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INFLUENCE OF GROUP SIZE AND FLORAL DISPLAY ON POLLINATOR BEHAVIOUR IN *MORICANDIA ARVENSIS*

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Abstract—Optimal foraging theory predicts that pollinators will visit dense floral patches over sparse ones. Understanding how the local abundance of floral resources influences pollinator behaviour is crucial for assessing the effect of floral traits on plant reproduction. In this study, we experimentally investigate the role of plant group size and floral display on pollinator foraging behaviour visiting *Moricandia arvensis* (Brassicaceae). We performed two field experiments: the first manipulated the number of plants per group (group size), and the second manipulated both the total number of flowers per group (group floral display) and group size. We then recorded the foraging behaviour of pollinators using probability of approaching the group, number of plants visited per group, bout length and floral visitation rate. Group floral display was the primary factor influencing pollinator foraging behaviour, except for the probability of approaching the group, where a significant interaction between group floral display and group size was observed. Specifically, the effect of larger floral displays on attracting pollinators increased disproportionately in larger groups. Because the increase in floral visitation rate due to larger displays was less than the increase in the floral display itself, visitation rate per flower was lower in groups with larger displays than in those with smaller displays. Although pollinator foraging behaviour depended largely on local floral resources, the number of plants per group partially shaped the effect of the group floral display on pollinator attraction and visitation rate. This interaction indicates complex effects of neighbouring floral traits on plant-pollinator interactions, which may have important consequences for mating patterns and plant reproductive success.

Keywords—Brassicaceae, floral density, neighbourhood, pollinator sharing, *Moricandia*, pollinator foraging behaviour

INTRODUCTION

According to optimal foraging theory, pollinators tend to choose dense floral patches over sparse ones (Heinrich & Raven 1972; Thomson 1981; Sih & Baltus 1987; Kunin 1993; Moeller 2004; Hegland & Boeke 2006; Biernaskie et al. 2009; Essenberg 2012; Hegland 2014). By affecting the behaviour and visitation rate of floral visitors, some features of the local plant neighbourhood may influence the mating patterns and reproductive success of individual plants (Klinkhamer et al. 2001; Knight 2003; Grindeland et al. 2005; Dauber et al. 2010; Martén-Rodríguez et al. 2012). Understanding how the local abundance of floral resources influences pollinator behaviour may help to know how the floral traits of the individual plants influence plant reproduction.

The relationship between visitation rate and floral density may be non-linear (Essenberg 2012): with positive effects at low densities, and weaker (Klinkhamer & de Jong 1990; Kunin 1997; Hegland & Bowke 2006; Dauber et al. 2010) or negative (Goulson 2000; Feldman 2006; Metcalfe & Kunin

2006; Veddeler et al. 2006) effects at higher densities. This variation depends mostly on the density of flowers in the surrounding environments, and on some plant and pollinator traits. Consequently, the precise shape of the relationship between floral visitation rate and density varies due to changes in several site-specific factors, including community context, plant population density, spatial plan structure, and the abundance and identity of pollinators (e.g., Stout et al. 1998; Nielsen et al. 2012; Essenberg 2013; Janovský et al. 2013; Hegland 2014; Seifan et al. 2014; Nottebrock et al. 2016). This context dependency highlights the necessity of unravelling the ecological complexity of the local intraspecific neighbourhoods.

Although the effect of the local density of floral resources has been largely studied, we still lack understanding of how the spatial configuration of the plant neighbourhood, beyond just floral density, might impact pollinator foraging behaviour. At the community level, both floral density and diversity enhance pollinator attraction and visitation activity within a patch, with their relative importance varying across pollinator groups (Hegland & Boeke 2006). At the intraspecific level, it is generally considered that pollinators respond primarily to the overall availability of floral resources (Dauber et al. 2010; Essenberg 2012). From the pollinator's perspective, this implies that a floral patch consisting of a single large plant is functionally equivalent to one composed of many small individuals. However, the configuration of a patch may lead to subtle difference that go unnoticed by humans but not by pollinators. For example, a patch composed of a single or only a few individuals may exhibit less variation in floral resources, such as nectar volume, composition or concentration, compared to patches made up of multiple individuals.

