

# POPULATION DEPENDENCE IN THE INTERACTIONS WITH NEIGHBORS FOR POLLINATION: A FIELD EXPERIMENT WITH *TARAXACUM OFFICINALE*<sup>1</sup>

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- *Premise of the study.* The fitness of plants depends on their immediate biotic and abiotic environmental surroundings. The floral neighborhood of individual plants is part of this immediate environment and affects the frequency and behavior of their pollinators. However, the interactions among plants for pollination might differ among populations because populations differ in floral densities and pollinator assemblages. Despite that, manipulative experiments of the floral neighborhood in different populations with a specific focus on pollinator behavior are still rare.
- *Methods.* We introduced mixtures of two species (*Salvia farinacea* and *Tagetes bonanza*) in two populations of *Taraxacum officinale* and examined their effect on pollinators' foraging behavior on *Taraxacum*.
- *Key results.* The effects of the heterospecific neighborhood differed among pollinator groups and between the two populations. Only honeybees consistently preferred both the most diverse (containing three species) and completely pure patches of *Taraxacum* in both populations. We found a strong and positive effect of patch diversity on visitation to *Taraxacum* in one population, whereas in the other population either no effect or a negative effect of plant diversity occurred, which we attribute to differences between populations in the ratio of pollinators to inflorescences. Pollinator visitation consistently increased with local *Taraxacum* density in both populations.
- *Conclusions.* Our study shows that a similar local neighborhood can differentially affect the frequency and foraging behavior of pollinators, even in closely situated populations. Experimental studies conducted in several populations would contribute to determine which factors drive the variation in pollination interactions among populations.

**Key words.** competition; composition of visits; facilitation; floral neighborhood; foraging behavior; local density; local diversity; *Salvia farinacea*; *Tagetes bonanza*; *Taraxacum officinale*; visitation rates.

Because plants are sessile, their fitness depends on the biotic and abiotic environment that immediately surrounds them. The floral neighborhood of individual plants is part of this immediate environment and may affect the frequency, identity, and behavior of pollinators that visit their flowers. This influence of the floral neighborhood is of particular relevance in ecology and evolution because it implies that the fitness of individuals depends, to some extent, on their close neighbors. The floral context of an individual is determined by the density of conspecifics and the density and composition of heterospecifics. Conspecific density may affect the frequency (Jennersten and Nilsson, 1993; Hegland and Totland, 2005), behavior (Schmitt, 1983; Kunin 1993), and identity (Conner and Neumeier, 1995; Lázaro et al., 2009) of visitors that an individual plant receives. On the other hand, coflowering species can influence positively (Lavery, 1992; Johnson et al., 2003; Ghazoul, 2006) or negatively (Waser, 1983; Campbell, 1985; Armbruster and McGuire, 1991; Brown et al., 2002) the pollinator visitation rates to focal species and can also affect other characteristics of the foraging behavior of pollinators, such as the number of flowers they con-

tact per visit to a plant (e.g., Klinkhamer et al., 1989; Karron et al., 1995) and how often they shift between plant species during foraging bouts (e.g., Johnson et al., 2003; Hersch and Roy, 2007). Finally, heterospecific neighbors can affect the diversity and composition of visitors that plants receive (Moeller, 2005; Lázaro et al., 2009), which may be important for plant fitness due to differences among pollinators in pollination efficiency (e.g., Herrera, 1990; Larsson, 2005). In general, it is conceivable that species-rich neighborhoods attract more pollinators and a more diverse pollinator assemblage to generalist plant species than neighborhoods with fewer species (Ghazoul, 2006; Lázaro et al., 2009) and that pollinators shift more often between plant species in mixed neighborhoods of species with similar floral traits (e.g., Waser, 1986; Chittka et al., 1997), potentially increasing the amount of heterospecific pollen transfer (Galen and Gregory, 1989; Caruso and Alfaro, 2000; Jakobsson et al., 2008). Patches with greater absolute abundance of a species are expected to experience higher visitation rates at the patch level (e.g., Jennersten and Nilsson, 1993). In addition, a decrease in the relative abundance of a species could result in a lower number of inflorescences contacted per visitor and longer foraging times on single plants, potentially generating negative effects on plant fitness associated to geitonogamous pollination (Charlesworth and Charlesworth, 1987; Klinkhamer and de Jong, 1993).

Despite these general expectations, it is also conceivable that the effects of the floral neighborhood on individuals of a species differ among populations because populations may vary in pollinator assemblages and plant densities. Plant density is

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known to directly influence the pollination interactions among plants (Rathcke, 1983). Moreover, plant density can also determine the identity of floral visitors (Conner and Neumeier, 1995; Lázaro et al., 2009) and the frequency of visits (Jennersten and Nilsson, 1993; Hegland and Totland, 2005). Variations in the pollinator assemblage—caused indirectly by differences in plant population density or directly by geographical variation in the composition of insects—may also affect the interactions among plants for pollination, since the abundance of certain pollinators can affect the behavior of others (Inouye, 1978; Chittka and Waser, 1997; Valido et al., 2002; Slaa et al., 2003). Several correlative studies (e.g., Bosch and Waser, 1999; Hegland and Totland, 2005; Lázaro et al., 2009) have documented relationships between the composition and density of neighborhoods and the interactions among plants for pollinator attraction. In addition, some experimental manipulations of plant densities and local heterospecific neighborhoods (Feinsinger et al., 1991; Stout et al., 1998; Bosch and Waser, 2001; Caruso, 2002; Grindeland et al., 2005; Ghazoul, 2006; Hersch and Roy, 2007) have documented their effect on pollinator visitation. However, these manipulative experiments are normally conducted in single populations/experimental gardens (e.g., Stout et al., 1998; Brown et al., 2002; Ghazoul, 2006) or in close locations used for replication instead for a comparison among populations (Feinsinger et al., 1991; Kunin, 1993; Karron et al., 1995; Bell et al., 2005). Experimental manipulations of the same factors in different populations and a comparison of the responses obtained are necessary to study the consistency between populations in the effects found.

In this study, we used an experimental approach to analyze in detail the effects of the floral neighborhood on pollinator visitation to the pollination-generalist *Taraxacum officinale* (Asteraceae), by introducing mixtures of two species (*Salvia farinacea* [Lamiaceae] and *Tagetes bonanza* [Asteraceae]) in two locations differing in *Taraxacum* population density. In particular, we asked how the heterospecific floral neighborhood and the local density of *Taraxacum* inflorescences affected (1) the pollinators' patch choice, (2) the visitation rates by the most common pollinators, (3) the diversity and composition of visitors to the focal species, (4) the number of inflorescences contacted by each pollinator during a visit to a patch, (5) the duration of pollinator visits to inflorescences, and (6) the frequency of shifts between *Taraxacum* and other species during foraging bouts within patches. We expected visitation and pollinator diversity to increase with the diversity of the neighborhood. Visitation at the patch level and foraging time on single inflorescences were expected to increase, whereas the number of inflorescences contacted per visitor was expected to decrease with *Taraxacum* density. Higher number of shifts between species was expected in mixed neighborhoods with similar species. We also expected the responses of pollinators to differ between the study populations.

