

Pollinator aggregative and functional responses to flower density: does pollinator response to patches of plants accelerate at low-densities?

Tracy S. Feldman

Feldman, T. S. 2006. Pollinator aggregative and functional responses to flower density: does pollinator response to patches of plants accelerate at low-densities? – *Oikos* 115: 128–140.

Plant reproduction is often reduced at low densities, due to reduced pollinator visitation rates. Recent theory suggests that a disproportionate increase in pollinator visits to patches of plants as heterospecific plant density increases (i.e. if visitation is a sigmoid function of patch density) can rescue sparse populations of a focal plant species from reduced reproductive success or population decline. A field experiment was performed to determine the shape of the pollinator visitation response to patches of differing density of the common weed *Brassica rapa*. Both the aggregative and functional response for the entire pollinator community were saturating rather than sigmoid, indicating that pollinator response does not accelerate when density increases. The results for the entire pollinator community were consistent among temporal and spatial replicates. Aggregative response curves for specific pollinator taxa were either linear (bombyliid flies) or saturating (syrphid flies, solitary bees, and Lepidoptera). Functional responses for these taxa were saturating (syrphid flies and solitary bees) or flat (bombyliid flies and Lepidoptera). Individual pollinators visited more plants during foraging bouts in high-density patches, but visits per plant decreased. Seeds per fruit and seeds per flower increased with increasing density. There is no evidence that pollinators disproportionately visit denser patches, or that the conditions for this mechanism of pollination facilitation are likely to be met in this generalist pollinator system.

T. S. Feldman, Biology Dept, Box 90338, Duke Univ., Durham, NC 27708-0338, USA, also at: Plant Biology Division, Samuel Roberts Noble Foundation, 2510 Sam Noble Parkway, Andmore, OK 73401-2124, USA (tsfeldman@noble.org)

At low densities, plants often experience reductions in pollinator visitation, leading to reduced fruit and seed production. These negative effects of low-density have been documented frequently, in both natural (Sih and Baltus 1987, Jennersten 1988, Jennersten and Nilsson 1993, Roll et al. 1997, Groom 1998, Wolf and Harrison 2001) and experimental (Kunin 1993, 1997, Steffan-Dewenter and Tschardt 1999) populations. In turn, if reproduction at low densities is insufficient to replace dying individuals (Lamont et al 1993, Groom 1998, Hackney and McGraw 2001), a population would

experience strong Allee effects, by which it would be doomed to extinction should it fall below a threshold density (Allee 1931, Stephens et al. 1999).

Mathematical models have demonstrated that under certain conditions, two plant species that flower simultaneously and share pollinators can rescue each other from both low reproduction and Allee effects (Bobisud and Neuhaus 1975, Feldman et al. 2004), a process called pollination facilitation. These models, along with field studies (Waser and Real 1979, Moeller 2004, T. S. Feldman, unpubl.), suggest four mechanisms by

Accepted 3 April 2006
Subject Editor: Jane Memmott

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ISSN 0030-1299

which pollinator response to plant density can lead to facilitation: aggregative response (Feldman et al. 2004), functional response (Bobisud and Neuhaus 1975), increasing pollination quality (T. S. Feldman, unpubl.), and numerical response (Murdoch 1977, Moeller 2004).

An aggregative response refers to the change in the number of pollinators visiting a patch per unit time as patch density increases. Feldman et al. (2004) modeled pollinator aggregative response, using a differential equation model of two plant species competing for space and pollinator services, and assuming that pollinators do not distinguish between the two plant species. They found that interspecific facilitation can occur if the pollinator aggregative response is initially an accelerating function of plant density, even if the initial accelerating phase is followed by a plateau at higher plant densities. These findings concur with a previous graphical model (Rathcke 1983). In the model of Feldman et al. (2004), sigmoid aggregative response implies that pollinators are choosing among patches of floral resources (composed of one or more species of co-flowering plants) on a landscape, and are increasingly likely to switch to a patch as its floral density increases. Thus, facilitation can occur if foragers choosing among resource patches disproportionately concentrate their foraging efforts on high-density patches (Hassell 1971, Murdoch and Oaten 1975). However, few studies have attempted to determine the functional form of the aggregative response of pollinators to plant density (but see Sih & Baltus 1987). Even fewer studies have explored pollinator choice among patches in a large landscape context (Rathcke 1988).

Pollination facilitation may also occur if individual pollinators respond in an accelerating fashion to increasing density of plants or flowers within a patch. This relationship describes a functional response, in which the visitation rate of individual pollinators changes as a function of flower density within a patch. Bobisud and Neuhaus (1975) modeled a uniform patch populated by three plant species, and found that facilitation is possible when pollinators do not distinguish between two of the plant species. Pollinator constancy leads pollinators to disproportionately increase visits to the two indistinguishable species as the density of one of them increases. This is akin to switching behavior of individual foragers, which can sometimes lead to a sigmoid functional response (Murdoch and Oaten 1975). Switching has been documented widely among insect predators (Murdoch 1969, Murdoch et al. 1984, Schenk and Bacher 2002, Elliott 2004) and pollinators (Heinrich 1976, Zimmerman 1981, Goulson et al. 1998, Nagamitsu et al. 2000). Although this mechanism could also lead to improper pollen transfer (Waser and Fugate 1986), excessive deposition of heterospecific pollen may not occur if plants deposit pollen on different regions on the bodies of pollinators.

Third, pollination facilitation may occur if the quality of pollinator visits increases in the presence of co-occurring plant species, even if there is no change in the quantity of visits in the presence of the co-occurring species. In this case, the increase in floral resources resulting from co-occurring species decreases the probability that pollinators will repeatedly visit additional patches containing other species in between repeated visits to the first patch. By doing so, they are more likely to carry compatible pollen back to the patch on their next visit (T. S. Feldman, unpubl.), which increases the amount of compatible pollen received in the presence of the co-occurring species.

Fourth, pollination facilitation may occur if plant density alters the pollinator numerical response (Moeller 2004). If populations of pollinators grow disproportionately larger when two plant species co-occur than when they occur separately, by extending the flowering season (Waser and Real 1979) or by increasing resource density, then each plant species may have higher visitation and reproductive success when co-occurring than when growing alone.