The identity of the plants in the neighbourhood also influences the expression of floral displays (Torices et al. 2018; Lewis & Friedman 2025). In *Moricandia moricandioides*, both advertising allocation (Torices et al. 2018) and signalling-reward relationships (Torices et al. 2021) have been shown to depend on the identity of neighbouring conspecifics. Plants growing with neighbouring conspecifics tend to produce more flowers, an effect that is further amplified when those neighbours are relatives (Torices et al. 2018). This pattern has been hypothesised to result from kin selection (Torices et al. 2018; Sun et al. 2021): by increasing floral display, individuals may indirectly boost their fitness via pollinator sharing with siblings. Understanding how pollinator behaviour responds to the spatial arrangement of plant groups is particularly relevant, as it can offer insights into the complex interactions between conspecific plants, their individual and group-level traits, and their floral visitors.

Here, we experimentally explore the effects of group size and floral display on the foraging behaviour of insects visiting the flowers of an insect-pollinated herb *Moricandia arvensis* L. (Brassicaceae). We conducted two field experiments: in the first, we assembled plant groups that varied in the number of individuals (*group size*); in the second, we assembled plant groups that varied in both total floral display (*group floral display*) and *group size*. Afterward, we assessed how these experimental manipulations affected: (1) the probability of attracting floral visitors to the entire group; (2) the number of different flowers visited upon arrival, (3) the number of different individual plants visited, (4) the consecutive number of flowers visited in the same individual plant; and (5) visitation rate per-flower. We hypothesize that the probability of attracting floral visitors to a group will increase primarily with group floral display, as larger displays are expected to be more visually conspicuous to pollinators. In contrast, other components of visitor foraging behaviour—such as the number of flowers and individuals visited, and the sequence of visits—are predicted to depend on the combined effects of group size and floral display.

MATERIALS AND METHODS

STUDY SYSTEM

We used the insect-pollinated weed *Moricandia arvensis* (Brassicaceae), an annual to short-lived perennial herb native to dry semi-arid and arid ecosystems of the Western Mediterranean. This species exhibits striking intra-individual floral plasticity, producing large cross-shaped lilac flowers in spring and small rounded white flowers in summer (Gómez et al. 2020). Both floral phenotypes are visited by different pollinator assemblages (Gómez et al. 2020; 2022). For this experiment, we used only the spring lilac-flowered phenotype at the onset of flowering. This phenotype was selected not only because it is easier to induce under controlled conditions, but also because the experiment was conducted in early spring, when *M. arvensis* naturally produces this floral form. Additionally, this species shares both floral traits and pollinators with its congener *M. moricandioides* (Gomez et al. 2016; 2022). The lilac phenotype closely resembles the flowers of *Moricandia moricandioides*, allowing us to discuss the broader implications of our findings in the context of that species as well. This spring phenotype is pollinated mostly by long-tongued Anthophorini bees (Gómez et al. 2016; 2020; 2022).

EXPERIMENTAL DESIGN

To explore the effect of group size and floral display on pollinator behaviour we observed pollinator visitation on two manipulative field experiments. The first experiment assessed the effect of plant group size manipulating the number of plants per group. The second experiment investigated the effect of the total number of flowers per group, manipulating both the number of flowers per group and the number of plants per group.

Study area

We conducted these experiments from March 13 to 17th 2016 at Barranco del Espartal, a seasonal watercourse in the semi-arid Guadix-Baza Basin (Granada, southeastern Spain; Fig. 1a). The vegetation is characterized by an open shrub-steppe dominated by *Artemisia herba-alba* Asso, *A. barrelieri* Bess. (Asteraceae), *Salsola oppositifolia* Desf. (Amaranthaceae), *Macrochloa tenacissima* L. (Poaceae), *Lygeum spartum* L. (Poaceae) and *Retama sphaerocarpa* L. (Fabaceae). The region has a continental Mediterranean climate with strong temperature fluctuations (ranging from -14ºC to 40ºC) and high seasonality (hot summers, cold winters).