## MATERIALS AND METHODS

**Study species and study areas**—We selected *Taraxacum officinale* (*Taraxacum* hereafter) as the study species. This perennial herb belongs to the Asteraceae family and bears yellow flowers arranged in inflorescences (floral heads). The species contain both diploid sexual and polyploid apomict individuals (Richards, 1970, 1973). It is a very common species that usually blooms alone in a relatively high abundance in several meadow plant communities of southern Norway. In addition, this species is highly visited by a wide range of generalist pollinators, including social and solitary bees, flies, beetles, wasps, ants,

and butterflies, so it can share pollinators with potential surrounding species. These characteristics made *Taraxacum* an ideal focal species for the purposes of our study.

We selected two populations of *Taraxacum*—Norderås (ca. 20 × 20 m) and Eplehagen (ca. 15 × 15 m)—on the property of the Norwegian University of Life Sciences in Ås, southern Norway, and separated by ca. 1 km. The populations do not differ in proximity to forests or roads and are both placed in open (potentially sunny) areas. In both populations, *Taraxacum* blooms alone from mid-May to mid-June. There was, however, a higher density of *Taraxacum* inflorescences at Norderås than at Eplehagen ( $F_{1,152} = 39.10$ ,  $P < 0.0001$ ; inflorescences/m<sup>2</sup> ± SE: 10.16 ± 0.51 vs. 6.62 ± 0.23 for Norderås and Eplehagen, respectively).

**Experimental design**—At the beginning of *Taraxacum* flowering, we haphazardly placed 20 blocks within areas containing *Taraxacum* in each population. Each block contained four plots (70 × 70 cm), placed in a quadrat and separated by 1 m. The minimum distance between blocks was 3 m. Each block was located within a relatively homogenous patch of *Taraxacum*, so all the plots within a block contained densities of *Taraxacum* inflorescences that were as similar as possible. To investigate how the floral neighborhood affected the visitation to *Taraxacum* inflorescences, we introduced into the plots potted individuals of *Salvia farinacea* (*Salvia* hereafter) and *Tagetes bonanza* (*Tagetes* hereafter) that were previously grown in a greenhouse. Thus, the four plots within a block were randomly assigned (by randomly throwing a stick) to one of the following neighborhood treatments: (1) *Salvia* treatment, containing six individuals of *Salvia*; (2) *Tagetes* treatment, containing six individuals of *Tagetes*; (3) mixed treatment, containing three individuals of *Salvia* and three individuals of *Tagetes*; and (4) control, only containing individuals of *Taraxacum*. Each individual of *Tagetes* and *Salvia* had only one inflorescence at the beginning of the experiment. The pots were located randomly within the plots because spatial arrangement and the interspersed of coflowering species can influence the strength of interactions for pollination (Feinsinger et al., 1986; Caruso, 2002). Only scattered inflorescences of *Taraxacum* remained among the plots. *Salvia* and *Tagetes* were used because their flowers are arranged in inflorescences, as in *Taraxacum*, and because they are easily cultivated and were ready to bloom simultaneously with *Taraxacum*. We chose one species belonging to the same family and with a similar flower color (*Tagetes*, Asteraceae; yellow) as *Taraxacum* and another belonging to a different family and with a different color (*Salvia*, Lamiaceae; blue) to test whether more pollinator shifts between plant species occur when insects perceive flowers of different species to be more similar (e.g., Waser, 1986; Chittka et al., 1997). The neighborhood treatments did not differ in density of *Taraxacum* inflorescences (treatment:  $F_{3,152} = 1.17$ ,  $P = 0.322$ ; treatment × population:  $F_{3,152} = 0.60$ ,  $P = 0.618$ ). Therefore, control plots had on average fewer total inflorescences than did the other plots (average for control ± SE: 4.51 ± 0.36; treatment plots: 11.25 ± 0.21; treatment:  $F_{3,152} = 142.38$ ,  $P < 0.0001$ ; treatment × population:  $F_{3,152} = 0.97$ ,  $P = 0.411$ ). However, because the number of *Taraxacum* inflorescences locally was highly variable, the number of total inflorescences for the control and the treatment plots overlapped considerably (total density in control plots ranged from 1 to 27 inflorescences; mixed plots: 7–26; *Salvia* plots: 7–24; *Tagetes* plots: 7–30). In addition, despite the overall higher local density of *Taraxacum* inflorescences at Norderås, plots from the two populations overlapped in *Taraxacum* density. At Norderås, *Taraxacum* density ranged from 1 to 27 inflorescences per plot, whereas at Eplehagen it ranged from 1 to 10. No other plant species bloomed in the experimental areas during this study.

**Data collection**—We observed pollinator visitation using 15-min observation periods, during the 6 sunny days from 23 May to 4 June in 2007; the flowering peak of *Taraxacum* in these populations this year. All observations were conducted between 0930 and 1730 hours. Both populations and all the plots within a block were observed simultaneously, using one or two observers per block and population, depending on the intensity of pollinator activity. The order of observation of blocks was random, with all the blocks in each population observed every day but each day changing the order in which the blocks were observed. Thus, at the end of the experiment all the blocks were observed at every time of the day the experiment was running (see below for details). During censuses, we noted the number and identity of flower visitors to inflorescences of the species in the plots. A visit was defined to have occurred when there was contact between the visitor's body and the reproductive organs (stigma or anther) of the flower. We categorized each visitor into the following groups: bumblebees (*Bombus* spp.), solitary bees (mainly Andrenidae, Anthophoridae, Halictidae, and Colletidae), honeybees (*Apis mellifera*), ants (Formicidae),

wasps (mainly *Ichneumonidae*, *Vespa* spp.), hover flies (*Syrphidae*), muscoid flies (mainly *Muscidae*, *Anthomyiidae*), beetles (*Coleoptera*), butterflies (*Lepidoptera*), and bees (*Bombus* spp.). We recorded the number and identity of inflorescences contacted by the same individuals. We also noted the time that the insect spent foraging in each inflorescence for 62% of the visits (1764 visits). The visit duration could not be recorded for all visitors during periods with too many insects foraging simultaneously in the plot or when the insect remained in the plot at the end of the observation period. In some cases (2.1% of the visits), we could follow the insect after leaving a plot, when it went to another plot in the same block or to a close block. However, insects could not be followed when they left for a plot located far from the observed plot. Because of the bias of these data, we did not use them in the analyses. In total, we recorded 5195 visits to all the three species and 3712 to *Taraxacum* (see Table 1 for the number of pollinator visits to *Taraxacum* recorded in each population) during 960 observation periods to single plots. Each plot was observed for 1.5 h total. After each observation period, we counted the number of open inflorescences of *Taraxacum*, *Salvia*, and *Tagetes* in the plots. At the beginning of the experiment each individual of *Tagetes* and *Salvia* had only one inflorescence, and although a few individuals of these two species had two inflorescences toward the end of the experiment, such small variation in inflorescence density had no effect on the results (not shown). Consequently, the inflorescence densities of *Salvia* and *Tagetes* in each observation period were not included in the final analyses.