It is unclear when and how frequently each of these mechanisms might occur in natural systems. Further, evidence for or against one of these mechanisms does not eliminate the possibility that one or more of the other mechanisms may be operating.

The combined aggregative and functional responses of pollinators to plant densities affect visitation to individual plants, which in turn may affect seed production. At higher densities, plants may actually experience reduced reproduction relative to plants in patches of intermediate densities. Even if more individual pollinators visit the patch, and visit more plants in these patches, they often visit a smaller proportion of flowers in larger patches (Sih and Baltus 1987, Andersson 1988, Klinkhamer et al. 1989, Goulson et al. 1998). Therefore, individual plants or flowers may actually receive fewer visits in higher-density patches (Jennersten and Nilsson 1993). Reduced numbers of visits to plants in high-density patches may be caused by handling time limitations (Herrera 1989), or by limited numbers of available pollinators. Thus, two opposing forces – the increase in the number of visits to patches and the number of visits to flowers within patches combined with a decrease in visitation to individual plants as density increases – affect plant reproduction in concert. If the number of pollinators visiting higher-density patches is enough to outweigh effects of a saturating visitation rate per pollinator, then plant reproduction will still increase in high-density patches. Previous studies on pollinator visitation to plants or patches of different sizes have documented increases (Sih and Baltus 1987), decreases (Andersson 1988), and no effect on plant reproduction (Robertson and MacNair 1995) as patch size increases.

In this paper, I focus on the pollinator aggregative response, arguably one of the less studied of the four mechanisms that can lead to pollination facilitation. I use a single self-incompatible animal-pollinated species, *Brassica rapa*, in a landscape-level experiment to test for accelerating pollinator aggregative response to increasing plant density. I also measure the pollinator functional response, which I expect to be saturating in monospecific plant patches (Murdoch and Oaten 1975). Few studies have attempted an experimental approach to distinguish between and characterize both of these pollinator responses, and to examine effects of the combined pollinator response on visitation to individual plants and plant reproduction. I used a single species to determine whether facilitation by way of an accelerating aggregative response could occur in this system, effectively mimicking the case in which pollinators do not distinguish between two plant species (I will discuss other cases below). Specifically, I answer the following questions:

- 1) What is the functional form of the pollinator aggregative response to plant density? Specifically, do the conditions under which pollination facilitation is possible occur in *B. rapa* (i.e. an accelerating visitation response at low densities)?
- 2) What is the functional form of the pollinator functional response to plant density?
- 3) How do the combined pollinator aggregative and functional responses to plant density affect visitation to individual plants?
- 4) How do the combined pollinator aggregative and functional responses to plant density affect fruit and seed production?

Methods

System

Brassica rapa (Brassicaceae), or turnip rape, is a self-incompatible annual plant, so it is possible to compare the lifetime female fitness of plants from different density treatments within a single season. *B. rapa* is widely naturalized in roadsides, waste ground, pastures, and fields in the US. Its flowers are visited by insects in several orders, including Hymenoptera, Diptera, Lepidoptera, and Coleoptera (pers. obs.). I planted seeds of rapid cycling *Brassica rapa* (from Wisconsin Fast Plants Program http://www.fastplants.org/home_flash.html) in the Biology Greenhouse at Duke University, and grew the plants in 4-inch pots under ambient light conditions. After plants began flowering, I removed all open flowers and moved the plants to field sites for the experiment described below.

Field experiment

In each of two mowed fields in Duke University Forest, Durham, NC, USA, I established sixteen 5×5 m patches, each of which was at least 75 m from neighboring patches. With this design, I attempted to isolate patches enough that pollinators would perceive each patch as distinct and perhaps, if flight to and from a nest (e.g. for bees) were costly, would be forced to choose one patch over another.

I randomly assigned patches to receive arrays of 1, 2, 4, 8, 16, 32, 40 or 64 evenly spaced, potted *B. rapa* plants with similar numbers of flowers (densities of 0.04, 0.08, 0.16, 0.32, 0.64, 1.28, 1.6 and 2.56 plants m⁻², respectively). Each density was replicated twice in each field, for a total of four replicates per density. I included more low-density treatments to improve my ability to determine if the pollinator response curve is linear, saturating, or accelerating at low plant densities. Each patch was covered with a wire-mesh enclosure (with 5 cm holes) to discourage deer herbivory while still allowing pollinators access to plants.

I ran two temporal replicates of the experiment, from 12–16 April and from 7–15 May 2003. Densities were randomly reassigned to patches in the second replicate. During the second temporal replicate, I replaced the 64-plant treatment with four additional replicates of the one-plant treatment (thus, n = 688 plants in replicate 1, and n = 416 in replicate 2).

For 1–2 fifteen-minute periods between 09:30 and 16:00 h, on each of four or seven days during the first or second experimental runs, respectively, I recorded the number of pollinator visits to patches and the number of plants each pollinator visited once it entered a patch (focal plants were observed if all plants could not be observed at once in the highest-density patches). I conducted no observations during periods with rain or heavy cloud cover. During the experiment, patches of each type were watched for a total of 8±0.12 h (mean ± standard deviation), except for the 64-plant treatment, which was watched for a total of 3.25 h. After the experimental period, I counted the number of flowers and the number of fruits produced on each plant, and used the ratio of fruits to flowers as a measure of fruit set. I then sampled three fruits from each plant from within the first ten flowers produced on the largest stalk (if possible, I sampled fruits from the first, third, and fifth nodes), and counted the number of seeds in each sampled fruit. In addition, I weighed seeds from at least one sampled fruit produced by 24 plants from the two lowest density treatments, and 43 plants from the 40-plant treatment. I weighed up to 6 seeds per fruit, as a group, divided by the number of seeds weighed to get the average weight per seed, and averaged these values among fruits for each plant. Since seed weights were not significantly different between the high and low-density treatments (two tailed t-test; T = 2.02; P = 0.848),

I did not determine seed weight for the other density treatments.