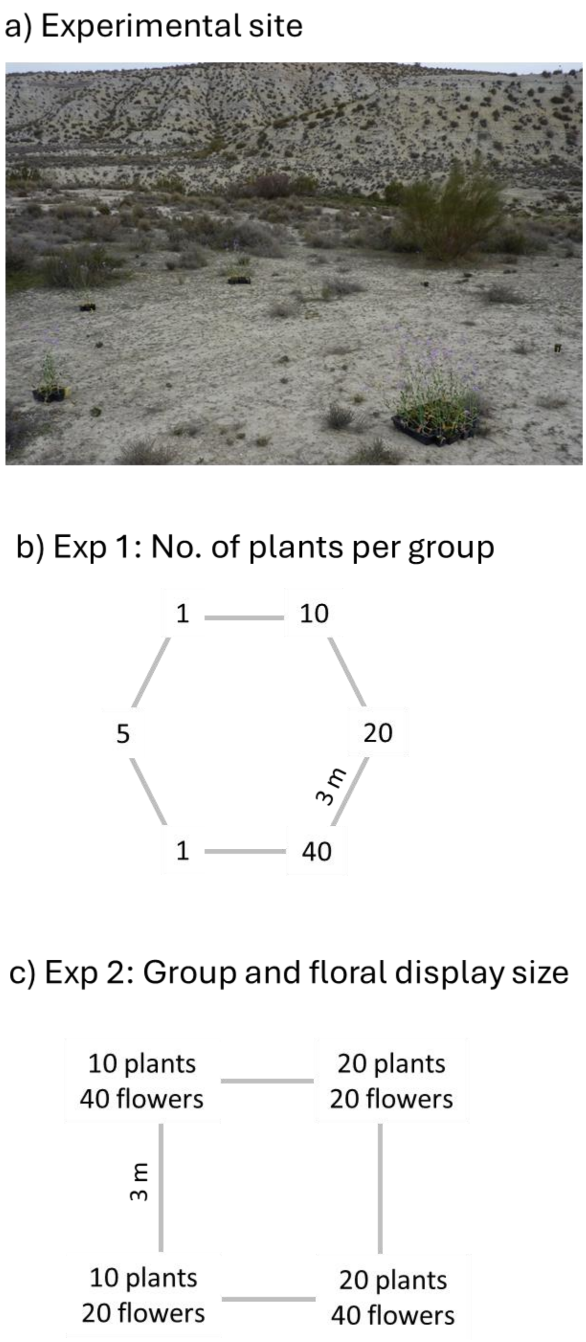

Figure 1. Experimental setup. (a) Barranco del Espartal, the site where the experimental arenas were established. (b) Experimental arena used to assess the effect of group size. (c) Experimental arena used to assess the effect of group floral display while controlling for group size. The exact location of each group type within each arena was randomly reshuffled before each census.

Experiment 1: Pollinator responses to plant group size

In the first experiment, we arranged groups of 1 (two replicates), 5, 10, 20 and 40 individuals forming a regular hexagon with 3 m of side length where all groups were consequently separated from each other by 3 m and placed at 3 m from the centre (Fig. 1b). We selected plants with similar size and similar number of flowers per individual ranging from 2 to 5 open flowers each. As a result, the average number of flowers per group increased proportionally with group size (mean, min–max): 4.4 (2-5) flowers in single-plant groups; 18.4 (13–

24) in 10-plant groups; 31.7 (31–32) in 20-plant groups; 153.0 (129–166) in 40-plant groups. Plants were cultivated in 0.5 L pots in a high-tech greenhouse at the University of Granada mimicking the spring conditions of Mediterranean Spain (day/night= 10/14 h, temperature=20/10 °C, average daily temperature = 14.2°C; see Gómez et al. 2021 for details), and were carried to the field every day. Plants came from seeds collected from the study area during the autumn of 2015. *Moricandia arvensis* blooms sequentially, with new flowers opening daily and each flower lasting approximately two days. To maintain consistency in floral display, plant selection was performed daily. Plants used on one day were not excluded from selection on subsequent days, and some individuals may have been reused in different group configurations. As treatment and plants were randomly assigned for reuse, the impact of any residual chemical or visual cues left by pollinators was considered negligible.

Experiment 2: Pollinator responses to group floral display and group size

In this second experiment, we teased apart the effect of the group floral display from the effect of group size. We set up four experimental groups composed of either 10 or 20 plants, with group floral displays of either 20 or 40 open flowers (Fig. 1c). We used the same pool of plants as in previous experiments, but sorting out individuals by the number of flowers they had opened every day. As a result, individual floral display varied across treatments. Groups with 20 flowers consisted of plants with one flower each in the 20-plant group, and two flowers each in the 10-plant group. Similarly, groups with 40 flowers included plants with two flowers each in the 20-plant group, and four flowers each in the 10-plant group. Thus, individual plants in the 10- and 20-plant groups with 40 flowers had four and two flowers per plant, respectively, while those in the 20-flower groups had two and one flower per plant, respectively. The four groups were arranged at the corners of a square of 3 m sides (Fig. 1c).