We used the number of arrivals to *Taraxacum* (i.e., the number of pollinator individuals who arrived to a plot and visited *Taraxacum*) as one of our response variables because this variable may indicate the attractiveness of *Taraxacum* inflorescences to different pollinators. We also obtained the visitation rate per inflorescence for each 15-min observation period, by dividing the total number of visits to inflorescences of *Taraxacum* by the number of open inflorescences of *Taraxacum* in that plot during the particular observation period. This variable was an estimation of the pollination activity per inflorescence. We also analyzed other aspects of the foraging behavior of pollinators that could be directly affected by the local neighborhood and that might influence the quality of the visits, such as the number of contacted inflorescences per visit within a plot, the time insects spent in individual inflorescences, and the frequency of shifts between plant species by individual insects. Last, we examined how the floral neighborhood affected the composition and the diversity of visitors to *Taraxacum*. We estimated pollinator diversity by following Sahl and Conner (2006) and used the Simpson's (1949) diversity index:  $1/D = \sum_{i=1}^S p_i^2$ , where  $p_i$  is the proportional visitation for pollinator group  $i$ , and  $S$  is the richness, i.e., the number of pollinator groups visiting a plant species. This index includes both richness and evenness and gives more weight to common taxa (Gurevitch et al., 2006), which prevents us from over-interpreting incidental visits.

**Statistical analyses**—We used generalized linear models to analyze the effect of the neighborhood treatment on the different response variables because the data did not fulfill the assumptions of normality. We used gamma distributions and log link functions for all the response variables except for the frequency of shifts between species, for which we used a binomial distribution with logit as a link function. We used repeated measures analyses to investigate how neighborhood treatment and *Taraxacum* density affected the number of arrivals to *Taraxacum* and the visitation rate per inflorescence in both study populations. In these models, population was included as a fixed factor, and block was included as a random factor (subject of the repeated measures). The

neighborhood treatment (control, mixed, *Salvia*, and *Tagetes*), date (the 6 d), and time of the day (divided into 4 periods, every 2 h) were within-subject fixed factors. The density of *Taraxacum* inflorescences was included as a covariable.

We used multivariate analyses to investigate how the floral neighborhood influenced the identity of visitors of *Taraxacum*. We used redundancy analyses (RDA; CANOCO v.4.5) because detrended correspondence analyses (DCA) showed short gradient lengths (<4), suggesting that linear models best captured the variance in the data (ter Braak and Smilauer, 2002). The sample units were the 15-min observation periods. We used the number of visits of each pollinator group to *Taraxacum* as dependent variables and the neighborhood treatments (control, mixed, *Salvia*, and *Tagetes*) and the number of inflorescences of *Taraxacum* as predictor variables. The number of inflorescences of *Taraxacum* was entered as a continuous variable, whereas the neighborhood treatments were entered as dummy variables (i.e., variables coding a particular level of a nominal variable—e.g., neighborhood treatment—that can take 0 or 1 values; ter Braak and Smilauer, 2002). We included date (6 d) and time of the day (4 time periods) as covariables because they can affect the composition of the visitor assemblage. We used 1000 Monte Carlo permutations to assess the statistical significance of the association between the composition of the pollinator visits and the floral neighborhood. First, we obtained the significance of the whole ordination model. Second, we tested separately the effects of each neighborhood treatment and the number of inflorescences of *Taraxacum* on the composition of pollinator visits.

Observation periods without pollinator visitation precluded the use of repeated measures analyses for the study of how the neighborhood treatment, density of inflorescences of *Taraxacum*, and population affected (1) the diversity of pollinator visits, (2) number of inflorescences contacted per visitor, (3) time spent per inflorescence, and (4) frequency of shifts between species. Therefore, and to avoid pseudoreplication in these analyses, we averaged the values for each plot, using only one independent measure per plot. Thus, these analyses included only population and neighborhood treatment (control, mixed, *Salvia*, and *Tagetes*) as fixed factors and the density of inflorescences of *Taraxacum* as a covariable.

All the previous analyses (except redundancy analyses) were conducted for all the pollinator groups pooled and also for each pollinator group separately (provided that at least 15 visits were observed in each population and that enough replications per treatment and population were recorded). Before the analyses, we checked the homogeneity of slopes, by testing for significant interactions between the fixed factors and the covariable; none of these interactions was significant. We did not include total inflorescence density as another covariable in the analyses because *Taraxacum* density and total density were highly correlated ( $r = 0.66$ ,  $N = 960$ ,  $P < 0.0001$ ). Only the factors and their second order interactions were included in the final models, because the degrees of freedom did not allow testing the third and fourth order interactions. These analyses were performed in either the program SAS (GENMODE v. 9.1; SAS Institute, 2002) or STATISTICA (v. 6; StatSoft, 2001). All obtained contrasts were corrected using sequential Bonferroni tests (Rice, 1989). Means are accompanied by their standard error throughout the text.

## RESULTS

**Number of arrivals to *Taraxacum***—The neighborhood treatment affected the number of individuals of both honeybees and bumblebees arriving to *Taraxacum* (Table 2, Fig. 1). However, while the effect of the neighborhood on the arrivals of honeybees was consistent between populations, the effect of neighborhood on the number of bumblebee arrivals was not (Table 2, Fig. 1). Honeybees most often arrived to *Taraxacum* inflorescences in the control and mixed plots in both populations (Fig. 1). Bumblebees, on the other hand, most often arrived to *Taraxacum* in the *Salvia* plots and most seldom to *Taraxacum* in the control plots at Norderås. At Eplehagen, there was no effect of local neighborhood on the arrivals of bumblebee individuals to *Taraxacum* (Table 2, Fig. 1). The number of arrivals when all the pollinator groups were analyzed together and the arrivals of honeybees, muscoid flies, and beetles increased with the density of *Taraxacum* inflorescences in the plots (Table 2). A higher total number of arrivals and beetles'

TABLE 1. The number of visits to *Taraxacum* conducted by each pollinator group within each population. Total number of visits recorded in the last row.

Pollinator	Norderås	Eplehagen
Bumblebees	79	15
Solitary bees	19	21
Honeybees	1553	890
Ants	10	1
Wasps	4	15
Muscoid flies	140	62
Hover flies	56	6
Butterflies	14	0
Beetles	784	43
<b>Total visits</b>	<b>2659</b>	<b>1053</b>



TABLE 2. Results of the generalized linear models (gamma distribution and log as a link function) on the effect of neighborhood treatments (control, mixed, *Salvia*, and *Tagetes*), population, date, time of the day, and density of inflorescences of *Taraxacum* (covariable) on the arrivals to *Taraxacum*. All: all pollinator groups pooled. The results for the pollinator groups that conducted at least 15 visits in each population are given separately. The  $\chi^2$  and *P* values are presented for each analysis. The dfs are common for all the analyses.