Data analysis

I tested for density effects on visitation rates to patches (visits per patch per hour), visits to plants per patch visit, visitation rates to plants within patches (visits per plant per hour), and fraction of flowers fruiting per plant (hereafter called fruit set), using analysis of deviance (using GLM models in Splus 6.1 2002), which uses likelihood ratio tests and appropriate error distributions to describe the data. I assumed that fruit set was binomially distributed and that both numbers of visits and numbers of seeds per fruit were Poisson-distributed. I used ANOVA to test for effects of patch density on the number of floral nodes per plant, assuming the data were normally distributed. For analyses of visitation data, I included temporal replicate, date (within temporal replicate), field, and patch (within field) as categorical covariates. For analyses of fruit set and seeds per fruit, I included temporal replicate, field and patch (within field) as categorical covariates. In addition, for unknown reasons, node production increased slightly as a function of density (including replicate, field, and position within field as covariates; $F=21.96$; $P<0.01$, partial correlation coefficient = 0.206). Because the number of flowers per plant differed among plants, I calculated the number of seeds produced per flower (seed production per fruit \times fruit set) to compare effects of treatments on seed production independent of the number of flowers per plant. Then I tested for effects of density on the number of seeds produced per floral node using analysis of deviance, assuming the data were Poisson distributed. Since I am mainly interested in effects of density on pollinator visitation and plant reproduction, I report only statistics and p-values for effects of density in the text, but I report all effects in tables.

To find the functional form of the pollinator aggregative and functional responses to increasing plant density, I fitted the parameters of following equation to the data using maximum likelihood methods:

$$V = \frac{aD^c}{1 + bD^c} \quad (1)$$

where V is the rate of pollinator visitation (number of pollinators per patch or number of plants visited per pollinator per foraging bout) and D is the number of plants in a five-by-five meter patch. When V is the rate of pollinator visitation to patches of plants, Eq. 1 describes an aggregative response, and when V is the number of plants each pollinator visits per foraging bout, Eq. 1 describes a functional response. The ratio of a/b is

the asymptotic visitation rate at high density, and $1/b$ is the plant density at which visitation is one half its maximum value. Parameters b and c determine the shape of the function. Equation 1 is flat if $b=c=0$, increases linearly with D if $b=0$ and $c=1$, saturates monotonically if $b>0$ and $c\leq 1$, and is sigmoidal if $b>0$ and $c>1$ (Fig. 1). I fitted parameters for flat, linear, and saturating ($c=1$) curves, and for the 3-parameter model (which is sigmoidal if $c>1$). The difference between the saturating model and the 3-parameter model where $c\leq 1$ is that in the latter case, c is allowed to vary (thus enabling me to determine whether the data are best described by a 2 or a 3 parameter model). Then, I used likelihood ratio tests to find parameter confidence limits and to determine which functional form fit the data best. When likelihood ratio tests showed that one model was not significantly different than another, I chose the simpler model as more parsimonious. To determine whether acceleration in the aggregative response at low densities might be obscured by data from high-density patches, I conducted additional likelihood ratio tests using data from only the four lowest densities, comparing an exponential model (where $b=0$ and $c<1$ in the saturating case; $c>1$ in the accelerating case) to linear and flat models.

In addition, different types of pollinators might respond differently to increasing plant density (Sih and Baltus 1987). If some pollinators are more effective than others (either through high frequency of visits or high effectiveness per visit), then the aggregative/functional response curves of the more effective pollinators may be more relevant than an aggregative/functional response curve that lumps all pollinator types. Thus, I used subsets of the data to determine the functional forms of both aggregative and functional response curves for four different insect taxa for which I had observed sufficient numbers of individuals: bombyliid flies, syrphid flies, solitary bees, and Lepidoptera.

In 21 of the 239 observation periods, fieldworkers observed only a subset of the plants in high-density patches. In this case, observers may not have detected all pollinators entering the patch (thus affecting the estimated aggregative response). I attempted to account for this potential bias by conducting a second analysis in which I divided visits to patches by the proportion of plants observed. This new estimate assumes that the visitation rate is proportional to the size of the patch, which may lead to overestimates of visitation to patches, because pollinators that enter the patch far from observed plants may later enter and be counted in the observed portion of the patch. Because these separate analyses yielded the same qualitative results in all but one case, I report results from analyses using unaltered visitation data unless otherwise stated.

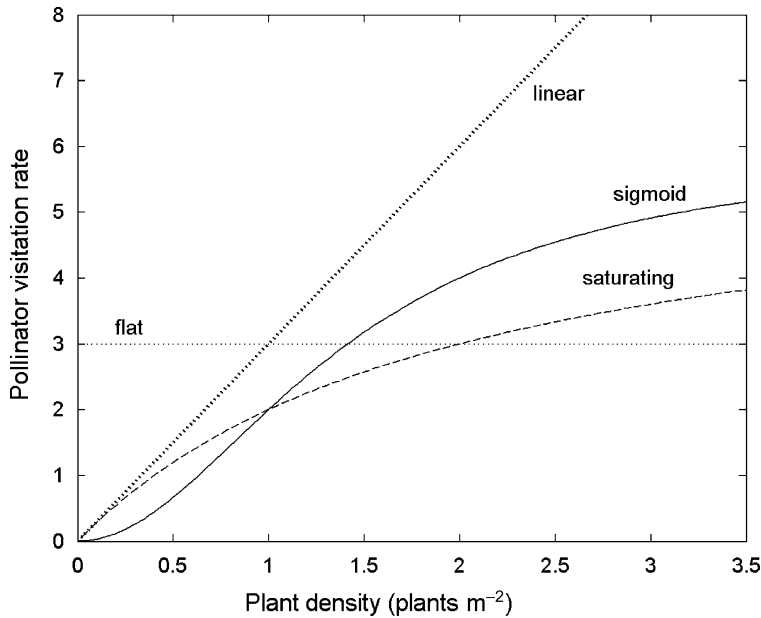


Fig. 1. Models of pollinator visitation rate as a function of plant density. The flat model (parameters $a = 3$, $b = c = 0$) is indicated by the thin dotted line. The linear model ($a = 3$, $b = 0$, $c = 1$) is indicated by the thick dotted line. The saturating model ($a = 3$, $b = 0.5$, $c = 1$) is indicated by the dashed line. The sigmoid model ($a = 3$, $b = 0.5$, and $c = 2$) is indicated by the solid line.

