

High density floral patches attract more pollinators, but not as an ideal free distribution

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Introduction

The creation of floral strips in agricultural field margins or the sowing of flowering plants such as phacelia (*Phacelia tanacetifolia*) and buckwheat (*Fagopyrum esculentum*) in orchards and vineyards are established methods for providing suitable habitat and resources for beneficial insects. By supplying shelter, nectar, alternative nutrition, and pollen (“SNAP”), the creation of florally-rich habitat can increase both the abundance and diversity of insect pollinators, such as wild bees, and arthropod predators such as hoverflies and hymenopteran parasitoids (González-Chang et al. 2019). Subsequently, these enhanced insect assemblages can provide increased ecosystem services such as crop pollination and natural management of insect pests (Blaauw & Isaacs 2014; Campbell et al. 2017; Woodcock et al. 2019). With a natural capital approach being slowly introduced to New Zealand farming, there may be additional scope for the creation of semi-natural habitats involving native flowering plants to be incorporated within intensive farming landscapes (see Fukuda et al. 2011; Macdonald et al. 2018; Curtis et al. 2019).

When integrating floral resources, native or otherwise, within agricultural landscapes it is valuable to ascertain how the arrangement and density of flowering plants influences their attractiveness to target insect taxa. In terms of pollinating insects, floral density can strongly influence foraging patterns, and, as insect flight is energetically demanding, foragers often focus on areas of high floral density to minimize flight costs and maximize rewards (e.g. Comba 1999; Zimmerman 1981; Dreisig 1995; Hegland & Boeke 2006). However, if too many insects are attracted to the same floral patches, competition for space, pollen, and nectar can intensify, and the frequency of visits to depleted flowers would tend to increase.

Forager distributions can sometimes be explained by an ideal free distribution (IFD), when the quality of all resource patches in an area equalizes, and optimally foraging animals distribute themselves to maximize individual payoffs (Fretwell 1969; Tregenza, 1995). Anthophilous insects often display such patterns, distributing themselves according to patch profitability (Thomson, 1981), and Dreisig (1995) described how high floral density patches hosted the greatest number of foraging bumblebees such that the nectar intake per flower was equalized.

The objective of this study was to gain empirical data on how different pollinator taxa (honeybees, bumblebees, and hoverflies) respond when simultaneously presented with different densities of floral resources. Additionally, by assessing the ratio of pollinators to flowers at each floral density we will assess whether each taxa may be following an ideal free distribution.

Materials and methods

This study was carried out at Rosemount Environmental Research Station, University College Dublin, on July 5th and 6th, 2021. White mustard (*Sinapsis alba*) plants were grown in plastic pots (12.5cm diam: 9cm depth) with 10 plants per pot. The plants were used in trials when flowering had commenced, and each plant averaged two or three floral units per pot.

Artificial stands of *S. alba* were set up on a lawn area in three locations spaced 2 m apart in a line (Fig. 1). Each location was randomly assigned to one of three treatments before the start of each observation period: (i) low floral density (1 pot with ~25 floral units); medium floral density (4 pots with ~100 floral units); or high floral density (9 pots with ~225 floral units). This gave one stand of each level of floral density per observation period.

Each day, six 30-minute pollinator surveys were conducted between 11am and 4pm, totalling 12 observation periods over the two days. Prior to observations, plants were presented on the lawn for 30 minutes to give insects time to detect them and become accustomed to the pots. During each survey, we recorded the number of bumblebees (*Bombus* spp.), honeybees (*Apis mellifera*), and hoverflies (Syrphidae) that interacted directly with open flowers. To standardize counts at each stand in terms of the total count

for that survey period, we also calculated the proportion of individuals at each stand for each survey.



Figure 1. Stands of *Sinapsis alba* at Rosemount Environmental Research Station, University College Dublin. Stands were arranged 2m apart in a line. From left to right: high floral density (9 pots with ~225 floral units); medium floral density (4 pots with ~100 floral units); low floral density (1 pot with ~25 floral units).