Variable	df	All		Bumblebees		Honeybees		Solitary bees		Muscoid flies		Beetles	
		$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>
Treatment	3	2.36	0.50	8.59	<b>0.035</b>	7.80	<b>0.049</b>	5.48	0.14	5.01	0.17	1.70	0.64
Population	1	6.87	<b>0.009</b>	0.35	0.55	1.68	0.20	0.62	0.43	0.38	0.54	15.58	<b>&lt;0.0001</b>
Date	5	16.55	<b>0.005</b>	6.12	0.30	17.44	<b>0.004</b>	13.46	<b>0.019</b>	8.80	0.12	18.42	<b>0.003</b>
Time	3	11.79	<b>0.008</b>	5.94	0.12	13.66	<b>0.003</b>	10.29	<b>0.016</b>	5.19	0.16	5.64	0.13
Treatment $\times$ Population	3	6.72	0.08	8.75	<b>0.033</b>	0.65	0.89	4.40	0.22	6.81	0.08	6.78	0.08
Treatment $\times$ Date	15	18.93	0.22	13.86	0.54	17.87	0.27	13.70	0.55	15.26	0.43	17.28	0.30
Treatment $\times$ Time	9	6.46	0.69	12.58	0.18	7.55	0.58	9.03	0.44	7.06	0.63	13.92	0.13
Community $\times$ Date	5	11.59	<b>0.041</b>	10.13	0.07	14.83	<b>0.011</b>	4.84	0.44	12.02	<b>0.035</b>	13.43	<b>0.020</b>
Community $\times$ Time	2	6.63	0.09	6.50	0.09	10.52	<b>0.015</b>	2.47	0.48	6.92	0.07	6.23	0.10
Date $\times$ Time	8	15.79	<b>0.046</b>	11.87	0.16	12.51	0.13	10.03	0.26	15.02	0.06	9.97	0.27
Inflorescences of <i>Taraxacum</i>	1	12.23	<b>0.0005</b>	1.40	0.24	11.24	<b>0.0008</b>	1.35	0.25	5.31	<b>0.021</b>	7.95	<b>0.005</b>

arrivals to inflorescences of *Taraxacum* were found at Norderås than at Eplehagen (all:  $3.81 \pm 0.17$  vs.  $1.69 \pm 0.10$ ; beetles:  $1.57 \pm 0.09$  vs.  $0.09 \pm 0.02$ , for Norderås and Eplehagen respectively; Table 2). The number of arrivals varied with date and time, and the interactions date  $\times$  population and time  $\times$  population were significant for some pollinator groups (Table 2).

**Inflorescence visitation rate**—The floral neighborhood treatment significantly affected total visitation rate to *Taraxacum* and the visitation rates of bumblebees and muscoid flies (Table 3, Fig. 2). The effects of the neighborhood were not consistent, however, between populations (Table 3, Fig. 2). The highest total visitation rate to *Taraxacum* inflorescences occurred in mixed plots at Norderås, whereas we found no difference in total visitation rate among treatments at Eplehagen (Fig. 2A). The visitation rate of bumblebees to *Taraxacum* was highest in the *Salvia* plots in both populations. However, in the *Tagetes* plots their rate was as high as in the *Salvia* plots at Eplehagen (Fig. 2B). The treatment with the lowest visitation rate by bumblebees also differed between populations: at Norderås, the bumblebee visitation rates were lowest in the control and *Tagetes* plots, while at Eplehagen they were lowest in the mixed plots. The visitation rate of muscoid flies was highest in the control and mixed plots and lowest in the *Tagetes* plots at Norderås, whereas it was highest in the control plots and lowest in the mixed plots at Eplehagen (Fig. 2B). Total visitation rate and the visitation rate of beetles decreased with the density of *Taraxacum* inflorescences in the plots (Table 3). The visitation rate of beetles was higher at Norderås than at Eplehagen ( $0.51 \pm 0.03$  vs.  $0.04 \pm 0.01$ , respectively; Table 3). Visitation rate varied with date and time, and the interactions date  $\times$  population and time  $\times$  population were significant for some pollinator groups (Table 3).

**Composition of visits**—The floral neighborhood affected the composition of pollinators of *Taraxacum* in both populations, as shown by the RDAs (Table 4). However, the models did not explain a high percentage of the total variance in pollinator composition (Table 4). The number of inflorescences of *Taraxacum* had a significant effect, both at Norderås and Eplehagen (Table 4). In addition, the mixed treatment had a significant effect on the composition of pollinators of *Taraxacum* at Norderås, and the *Salvia* treatment had a marginally significant effect at Eplehagen (Table 4). Short distances among pollinator

groups and neighborhood variables in the RDAs' ordinations (Fig. 3) indicate a high association between them. At both populations, honeybee visits increased with the number of inflorescences of *Taraxacum* (Fig. 3). At Norderås, the number of visits of bumblebees also increased with the number of inflorescences of *Taraxacum*, as did (although more weakly) the visits of

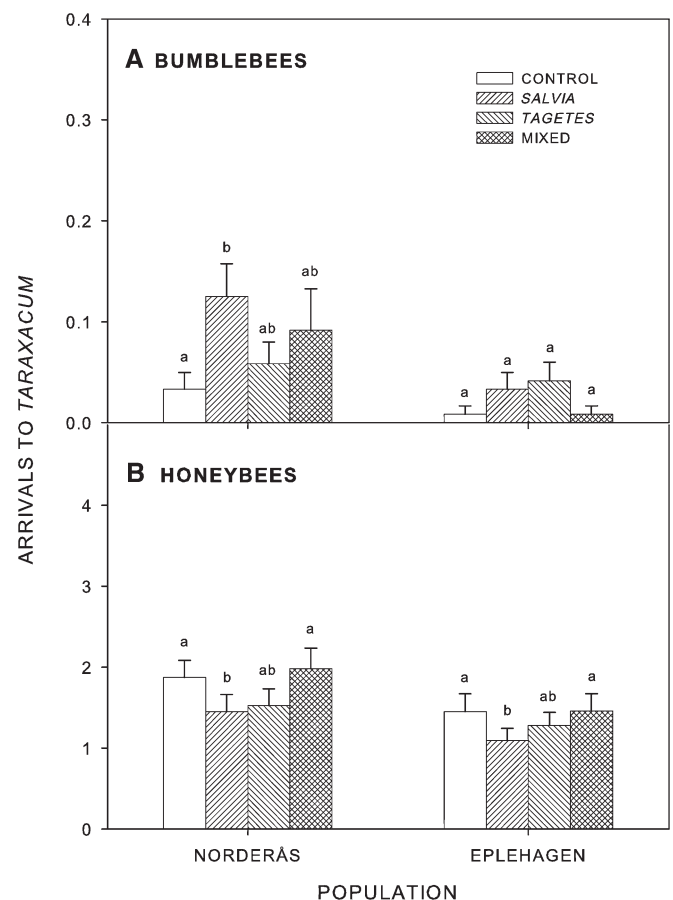


Fig. 1. Mean number of arrivals ( $\pm$ SE) of (A) bumblebees and (B) honeybees to *Taraxacum* inflorescences under different neighborhood treatments in each population. Bars with different letters represent significant differences within a population. Note difference in scale on y-axes.

TABLE 3. Results of the generalized linear models (gamma distribution and log as a link function) on the effect of neighborhood treatments (control, mixed, *Salvia*, and *Tagetes*), population, date, time of day, and density of inflorescences of *Taraxacum* (covariable) on the visitation rate to *Taraxacum* inflorescences. All: all pollinator groups pooled. The results for the pollinator groups that conducted at least 15 visits in each population are given separately. The  $\chi^2$  and  $P$  values are presented for each analysis. The dfs are common for all the analyses.