Results

Visitor taxa

Insect visitors to *Brassica rapa* plants in the experimental patches included Diptera, Hymenoptera, Lepidoptera, and Coleoptera (Table 1). Syrphid flies and bombyliid flies were the most common Dipteran visitors (Table 1). Although syrphids made the most visits to patches, they visited a smaller percentage of plants per foraging bout than did bombyliid flies, solitary bees, social bees, or Lepidoptera (Table 1). Solitary bees (including species in the family Halictidae) and social bees (*Bombus* spp.) were the most common Hymenopteran visitors (no honey bees were observed). Lepidoptera included cabbage whites (*Pieris rapae*), painted ladies (*Vanessa* sp.), eastern tailed blues (*Everes comyntas*), spring azure (*Celastrina ladon*), dusky-winged skipper (*Erynnis* sp.), cloudy-winged skipper (*Thorybes* sp.), other skippers (Hesperiidae), and a few species of moths. Beetles included Chrysomelidae (*Diabrotica* sp.),

Elateridae, and Cantharidae. These might be florivores rather than pollinators.

Number of pollinator visits to patches (aggregative response)

The number of pollinator visits to experimental patches per unit time increased with increasing numbers of plants per patch (analysis of deviance $\chi^2 = 388.52$; $P \ll 0.01$, partial correlation coefficient of density effects on visitation = 0.028; Fig. 2A). Visitation rate to patches was also affected by date within temporal replicate, field, and patch within field (Table 6). There were significant interaction effects between patch density and field, and between patch density and temporal replicate, but separate analysis of patch density effects from each temporal replicate/field combination yielded the same qualitative results.

Visits per patch per hour increased as a saturating function of the number of plants per patch. The best-fit

Table 1. Insect types observed visiting *Brassica rapa* during experimental replicates and the percent of visits to patches by each pollinator type.

Visitor taxon	Percent of visits to patches of <i>B. rapa</i> (N = 1081)	Percentage of observed visits to <i>B. rapa</i> Plants (N = 1698)	Mean number of observed plants visited per foraging trip
<i>Diptera</i>	67.06	49.59	1.16
Syrphidae	61.70	40.11	1.02
Bombyliidae	4.16	8.42	3.18
other	1.20	1.06	1.39
<i>Hymenoptera</i>	25.73	37.69	2.30
Solitary Bees	22.58	34	2.36
<i>Bombus</i> spp.	0.74	1.52	1.25
other	2.41	2.12	2
<i>Lepidoptera</i>	6.29	12.13	3.06
Other insects	0.93	0.59	1

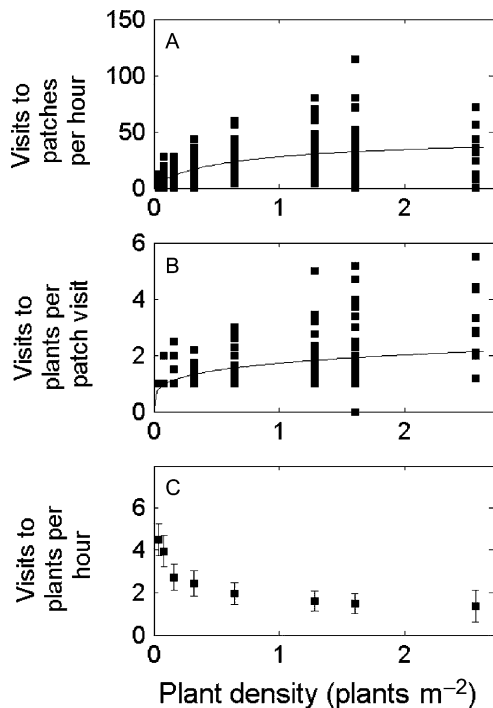


Fig. 2. (A) Pollinator visits to patches per hour (aggregative response) increases as a saturating function of plant density. (B) Visits to plants by pollinators per patch visit (functional response) increases as a saturating function of plant density. (C) Visits to individual plants decreases as plant density increases (mean \pm poisson confidence intervals). Solid lines in (A) and (B) indicate mean fitted curves.

curve is saturating because the fitted value (and even the upper confidence limit) of the shape parameter c is less than one (Table 2). Likelihood ratio tests indicated that the visitation response to patches as plant density increased was saturating rather than linear or flat (Table 3). In addition, likelihood ratio tests indicated that data from only the four lowest densities showed the same pattern – the best-fit model was saturating rather than accelerating, linear, or flat (the best-fit value with 95% confidence limits for parameter c was 0.6 (0.5, 0.61)). Because field and temporal replicate affected visits to patches per hour, I analyzed data separately from each field and from each temporal replicate. In each case, the pattern was the same – the best-fit model was a saturating aggregative response curve.

I performed the same tests separately for four subgroups of pollinators: bombyliid flies, syrphid flies, solitary bees, and Lepidoptera (Fig. 3A–3D). Fitted parameters for the best-fit models are listed in Table 2. For both solitary bees and syrphid flies, the 3-parameter model fit best (from a likelihood ratio test between saturating and full models, $\chi^2 = 62.62$ and 4.48; $P < 0.01$ and 0.05, respectively). Although the best-fit curve was saturating for solitary bees ($c < 1$), it was borderline sigmoidal in the syrphid flies ($c > 1$; Table 2). For

bombyliid flies, a linear model fit significantly better than did a flat model ($\chi^2 = 166.09$; $P < 0.01$), but the linear curve was not significantly different from either a saturating or full model ($\chi^2 = 0.26$ and $\chi^2 = 0.71$, respectively). For Lepidoptera, a saturating curve fit best (Table 2).

Separate curve-fitting analyses using visitation data adjusted to account for observation periods when not all plants were observed yielded the same qualitative results for all pollinator types except syrphid flies. For syrphid flies, the sigmoid model did not fit significantly better than a saturating model when I conducted analyses with adjusted data. Thus, I report results from both analyses for syrphid flies, in Table 2. Because there were effects of temporal replicate on visits by syrphid flies to patches per hour, I analyzed data separately from each temporal replicate. In both replicates, the best-fit model was a saturating aggregative response curve (Table 2, Fig. 3B).