Nonparametric Friedman tests were used to determine if there were significant differences in the numbers (and proportions) of bumblebees, honeybees, and hoverflies among the low, medium, and high floral densities. To show if the pollinators were displaying an IFD, the observed counts for each pollinator group at each level of floral density were compared with the expected counts using chi-squared goodness of fit tests.

Results

In total, 79 bumblebees, 127 honeybees, and 145 hoverflies were recorded in the twelve surveys. The recorded numbers and proportion of individuals for all three pollinator groups exhibited clear positive associations with floral density (Figure 2). Subsequently, for all three pollinator groups there were significant differences among the three floral density treatments (Bumblebees, $P = 0.004$, Honeybees, $P < 0.001$; Hoverflies $P < 0.001$; Figure 2).

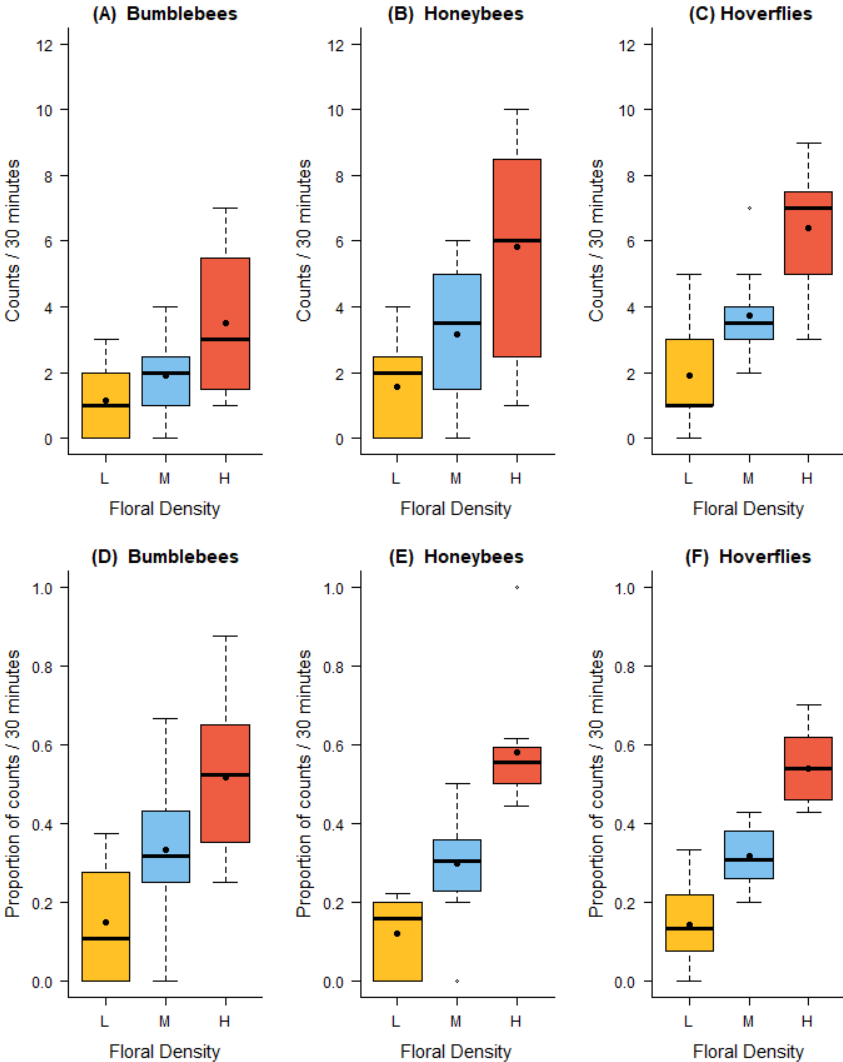


Figure 2. Counts (and proportions of counts) per 30-minutes at stands of *Sinapsis alba* (A, D) bumblebees, (B, E) honeybees, and (C, F) hoverflies. Floral density: L = low (~25 floral units); M = medium (~100 floral units); H = high (~225 floral units). Means as dark black circles, medians as solid black lines, inter-quartile ranges as boxes, max / min values given by whiskers, and small circles indicate outliers.