Variable	df	All		Bumblebees		Honeybees		Solitary bees		Muscoid flies		Beetles	
		$\chi^2$	$P$	$\chi^2$	$P$	$\chi^2$	$P$	$\chi^2$	$P$	$\chi^2$	$P$	$\chi^2$	$P$
Treatment	3	3.32	0.34	8.77	<b>0.033</b>	6.56	0.09	4.75	0.19	3.65	0.30	1.43	0.70
Population	1	3.52	0.06	0.07	0.80	2.12	0.15	0.00	0.94	0.24	0.63	15.37	<b>&lt;0.0001</b>
Date	5	17.65	<b>0.003</b>	7.95	0.16	17.36	<b>0.004</b>	13.97	<b>0.016</b>	11.92	<b>0.036</b>	18.23	<b>0.003</b>
Time	3	14.02	<b>0.003</b>	6.98	0.07	13.24	<b>0.004</b>	9.83	<b>0.020</b>	6.10	0.11	5.89	0.12
Treatment $\times$ Population	3	7.90	<b>0.048</b>	6.44	<b>0.042</b>	5.52	0.14	7.02	0.07	8.83	<b>0.032</b>	6.22	0.10
Treatment $\times$ Date	15	16.65	0.34	15.69	0.40	18.12	0.26	13.27	0.58	16.71	0.34	18.36	0.24
Treatment $\times$ Time	9	7.74	0.56	12.19	0.20	7.31	0.60	8.67	0.47	7.23	0.61	15.04	0.09
Community $\times$ Date	5	10.18	0.07	9.96	0.08	14.06	<b>0.015</b>	6.25	0.28	9.90	0.08	16.65	<b>0.005</b>
Community $\times$ Time	2	10.23	<b>0.017</b>	4.92	0.18	12.60	<b>0.006</b>	2.82	0.42	5.35	0.15	5.01	0.17
Date $\times$ Time	8	6.45	0.60	9.55	0.30	10.65	0.22	9.68	0.29	13.63	0.09	7.39	0.50
Inflorescences of <i>Taraxacum</i>	1	8.00	<b>0.005</b>	0.15	0.70	0.44	0.51	0.80	0.37	2.30	0.13	9.24	<b>0.002</b>

solitary bees, ants, muscoid flies, and beetles (Fig. 3A). At Norderås, *Taraxacum* inflorescences in mixed plots received more bumblebee and honeybee visits and fewer hover fly and butterfly visits than did the other plots (Fig. 3A). At Eplehagen, not only the visits of honeybees, but also the visits of hover flies, muscoid flies, and beetles increased with the number of inflorescences of *Taraxacum* (Fig. 3B). At Eplehagen, inflorescences of *Taraxacum* in *Salvia* plots tended to receive more bumblebee, beetle, and wasp visits and fewer honeybee and hover fly visits (Fig. 3B).

**Diversity of pollinator visits**—The neighborhood treatment did not affect the diversity of pollinator groups visiting *Taraxacum* (treatment:  $\chi^2_3 = 6.24$ ,  $P = 0.10$ ; interaction population  $\times$  treatment:  $\chi^2_3 = 5.70$ ,  $P = 0.13$ ). There was a higher diversity of pollinator groups visiting *Taraxacum* at Norderås than at Eplehagen ( $1.54 \pm 0.03$  vs.  $1.17 \pm 0.02$  respectively;  $\chi^2 = 121.02$ ,  $P < 0.0001$ ). The density of *Taraxacum* inflorescences was not related to the diversity of visits that it received ( $\chi^2 = 0.04$ ,  $P = 0.85$ ).

**Number of inflorescences contacted per visitor**—The neighborhood treatment had a significant effect on the number of inflorescences visited by individual pollinators when all pollinator were pooled (Table 5A). However, the effect of the treatment differed between the two populations, as shown by a significant treatment by population interaction (Table 5A). More inflorescences were contacted per visitor in the mixed than in the *Salvia* plots at Norderås ( $1.42 \pm 0.06$  vs.  $1.29 \pm 0.05$ , for mixed and *Salvia* plots, respectively; the other plots had intermediate values), while more inflorescences were contacted per visitor in the control than in the *Tagetes* plots at Eplehagen ( $1.37 \pm 0.09$  vs.  $1.19 \pm 0.04$ , for control and *Tagetes* plots, respectively; the other plots had intermediate values). The number of inflorescences contacted per visitor increased significantly with the number of inflorescences of *Taraxacum* when all the pollinator groups were analyzed together (Table 5A). Honeybees, muscoid flies, and beetles contacted more inflorescences per foraging bout in a plot at Norderås than at Eplehagen (honeybees:  $1.73 \pm 0.07$  vs.  $1.34 \pm 0.05$ ; muscoid flies:  $1.08 \pm 0.04$  vs.  $1.03 \pm 0.03$ ; beetles:  $1.03 \pm 0.01$  vs.  $1.00 \pm 0.00$ ; Table 4A).

**Duration of visits to inflorescences**—The neighborhood treatment had a consistent and significant effect on the duration

of visits to inflorescences when all the pollinator groups were analyzed together (Table 5B). The time spent per inflorescence was significantly lower in *Tagetes* plots (*Tagetes* vs. the mean of the other treatments:  $37.61 \text{ s} \pm 3.88$  vs.  $57.25 \text{ s} \pm 4.48$ ). The duration of honeybee visits to an inflorescence significantly decreased with the number of inflorescences of *Taraxacum* in the plots (Table 5B). Longer visits occurred at Eplehagen than at Norderås when all the pollinator groups were pooled and also for muscoid flies (all:  $56.83 \text{ s} \pm 5.62$  vs.  $46.96 \text{ s} \pm 3.67$ ; muscoid flies:  $190.45 \text{ s} \pm 36.31$  vs.  $79.31 \text{ s} \pm 11.06$ ; Table 5B).

**Shifts between *Taraxacum* and other species**—Most of the visitors to *Taraxacum* (96.6%) were species-constant during visitation to plots where more than one species was present (i.e., mixed, *Salvia*, and *Tagetes* plots). Of the 3.4% of the visitors that shifted between *Taraxacum* and other species, 70.4% shifted between *Taraxacum* and *Tagetes*. The number of shifts between species was not significantly related to the number of inflorescences of *Taraxacum* ( $\chi^2 = 0.42$ ,  $P = 0.52$ ) or the neighborhood treatment ( $\chi^2_2 = 3.70$ ,  $P = 0.16$ ), and there was no treatment by population interaction ( $\chi^2_2 = 0.93$ ,  $P = 0.63$ ). However, visitors to *Taraxacum* shifted more between species at Norderås than at Eplehagen (4.0 and 2.2% of the visitors shifted at Norderås and Eplehagen, respectively;  $\chi^2 = 5.35$ ,  $P = 0.021$ ).