Pollinator visitation to individual plants (functional response)

The number of plants visited per pollinator visit to a given patch increased as a function of plant density (analysis of deviance $\chi^2 = 6.92$; $P < 0.01$; partial correlation coefficient of density effects on visitation = 0.0145; Fig. 2B). There was a significant interaction between patch density and temporal replicate, but separate analyses of data from each replicate yielded similar qualitative results – plants visited per visitation bout increased with plant density, although the effect of density was not significant in either replicate alone (Table 6).

The number of visits to individual plants per foraging bout (the functional response) increased as a saturating function of plant density (Table 4). Likelihood ratio tests indicated that the visitation response to patches as plant density increased was saturating rather than flat or linear (Table 5). Because there were effects of temporal replicate on visits per foraging bout, I analyzed data separately from each each temporal replicate. In the first replicate the best-fit model was flat, but in the second replicate the best-fit model was a saturating curve.

I performed the same tests separately for four subgroups of pollinators: bombyliid flies, syrphid flies, solitary bees, and Lepidoptera (Fig. 4A–4D). Fitted parameters for the best-fit models are listed in Table 4. For both solitary bees and syrphid flies, the full model fit best (from a likelihood ratio test between saturating and full models, $\chi^2 = 5.74$ and 8.10, respectively; $P < 0.01$ in each case; Table 4). In each case, the fitted curve was saturating, because the shape parameter c was less than one. For bombyliid flies and Lepidoptera, the full model, saturating model, and linear model did not fit significantly better than a flat model (Table 4).

Table 2. Maximum likelihood parameter estimates, for Eq. 1, fit to the number of visits to patches per hour as a function of density (aggregative response).

Best-fit model	N	Parameters	Mean (lower 95% confidence limit, upper 95% confidence limit)
Full data set full model**	239	a	64.25 (49.37, 84.05)
		b	1.30 (0.79, 1.97)
		c	0.81 (0.71, 0.92)
Bombyliid flies linear	239	a	1.09 (0.93, 1.25)
Syrphid flies sigmoid	239	a	117.78 (81.20, 176.06)
		b	6.29 (0, 9.94)
		c	1.16 (1.01, 1.32)
Replicate 1 saturating	98	a	72.87 (50.90, 111.74)
		b	11.25 (7.27, 18.60)
Replicate 2 saturating	141	a	80.53 (71.20, 91.42)
		b	2.24 (1.83, 2.73)
Syrphid flies*** saturating	239	a	79.82 (71.05, 90.06)
		b	3.75 (3.18, 4.43)
Solitary bees full model**	239	a	5.70 (5.34, 6.17)
		b	0 (0, 0.06)
		c	0.60 (0.54, 0.66)
Lepidoptera saturating	239	a	3.48 (2.57, 4.81)
		b	0.96 (0.50, 1.71)

**shape parameter for the fitted curve is below 1, indicating that the shape is saturating

***test accounting for numbers of plants observed. In all other pollinator types (and in the full data set, there were no other qualitative differences in these results

Combined effects of pollinator aggregative and functional responses

Visitation rates (pollinator visits per hour) to individual plants decreased as a function of the number of plants per patch (analysis of deviance $\chi^2 = 38.23$; $P < 0.01$; partial correlation coefficient of density effects on visitation = -0.025 ; Fig. 2C). This was affected by date within temporal replicate, field, and patch within field (Table 6). Although there was a significant interaction between patch density and temporal replicate, separate analyses using data from each replicate yielded similar qualitative results with respect to effects of patch density. Thus, as plant density increased, pollinator visits did not increase as steeply as the number of plants per patch.

Fruit set was not detectably affected by the number of plants per patch (analysis of deviance $\chi^2 = 0.15$; $P = 0.7$; Fig. 5A). However, the number of seeds per fruit increased as a function of the number of plants per

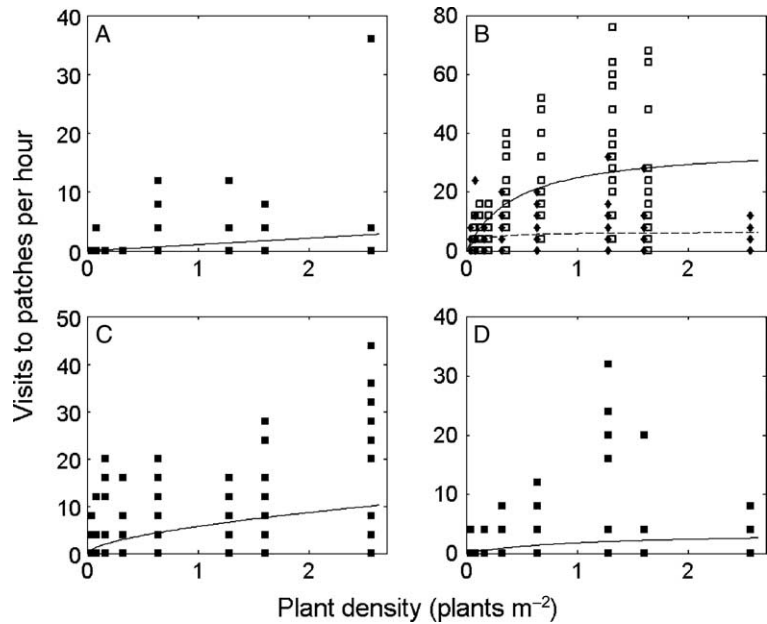
patch ($F = 13.18$; $P \ll 0.01$; partial correlation coefficient of density effects on per-fruit seed production = 0.070 ; Fig. 5B). The number of seeds per fruit was also affected by temporal replicate, field, and patch within field (Table 7). There were significant interaction effects between temporal replicate and patch density, and between field and patch density. Separate analyses of data for each replicate and field combination showed similar results to the analysis of the full data set (a significant positive effect of patch density), except the second replicate, which showed a non-significant negative effect of patch density.

Further, seeds produced per floral node (mean seeds per fruit \times fruit set) increased as a function of the number of plants per patch ($\chi^2 = 9.77$; $P = 0.01$; partial correlation coefficient of density effects on total seed production = 0.06 ; Fig. 5C). This was affected by temporal replicate, field, and patch within field (Table 7). There was a significant interaction effect

Table 3. Results from likelihood ratio tests between four models (sigmoid, saturating, linear, and flat), fitting aggregative response for all pollinator taxa combined.