We observed visitors to the flowers in 19 surveys lasting between 30 and 60 minutes spread over three different days, totalling 630 minutes. The plant location was randomly re-shuffled in each survey. Three different observers were recording floral visitors at the same time. In this way, we were able to track each single insect, paying special attention to whether it moved from one experimental group to another, or when it permanently left the experimental groups. For each floral visitor, we recorded which groups it visited, the number of flowers visited within each group, and the number of flowers visited on each individual plant within the group. Insects that made contact with the anthers were recorded.

Visiting insects were identified in the field according to their functional group, using the classification provided in Gómez et al. (2022). Most visits were performed by long-tongued large bees (86.0 % of all visits), mostly *Anthophora* sp. (64.7 %), but also *Eucera* sp. (21.2%). We also observed hummingbird hawkmoths (12.8 %), small bees, hoverflies, butterflies and Anthomyiidae flies. These last three groups accounted for less than 1.5 % of the visits.

Statistical analyses

We determined whether group characteristics influenced flower visitors by means of General Linear Mixed Models (GLMMs). In experiment 1, we investigated the effect of group size on five different features of pollinator behaviour: the probability of visitors approaching each plant group (i.e., movement towards and visitation of the group, regardless of the number of flowers visited within it), the number of flowers visited per insect, the per-flower visitation rate, the number of plants visited within each group per individual insect, and the consecutive number of flowers visited on the same plant (hereafter *bout length*). The probability of visitor approaching a group was modelled using a binomial distribution, the number of flowers and plants visited was modelled using a negative binomial distribution, and the visitation rate and bout length were modelled using Gaussian and Poisson distributions, respectively. For this experiment, group size was the only explanatory variable, whereas survey was included as random factor.

In experiment 2, we analysed the effect of *group size* (10 vs. 20 individuals), *group floral display* (20 vs. 40 flowers) and their interaction on the same response variables explained above. The interaction was assessed using type-III tests. When the interaction term was not statistically significant, main effects were assessed by type-II tests.

All GLMMs were fitted using 'lme4' package in R software (Bates et al., 2015). Statistical differences between group size levels in the first experiment were assessed by least-square means differences using the package 'lsmeans' (Lenth, 2016). All *P*-values were corrected for multiple comparisons using Holm's adjustment.

RESULTS

POLLINATOR RESPONSES TO PLANT GROUP SIZE

We recorded a total of 2,043 flower contacts from 216 individual insects. Larger plant groups attracted significantly more visitors (n = 485, d.f. = 4, $\chi^2 = 43.1$, $P < 0.001$, Fig. 2a, Supplementary Table 1), increasing both the number of flowers visited (n = 151, d.f. = 4, $\chi^2 = 38.7$, $P < 0.001$, Fig. 2b, Supplementary Table 1) and the number of different plants visited per individual pollinator (n = 152, d.f. = 4, $\chi^2 = 54.9$, $P < 0.001$, Fig. 2c, Supplementary Table 1). Nevertheless, per-flower visitation rate decreased with group size (n= 151, d.f. = 4, $\chi^2 = 52.4$, $P < 0.001$, Fig. 2d, Supplementary Table 1). Bout length was not statistically different between group sizes (n= 877, d.f. = 4, $\chi^2 = 3.0$, $P = 0.562$, Fig. 2e, Supplementary Table 1), although variation on bout length was higher in smaller groups (Fig. 2e).

POLLINATOR RESPONSES TO GROUP FLORAL DISPLAY AND GROUP SIZE

Group floral display affected insect attraction more than group size (Table 1, Fig. 3a, Supplementary Table 2). However, a significant interaction between them was observed (Table 1). The effect of greater floral display in pollinator attraction to the group was disproportionately greater in larger groups (Fig. 3a, Supplementary Table 2). On the other hand, larger groups with smaller floral arrangements received almost the same number of visits as smaller groups with the same floral arrangement (Fig. 3a, Supplementary Table 2).