## DISCUSSION

Because of the sessile nature of plants, their fitness relies on their immediate environmental surroundings. The floral neighborhood of individual plants is part of this immediate environment and affects the frequency and behavior of their pollinators. Our study has shown that a similar local floral neighborhood can differently affect the frequency, composition, and foraging behavior of pollinators of even closely situated populations. Field experiments like ours are rarely conducted in more than one population, and when several close sites (distance up to a few hundred meters) are used, the results for the different sites are not statistically compared, but instead used as replicates of the experiment (Feinsinger et al., 1991; Kunin, 1993; Bell et al., 2005). However, population-dependent interactions among neighbors for pollination are expected if interactions (competition or facilitation) for pollinator attraction depend on population

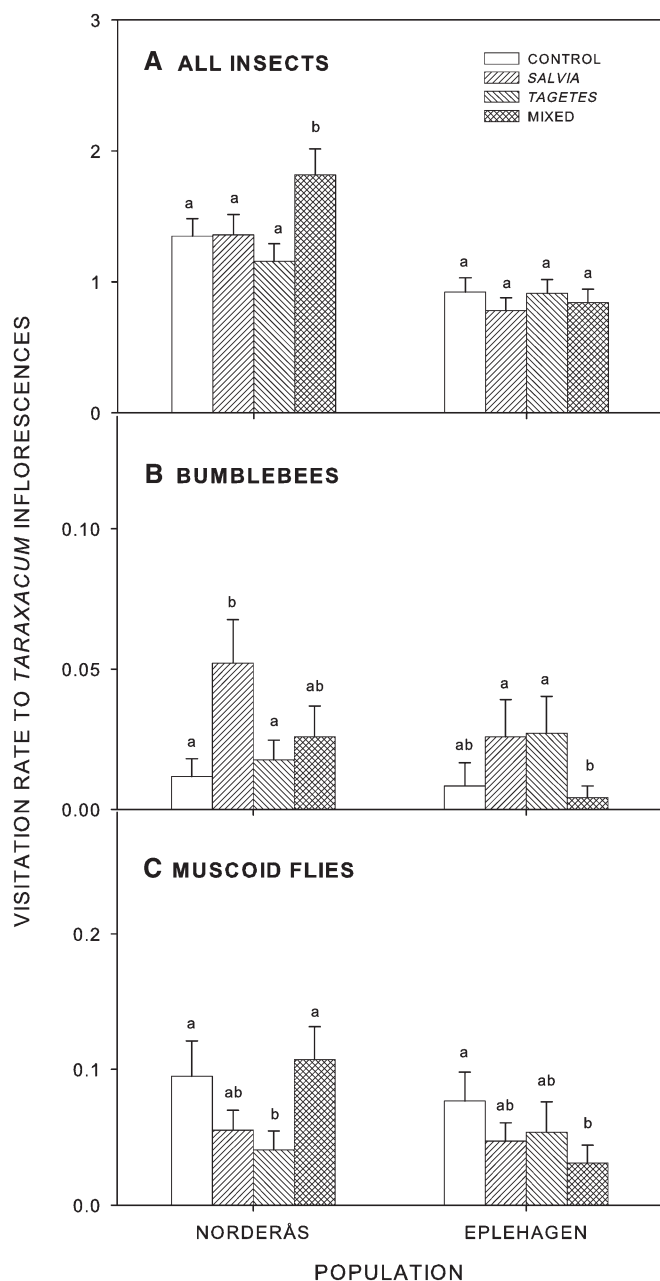


Fig. 2. Mean visitation rate ( $\pm$ SE) by (A) all the pollinators pooled together, (B) muscoid flies, and (C) bumblebees to *Taraxacum* inflorescences under different neighborhood treatments in each population. Bars with different letters represent significant differences within a population. Note difference in scale on y-axes.

size and density (Rathcke, 1983) and if the abundance of a pollinator affects the behavior of others (Inouye, 1978; Chittka and Waser, 1997; Valido et al., 2002; Slaa et al., 2003). Our study populations differed in *Taraxacum* density and, perhaps partly due to that (e.g., Jennersten and Nilsson, 1993; Conner and Neumeier, 1995), in their pollinator assemblage (Table 1). Although with our data we cannot determine which factors are driving the differences we found between the populations, the fact that the same experimental set up affected the pollinator behavior differently in the two localities, warns against extract-

TABLE 4. Redundancy analyses on the relationships between the floral neighborhood and the composition of pollinators of *Taraxacum* inflorescences at (A) Norderås and (B) Eplehagen. Covariables: date (Da) and time of the day (Ti); %V: percentage of explained variance by the different explanatory variables. The sum of all eigenvalues is after accounting for the covariables. Only significant or marginally significant variables ( $P < 0.1$ ) are shown, although all variables specified in the methods were included in the analyses.

Population	Effect	Covariables	%V	F	P
A) Norderås	Full model (all effects)	Da, Ti	9	11.73	0.001
	<i>Taraxacum</i> inflorescences	Da, Ti	7	41.39	0.001
	Mixed treatment	Da, Ti	1	4.13	0.029
	Sum of all canonical eigenvalues / sum of all eigenvalues: 0.084 / 0.932				
B) Eplehagen	Full model (all effects)	Da, Ti	7.5	9.57	0.001
	<i>Taraxacum</i> inflorescences	Da, Ti	7	35.04	0.001
	Salvia treatment	Da, Ti		2.82	0.09
	Sum of all canonical eigenvalues / sum of all eigenvalues: 0.074 / 0.991				

ing conclusions based on results from single populations and highlights the complexity of the interactions between plant species for pollinator visitation.

**Effects of the heterospecific neighborhood on visitation patterns**—Pollinator groups were affected differently by the local heterospecific neighborhood, as expected based on their biology and foraging behavior. Social bees have high energetic demands and usually show search patterns that follow the blossom density distribution (Dukas and Real, 1993; Chittka et al., 1997; Goulson, 2003), whereas flies and beetles have shown encounter rates and residency times that are less influenced by blossom density (Hegland and Boeke, 2006). In our study, beetles were only affected by *Taraxacum* density, but not by the heterospecific neighborhood. In addition, although the floral treatments affected visitation rate of flies in this study (Fig. 2), we found that the heterospecific neighborhood played a stronger role in the attraction of bees than in the attraction of muscoid flies to the plots (see Table 2, Fig. 1) and that more variables related to the pollinator behavior were affected by the treatment in bees than in flies. We also expected specialist insects to prefer dense flowering patches of its preferred plant species in order to forage economically (Stephens and Krebs, 1986). Such preference for dense flowering patches of the favorite species might be the reason for the tendency of bumblebees to choose plots containing *Salvia* together with the two other species, and particularly the plots with only *Salvia*.