Better-fit model	Alternative model	df	χ^2	P
Full model (3 parameters allowed to vary)	saturating (c = 1)	1	11.1	<0.01
Full model (3 parameters allowed to vary)	linear (b = 0, c = 1)	2	1276.39	<0.01
Full model (3 parameters allowed to vary)	flat (b = c = 0)	2	1621.74	<0.01
Saturating	linear	1	1265.296	<0.01
Saturating	flat	1	1610.65	<0.01

Fig. 3. Aggregative response of four taxonomic groups of pollinators to increasing density of *B. rapa*. Solid lines indicate mean fitted curves. (A) bombyliid flies, (B) syrphid flies (closed diamonds indicate data for replicate 1, and open squares indicate data for replicate 2), (C) solitary bees, and (D) Lepidoptera.



between density and temporal replicate. Separate analyses of data for each replicate showed similar qualitative results, but the positive effect of patch density was not significant in the first temporal replicate.

Discussion

Increasing plant density had a strong positive influence on both the number of pollinator visits to patches and the number of plants visited per pollinator foraging bout. This in turn affected visitation to individual plants and seed production in *B. rapa*. However, I found little

evidence that visitation accelerated at low plant density, one mechanism that can allow pollination facilitation. In the following paragraphs, I discuss factors that may affect the shape of the pollinator aggregative and functional responses and consequences of combined pollinator responses for plant visitation and reproduction, and I review some reasons why facilitation has seldom been detected in nature.

Pollinator aggregative response

In this study, the shape of the pollinator aggregative response to *B. rapa* plant density is saturating, implying

Table 4. Maximum likelihood parameter estimates, for Eq. 1, fit to the number of visits to plants per foraging bout as a function of density (functional response).

Best-fit model	N	Parameters	Mean (lower 95% confidence limit, upper 95% confidence limit)
Full data set full model**	214	a	1.72 (1.52, 6.55)
		b	0 (0, 2.80)
		c	0.23 (0.14, 0.53)
Bombyliid flies flat	26	a	2.03 (1.53, 2.62)
Syrphid flies*** full model **	174	a	1.66 (1.44, 7.00)
		b	0 (0, 3.28)
		c	0.23 (0.12, 0.56)
Solitary bees full model**	102	a	1.95 (1.65, 10.77)
		b	0 (0, 4.45)
		c	0.38 (0.15, 0.77)
Lepidoptera flat	39	a	2.03 (1.62, 2.51)

*shape parameter for the fitted curve is below 1, indicating that the shape is saturating

***test accounting for numbers of plants observed. In all other pollinator types (and in the full data set, there were no other qualitative differences in these results

Table 5. Results from likelihood ratio tests between four models (sigmoid, saturating, linear, and flat), fitting functional response for all pollinator taxa combined.

Better-fit model	Alternative model	df	χ^2	P
Full model (3 parameters allowed to vary)	saturating ($c = 1$)	1	9.53	<0.01
Full model (3 parameters allowed to vary)	linear ($b = 0, c = 1$)	2	210.64	<0.01
Full model (3 parameters allowed to vary)	flat ($b = c = 0$)	2	24.78	<0.01
Saturating	linear	1	201.11	<0.01
Saturating	flat	1	15.25	<0.01
Flat	linear	NA	185.86	<0.01

that pollinators do not ignore patches at very low densities. In part, perhaps the curve does not accelerate at low densities because patches were not sufficiently far apart to make flight between patches costly to pollinators. Thus pollinators may perceive the entire field as a single patch. Further, visitors to *B. rapa* also visited several other plant species that bloomed in and around the experimental fields. Either of these factors may have effectively decreased the perceived patchiness of the landscape by the generalist pollinators of *B. rapa*. It is important to understand the spatial and temporal scale at which pollinators perceive resource patches if we wish to determine pollinator aggregative responses to plant density and to predict the resultant effects on plant reproductive success. In the context of the present study, one could test this idea by repeating the experiment using different distances between experimental patches.

The model by Feldman et al. (2004) predicts that if pollinators respond to increasing heterospecific density in the same way that they did to increasing conspecific density in this study, then interspecific pollination facilitation is not likely to occur via pollinator aggregative and functional responses in this system. One assumption that affects the above prediction is that

pollinators do not distinguish between flowers of the plant species they visit. This assumption is common in models and discussions of pollination facilitation (Bobisud and Neuhaus 1975, Goulson 1994, Feldman et al. 2004). Indeed, pollinators often behave as if they do not distinguish between plant species in studies of competition for pollinators (Waser 1978, Campbell and Motten 1985, Kunin 1993) and pollination facilitation (Schemske 1981).

Pollinator preference for one of two plant species might enhance facilitation in two possible ways. First, facilitation of the less preferred species might occur if, as the density of the preferred plant species in the patch increases, pollinators are increasingly attracted to the patch, but some "spill over" onto the less-preferred species (this mechanism requires that pollinators do, intentionally or mistakenly, make some visits to the less preferred species). Second, facilitation of the preferred species might occur if an increase in the density of the less-preferred plant species attracts more pollinators to the patch, which then visit the preferred species (this mechanism requires that pollinators are at least partially attracted by less-preferred species). To my knowledge, these possibilities have yet to be tested. My experiment