Although there were clear positive relationships between forager numbers and floral density, the observed counts for bumblebees, honeybees, and hoverflies all differed significantly from those expected by chance if each group was following an IFD. The observed counts for each pollinator group were over two times greater than the expected counts at stands of low floral density (Table 1). Conversely, the observed counts for each pollinator group at the high floral density stands were lower than expected counts (Table 1).

Table 1. Observed (Obs) counts of bumblebees, honeybees, and hoverflies at stands of *Sinapsis alba* of different flower density. P-values estimated from chi-squared goodness of fit tests for 2 df and expected counts (Exp) based on ideal free distribution of insects among stands of flowers.

Group	Floral Density	Floral Units	Obs.	Exp.	χ^2	<i>p</i>
Bumblebees	Low	25	14	5.6	13.9	< 0.001
	Medium	100	23	22.6		
	High	225	42	50.8		
Honeybees	Low	25	19	9.1	12.6	< 0.002
	Medium	100	38	36.3		
	High	225	70	81.6		
Hoverflies	Low	25	23	10.4	18.6	< 0.001
	Medium	100	45	41.4		
	High	225	77	93.2		
Total	Low	25	56	25.1	44.4	<<0.001
	Medium	100	106	100.3		
	High	225	189	225.6		

Discussion

Patterns of pollinator foraging activity at stands of *S. alba* were generally consistent with the expectations for optimally foraging animals, as the numbers of foraging pollinators were greatest at high floral density. These results reinforce similar findings of previous studies investigating pollinator

foraging patterns, both using natural stands of flowers and artificial stands created using potted plants flowers (e.g. Kunin 1997; Seifan et al. 2014; Akter et al. 2017; Mahon & Hodge 2022).

Although there were clear positive associations between forager numbers and floral density for all three pollinator groups, the pollinator/floral unit ratio was actually highest in the low density stands. This pattern suggests that the insects in the high-density floral patches may have actually experienced reduced competition in terms of access to flowers. Conversely, it may have also been the case that individual floral units in the high-density patches received fewer visits from pollinators compared with the low-density plants, although further study involving the monitoring of pollinator visits to individual flowers is required to provide evidence of this.

In terms of planting schemes to attract wild (and managed) pollinators into agricultural landscapes, the results obtained here do not lead to straightforward recommendations. Compact, high-density patches of flowers attracted high numbers of all three pollinator groups we investigated, so areas planted in such a way would likely support a high density (and diversity) of pollinating insects. However, the low-density patches of flowers, although attracting lower numbers of insects in an absolute sense, attracted more insects per flower than the high-density patches. So, if the number of flowering plants is fixed, a series of small flower patches rather than a single large patch could actually result in attracting more insects overall, and future studies would benefit from exploring this possibility.

We accept that our survey protocol included several potential weaknesses, some of which could have precluded the recording of an IFD. For example, the observation periods of 30 minutes may have been too short for the foragers to fully perceive differences in patch quality (Abrahams 1986), or to allow the numbers of foragers at the high density stands to stabilize as a result of individuals remaining at these sites for longer periods (Zimmerman 1982). We also scored the overall use of each patch in terms of the cumulative number of individuals over the 30-minute survey period, and not the peak number of individuals present at any one time. Future studies might expand on these investigations by using different flower species, with different colours and/ or flower morphologies, and also experiment with the arrangement of plants (e.g squares, circles, crosses, lines) and spacing of plants within and between the different density patches. In New Zealand

agricultural and horticultural settings, there are many examples of floral subsidies being provided by exotic species such as *Phacelia tanacetifolia* and buckwheat (*Fagopyrum esculentum*) (e.g. Irvin et al. 2006). A more desirable aim would be to examine the response of native pollinating insects to native flowering plants incorporated into typically-intensive New Zealand farming landscapes as a means of enhancing biodiversity and associated ecosystem service value.

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