The responses of pollinators to the floral neighborhood also varied between populations, as expected based on the differences between populations in *Taraxacum* density and composition of the pollinator assemblage. The only visitor that showed a relatively consistent pattern between populations was the honeybees, which were also the most abundant visitors (Table 1). In both populations, honeybees were most attracted to *Taraxacum* when it occurred in control and mixed plots. *Taraxacum* in the *Salvia* plots received the fewest honeybee arrivals, whereas *Taraxacum* in the *Tagetes* plots received an intermediate number. Even though the control plots had fewer total inflorescences than the treatment plots, the controls might be especially attractive to honeybees because the relative abundance of *Taraxacum* inflorescences (which is the most visited

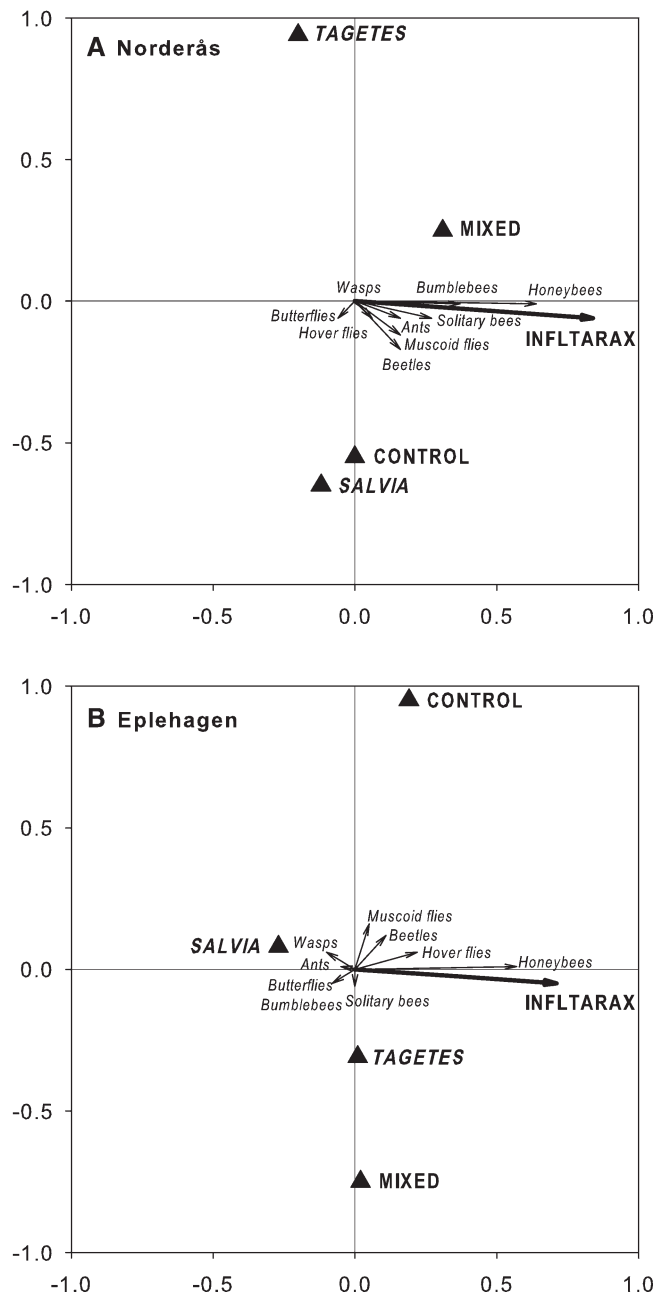


Fig. 3. Biplots of the redundancy analyses conducted for each population and used to study the relationship between the composition of visitors (thin arrows, italic lowercase; length of arrows was doubled to improve clarity) and the local neighborhood (uppercase; thick arrows for continuous variables and filled triangles for dummy variables). INFLTARAX: number of inflorescences of *Taraxacum*; TAGETES: *Tagetes* treatment; SALVIA: *Salvia* treatment; MIXED: mixed treatment; CONTROL: control. Date and time of the day were introduced as covariables in the models (see text for details). Populations: (A) Norderås; (B) Eplehagen.

plant in this study; see *Data collection* in Materials and Methods) was highest in them. On the other hand, higher visitation to mixed plots could be due to a facilitative effect of the multispecies floral displays, attributed to resource complementarity (Ghazoul, 2006). However, we have not found evidence to sup-

port the resource complementarity hypothesis because insects rarely shifted between plant species. Last, the intermediate state of *Tagetes* plots could perhaps be related to an inability of honeybees to discriminate yellow-flowered *Tagetes* from *Taraxacum* at a distance, leading honeybees to select plots with higher absolute numbers of yellow flowers when approaching a plot from a long distance, whereas perhaps they can distinguish them well when the approach is from a shorter distance.

The neighborhood treatment had different effects on visitation by other pollinator groups. Thus, the arrivals of bumblebees (at Norderås) and their visitation rates (at both populations) were highest when *Taraxacum* inflorescences occurred in the *Salvia* plots. This result is not surprising because *Salvia* is a very attractive species for bumblebees (74.1% recorded visits of bumblebees were to *Salvia* individuals), and facilitation often occurs when the focal, less attractive species grows close to an attractive plant species (the magnet-species affect; e.g., Lavery, 1992; Johnson et al., 2003). Nevertheless, the neighborhood treatment that had the lowest visitation rate of bumblebees differed between populations (Norderås: control and *Tagetes* plots, Eplehagen: mixed plots). A comparable result was also found for muscoid flies: while *Taraxacum* in mixed plots experienced the highest visitation rate by muscoid flies at Norderås, the lowest visitation rates were found in the mixed plots at Eplehagen. In both populations, however, the highest visitation rates occurred in the control plots, which may be due to their preference for patches with a high relative density of *Taraxacum*, even when they have the lowest total density.

A greater and/or more positive effect of high local floral diversity (represented by the mixed plots) at Norderås than at Eplehagen was repeatedly shown in our study. Thus, we not only found higher visitation rates to the mixed plots at Norderås (vs. the lack of, or negative effect of, this treatment on visitation rates by the same pollinator groups at Eplehagen), but also the mixed plots had a greater effect on the composition of visitors to *Taraxacum* and on the total number of inflorescences contacted per visitor at Norderås than at Eplehagen. The lack of a mixed plot effect on visitation at Eplehagen could be partly due to a much lower pollinator visitation there than at Norderås (Table 1), potentially masking any treatment effect. However, a lower visitation cannot explain the negative effect of the mixed treatment on visitation at Eplehagen. We believe the differences between the study populations in the effects of the mixed treatment are caused by their differences in the ratio of pollinators to inflorescences. Thus, more resources (pollinators) for the plants at Norderås than at Eplehagen may be responsible for the higher number of arrivals and visitation rates to inflorescences, the greater number of inflorescences contacted per visitor, and the lower duration of visits, and the higher number of shifts between plant species at Norderås than at Eplehagen. Because there are more pollinators per inflorescence at Norderås, *Taraxacum* is likely to compete less intensively for pollinator visits at this population than at Eplehagen (where the lower number of insects might drive higher competition by plant species). These differences in the ratio of pollinators to inflorescences could explain the positive effect of mixed plots on visitation to *Taraxacum* through facilitation by plant diversity (Ghazoul, 2006) at Norderås and a negative effect through competition for pollinator attraction (e.g., Rathcke, 1983) at Eplehagen. However, experimental manipulations using a gradient in the proportion of pollinators to inflorescences would be needed to test this hypothesis. Indeed, our study cannot reveal the factors driving the differences between the study populations. There could be



TABLE 5. Results of the generalized linear models (gamma distribution and log as a link function) on the effect of neighborhood treatments (control, mixed, *Salvia*, and *Tagetes*), population, and density of inflorescences of *Taraxacum* on (A) number of inflorescences contacted per visitor and (B) duration of the visits to inflorescences. All: all pollinator groups pooled. The results for the pollinator groups that conducted at least 15 visits in each population and for which enough replications per treatment and population were recorded are given separately. The  $\chi^2$  and *P* values are presented for each analysis. The dfs are common for all the analyses.