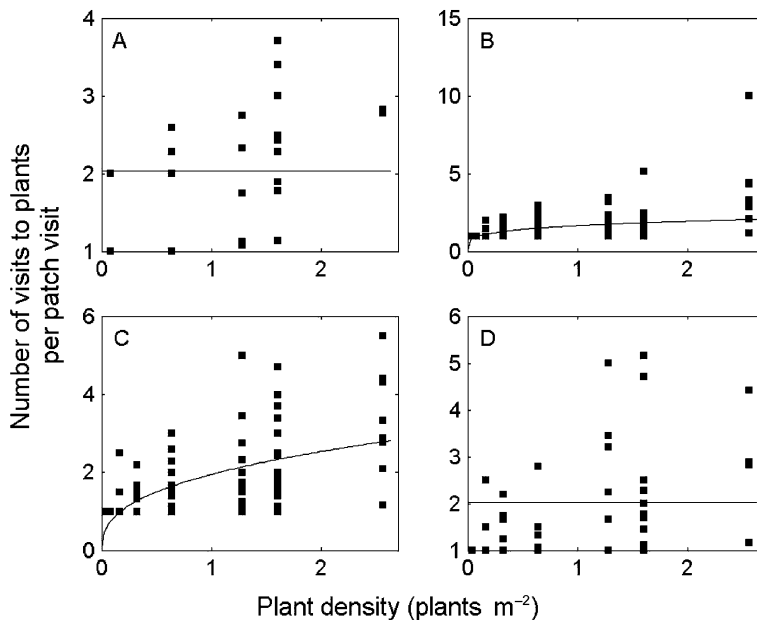


Fig. 4. Functional responses of four taxonomic groups of pollinators to increasing density of *B. rapa*. Solid lines indicate mean fitted curves. (A) Bombyliid flies, (B) syrphid flies, (C) solitary bees, and (D) Lepidoptera.

Table 6. Summary of statistical results for visitation data.

Response variable	Significant main effects	Significant interaction effects	df	Deviance	P
Visits to patches per hour (N = 239)	density		1	388.52	< 0.01
	date in replicate		11	149.91	< 0.01
	field		16	305.51	< 0.01
	patch within field		30	578.48	< 0.01
		density × field	1	73.45	< 0.01
Number of plants visited per foraging bout (N = 214)	density	density × temporal replicate	1	54.76	< 0.01
			1	6.92	< 0.01
		density × temporal replicate	1	7.57	< 0.05
Visits to plants per hour (N = 239)	density		1	38.23	< 0.01
	date in replicate		12	24.06	< 0.01
	field		16	32.88	< 0.01
	patch within field		30	80.36	< 0.01
		density × temporal replicate	1	6.19	< 0.02

applies to the case in which pollinators do not distinguish between plant species, and to the case of a preferred species in a multispecies system in which pollinators so strongly prefer one species that they ignore the others.

The species composition of the pollinator community may affect the shape of the net aggregative response

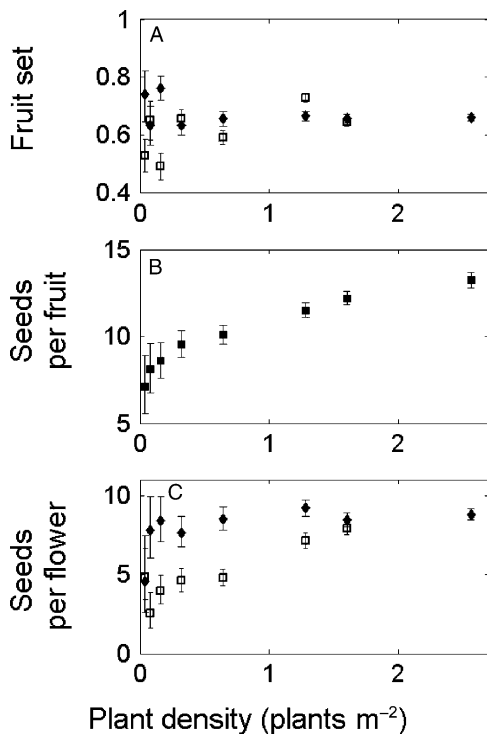


Fig. 5. (A) Proportion of fruits produced as a function of plant density (mean percent fruit set \pm binomial confidence intervals). (B) Seeds produced per fruit increase as plant density increases (mean \pm poisson confidence intervals). (C) Seeds produced per floral node increase as plant density increases (mean \pm poisson confidence intervals). In (A) and (C), solid diamonds indicate data for replicate one, and open squares indicate data for replicate two.

curve. Data from Sih and Baltus (1987) indicate that different pollinator species may have different aggregative response curves. However, if all pollinators are equally effective, then the pollinator response curve for all pollinator species combined may be used to predict whether pollination facilitation is possible. If the overall curve is saturating, then plant reproduction may reflect a balance of effects of pollinators with a sigmoid functional response and those with a saturating or linear response at low densities. However, if a subset of pollinators is responsible for a large share of the pollinations (either through effective visits or frequent visits), then the shape of the response curve for this subset of pollinators could determine whether pollination facilitation is possible. In this study, three of the four primary insect groups that visit *B. rapa* exhibit either saturating or linear visitation response curves. Although one group (Syrphidae) showed a slight sigmoid aggregative response, the response for each temporal replicate was saturating, indicating that the result for the combined replicates was probably driven by differences in numbers of visits to patches in the two temporal replicates. Thus, even if syrphid flies are the most effective pollinators of *B. rapa*, facilitation is unlikely to occur in this system. Further, syrphids often remain on single plants for long periods of time (T. S. Feldman, pers. obs.; on average, only one visit was observed per foraging bout; Table 1), and so may be very inefficient pollinators of this self-incompatible plant.

Pollinator functional response

Because I used a single plant species in this experiment, and there were no other plant species within the patches from which pollinators might switch, I expected the pollinator functional response to be saturating (Murdoch and Oaten 1975). Indeed, the functional response of the combined community of visitors was a

Table 7. Summary of statistical results for fruit and seed production data.

Response variable	Main effects	Significant interaction effects	df	Deviance (*)/F	P
Nodes produced per plant (N = 1062)	density		1	21.96	<0.01
	temporal replicate		1	30.58	<0.01
	field		16	12.08	<0.01
	patch within field		30	12.53	<0.01
Percent fruit production per plant (N = 1062) *	density		1	0.153	0.695 NS
Seed production per fruit * (N = 1062)	density		1	27.83	<0.01
	temporal replicate		1	69.18	<0.01
	field		16	273.73	<0.01
	patch within field		30	137.32	<0.01
		density × field	1	13.02	<0.01
		density × temporal replicate	1	102.11	<0.01
Seed production per floral node* (N = 1062)	density		1	9.77	<0.01
	temporal replicate		1	82.08	<0.01
	field		16	135.41	<0.01
	patch within field		30	227.99	<0.01
		density × field	1	17.05	<0.01
		density × temporal replicate	1	96.65	<0.01

saturation function of *B. rapa* density. Even if pollinators responded to the entire field as a patch, visiting plants that bloomed in and around the experimental fields (especially during the second replicate), the saturating functional response curves indicate that in this system, pollination facilitation cannot occur by disproportionate increases in visits per pollinator per foraging bout. This result was consistent among individual pollinator groups for which data were sufficient to distinguish among models.