Source	df	All		Honeybees		Muscoid flies		Beetles	
		$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>	$\chi^2$	<i>P</i>
A) Inflorescences contacted									
Treatment	3	1.18	0.76	2.96	0.40	7.03	0.07	3.79	0.29
Population	1	0.05	0.83	23.94	<b>&lt;0.0001</b>	3.85	<b>0.049</b>	4.28	<b>0.039</b>
Treatment × Population	3	7.89	<b>0.048</b>	7.47	0.06	0.78	0.85	3.37	0.34
Inflorescences of <i>Taraxacum</i>	1	9.04	<b>0.003</b>	0.02	0.89	3.43	0.06	1.18	0.28
B) Duration of visits									
Treatment	3	17.45	<b>0.0006</b>	2.90	0.41	0.56	0.91	0.56	0.91
Population	1	4.76	<b>0.029</b>	0.01	0.93	13.15	<b>0.0003</b>	1.82	0.18
Treatment × Population	3	0.78	0.86	4.14	0.25	1.78	0.62	0.21	0.98
Inflorescences of <i>Taraxacum</i>	1	0.60	0.44	6.78	<b>0.009</b>	1.07	0.30	1.23	0.27

environmental differences between the two populations driving the higher density of *Taraxacum* inflorescences at Norderås; such environmental differences between populations could alter the quality and quantity of floral resources available and subsequently affect pollinator visitation. Future studies with many populations to determine the factors related to the differences in visitation patterns will help us to understand how the floral neighborhood influences visitation in different contexts. Time limitations are also important to consider. We have data on visitation patterns from one field season, and interactions between plants and pollinators are known to vary among years (e.g., Petanidou and Potts, 2006; Olesen et al., 2008). Using an identical experimental set up across years would allow us to determine whether the differences among localities are maintained over time.

Finally, we did not find the expected effect of local neighbors on the shifts between species. The majority of visitors were species-constant (Waser, 1986), at least during visits within a plot during an observation period. Nevertheless, when shifts occurred, they were mostly between *Taraxacum* and *Tagetes*. Flower constancy is expected to be lower when insects perceive flowers of different plant species to be more similar (e.g., Waser, 1986; Chittka et al., 1997; Johnson et al., 2003; Slaa et al., 2003) and may be the reason for the higher number of shifts between these two species. Although such behavior could potentially result in improper pollen transfer with its negative effects on fitness (Galen and Gregory, 1989; Caruso and Alfaro, 2000; Jakobsson et al., 2008), this scenario would be unlikely in these artificial communities because the number of switches between species is extremely low.

**Relationships between local *Taraxacum* density and visitation patterns**—The relationships between the local density of *Taraxacum* inflorescences and several aspects of the visitation pattern of different pollinators were the most consistent results found in our study. Thus, we found a consistent positive relationship between local density of *Taraxacum* inflorescences and the arrivals of honeybees, muscoid flies, and beetles and between local *Taraxacum* density and visitation rates of all insects and beetles. In addition, local *Taraxacum* density was the most important factor for its composition of pollinators in different patches, as shown by the multivariate analyses. Pollinator approaches usually increase as local density increases (Klinkhamer et al., 1989; Feinsinger et al., 1991; Brody and

Mitchell, 1997; Dreisig, 1995; Bosch and Waser, 1999, 2001), which is normally related to a higher attraction effect (Medel et al., 2003) and/or foraging economy (e.g., Goulson, 2003). However, the translation of more arrivals to dense patches into a higher per-flower visitation seems to be idiosyncratic to the particular plant species and pollinator system (e.g., Jennersten and Nilsson, 1993; Kunin, 1997; Bosch and Waser, 1999) and that could explain why visitation rates did not increase with local density for all the pollinator groups whose arrivals increased with local *Taraxacum* density. Interestingly, although most of the insects preferred to visit patches with a high density of *Taraxacum* inflorescences, only muscoid flies and honeybees preferred the control plots. This preference could be because absolute density had greater effects than relative density on the behavior of most of the pollinator groups in our populations and/or because most pollinator groups in our populations also respond positively to the total inflorescences density and/or diversity. Hegland and Boeke (2006) found that blossom density was the best predictor of both flower visitor richness and activity. However, although we found associations between *Taraxacum* density and the composition and frequency of visitors, we did not find any relationship between the local density of *Taraxacum* and the diversity of visitor groups. Last, we also found that the number of *Taraxacum* inflorescences contacted per visitor consistently increased with the number of inflorescences of *Taraxacum* when all the visitor groups were pooled and that the duration of honeybee visits to individual inflorescences consistently decreased with increasing inflorescences density. These relationships were expected because at high flower or inflorescence density, pollinators may spend less time on each one, favoring cross-pollination (e.g., Karron et al., 1995) and increasing the quality of pollination service in dense plots and populations (e.g., Jennersten and Nilsson, 1993; Karron et al., 1995; Field et al., 2005).

**Foraging behavior and the scale of the experiment**—The size of the floral neighborhood affecting visitation of a plant may depend on the search behavior, the foraging range, and the diet breadth of its pollinators (Ghazoul, 2005). Foraging ranges of flying pollinators increase with body size and vary from hundred of meters to several kilometers; therefore, their behavior is affected by the floral distribution at the landscape scale (Steffan-Dewenter and Tschamtker, 1999; Steffan-Dewenter et al., 2002; Klein et al., 2003; Westphal et al., 2003). In addition to



this landscape effect, the floral distribution and composition at small local patch scales is known to affect foraging patterns and short-term foraging decisions of pollinators (Ghazoul, 2005). This is not surprising because pollinators usually limit their foraging flights to short distances (up to a few meters) despite being able to move much further, often moving between neighboring plants while foraging (e.g., Olesen and Warncke, 1989; Widen and Widen, 1990; Totland, 1994; Smithson and Macnair, 1997; Wesselingh and Arnold, 2000). Here we have shown that the insects respond to the local neighborhood at a very small scale, as other studies have done before for a number of pollinators (e.g., Ghazoul, 2006; Hegland and Boeke, 2006; Lázaro et al., 2009; Jakobsson et al., 2009). Although we are unable to reveal the response of pollinators to the larger-scale neighborhood, i.e., at the meadow and landscape scale, it is unlikely that we have obtained confounding results in which the effects of plant composition at the local and the meadow-scale are mixed because the experiment was distributed across the whole of the meadows, i.e., the meadows were entirely homogeneous at this scale. Therefore, our results may represent well the effect that the immediate neighbors had on *Taraxacum* in our artificial communities, independently of other nonmeasured effects at larger spatial scales. The extent that the floral distribution at the landscape scale can modify the local foraging behavior in our system is unknown, but could be another reason for the differences found between the study areas.

**Conclusions**—In this study, we have shown that the local neighborhood affected the frequency, composition, and foraging behavior of *Taraxacum*'s pollinators. Even though our experimental plant communities were artificial and simple, the responses were highly dependent on pollinator group and differed profoundly between the two populations, thus revealing a substantial complexity of interactions among plants and pollinators for pollination (which undoubtedly is even higher in natural, nonmanipulated communities). More experiments conducted in many populations are needed to increase our knowledge about interactions with neighbors for pollination and their underlying mechanisms because such interactions may be important for population resistance to perturbations and the evolution of floral traits.

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