Both aggregative and functional response curves are likely not fixed for a given plant species and its pollinators, but rather change as the species identity of neighboring flowers changes, as the abundance and species identity of the pollinator community changes, or as the season progresses. For instance, changes in the abundance of neighboring plants could cause pollinators to switch to denser patches or more abundant plant species, leading to sigmoid aggregative and functional responses, respectively. Even though more potentially competing plants were blooming later in the season in this study, pollinators may also have been more abundant then, because patches received more pollinator visits in the second temporal replicate. However, I found no evidence that visitation curves actually did vary between saturating and sigmoid for a *B. rapa*. Although visitation response curves varied spatially and temporally, both temporal and spatial replicates showed the same general pattern of a saturating visitation response.

Combined effects of aggregative and functional responses

Although both visitation to patches and visits to plants per foraging bout increased with increasing plant

density, per-plant visitation decreased. Therefore, positive effects of visitation to patches and of visits to plants per bout within patches may nonetheless result in lower per-plant visitation at high densities. This pattern occurs when the pollinator aggregative and functional responses saturate at higher patch densities, and an increase in the number of plants causes an incrementally smaller increase in visitation. Saturating aggregative response curves result in part because pollinators cannot visit patches at more than some maximum rate, and in part because the regional pool of pollinators may be limited. Similarly, saturating functional response curves result because pollinators cannot visit plants above some maximum rate, due to handling time at flowers (Soberon and Martinez del Rio 1981, Herrera 1989, Ingvarsson and Lundberg 1995). Although Jennersten and Nilsson (1993) found a saturating pattern at the patch scale, many studies have documented a similar pattern on a smaller scale, when measuring pollinator visitation to different inflorescence sizes. In several studies, pollinators visit larger plants more often than smaller plants, and yet visit a smaller percentage of flowers per plant on larger plants than on smaller plants (Geber 1985, Klinkhamer and de Jong 1990, Mitchell 1994, Robertson and Macnair 1995). At the scale of an individual plant, this may promote outcrossing (decreasing geitonogamy on larger plants), but at the scale of a patch, this may leave some plants unfertilized, negatively affecting per-plant fruit production in more dense patches (Jennersten and Nilsson 1993).

For the self-incompatible *B. rapa*, even with decreased per-plant visitation at higher densities, seed production increased with plant density, because pollinators were more likely to have previously visited other *B. rapa* plants in higher-density patches. Thus, pollinators visiting plants in high-density patches were likely carrying

larger quantities of compatible pollen, so each visit could fertilize more ovules.

Pollination facilitation

The results of this study suggest that the mechanism of pollination facilitation by way of an accelerating aggregative response is unlikely for *B. rapa*. However, it is not clear whether these results reflect natural systems in general, or if other mechanisms by which pollination facilitation can occur are operating in this species.

Goulson (1994) and others have suggested that facilitation in pollination systems (and thus, interspecific rescue from low-density effects) requires very stringent conditions, and should occur rarely in nature. Indeed, few studies of co-flowering plants have found evidence for facilitation of visits to plants (Thomson 1981, 1982, Johnson et al. 2003) or reproductive success (Schemske 1981, Pellmyr 1986, Laverty and Plowright 1988, Laverty 1992, Alexandersson and Ågren 1996, Roy 1996, 1994, Moeller 2004, T. S. Feldman, unpubl.) relative to those that have found evidence of competition for pollination (Waser 1978, Campbell 1985, Campbell and Motten 1985, Galen and Gregory 1989, Randall and Hilu 1990, Feinsinger et al. 1991, Kunin 1993, Lammi and Kuitunen 1995, Brown and Mitchell 2001, Brown et al. 2002) or no effect one flowering plant species on another's reproductive success (McGuire and Armbruster 1991, Armbruster and McGuire 1992). Facilitation has been documented most often in nectarless species (Pellmyr 1986, Laverty 1992, Alexandersson and Ågren 1996, Ferdly et al. 1999, Johnson et al. 2003, but see Lammi and Kuitunen 1995), which receive more visits and produce more seeds in the presence of other, nectar-producing plant species. If facilitation occurs due to sigmoid pollinator responses in natural systems, pollinators may exhibit sigmoid aggregative or functional responses in systems where facilitation is known to occur. However, I know of no studies that document facilitation and also characterize the shapes of the aggregative or functional responses of pollinators.

Perhaps most studies of co-flowering plant species are conducted in populations where conditions are unfavorable for facilitation (i.e. where pollinators discriminate among different flowers and do not switch to plants growing in higher density patches). Alternatively, facilitation may commonly occur on a local scale via increased quality of pollinator visits in the presence of co-flowering species (T. S. Feldman, unpubl.) if pollinators are less likely to visit additional patches of other species in between visits to a patch with co-flowering species. Facilitation may also more commonly occur via the numerical responses of pollinators when several plant species bloom together, either increasing local resources at a given time or lengthening the flowering

season, such that pollinator species increase in abundance in subsequent years, in turn increasing visitation (Waser and Real 1979, Moeller 2004). In this case, the aggregative and functional responses to patches within a flowering season would not be sufficient to predict whether longer-term facilitation will occur.

Acknowledgements – I would like to thank William F. Morris for many useful discussions and for advice on the methods and for comments on several drafts of the manuscript. Thanks to James S. Clark for additional advice on the methods. Thank you to members of the Wilson and Morris labs, who all provided useful discussion and help with the manuscript. I am extremely grateful to Courtney Fitzpatrick, Heidi and Colin Hempel-Frazier, Olivia Fu, Sharleen Johnson, Barbara Keighton, Jennifer A. Nelson, Lea C. Ray and Robin A. Smith, for providing help with fieldwork and setting up experiments, and to Sharleen Johnson for help with processing data. Richard Broadwell and Judson Edeburn helped provide access to field sites in Duke Forest. NSF supported this research, through a Doctoral Dissertation Improvement Grant (Feldman).

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