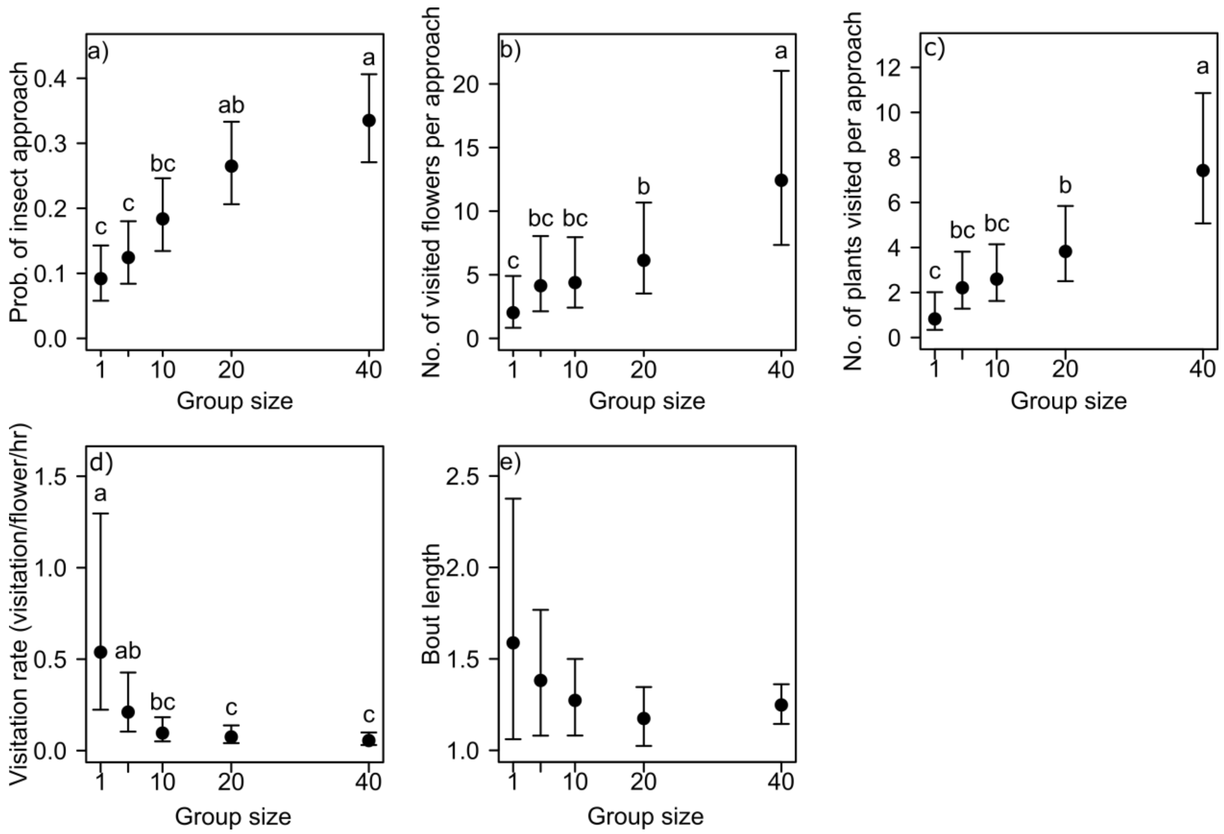

Figure 2. Effect of plant group size on pollinator visitation behaviour. Least-square means (± 95% CI) of (a) the probability of insect approach to a group, (b) the number of flowers visited within the group per each approach, (c) the number of plants visited per each insect approach, (d) visitation rate in terms of the number of flowers visited per total number of flowers in the group per hour, and (e) the bout length. Different letters indicate significant differences between groups (*P* < 0.05, all *P*-values were corrected for multiple comparisons using Holm's adjustment; Supplementary Table 2).

Table 1. Main effects of group size, group floral display and its interaction on the floral visitors. All effects were assessed using type-III tests. When the interaction term was not statistically significant, main effects were assessed by type-II tests. GLMMs were fitted independently for each one of the six response variables. Census was included as random factor.

Variables	n	d.f.	χ^2	*P*
Prob. of approach	440			
Group floral display (F)		1	3.43	**<0.001**
Group size (G)		1	5.89	0.123
F x G		1	4.22	**0.040**
No. of flowers visited	199			
Group floral display (F)		1	9.12	**0.003**
Group size (G)		1	0.10	0.753
F x G		1	0.22	0.639
No. of plants visited	199			
Group floral display (F)		1	5.84	**0.016**
Group size (G)		1	3.41	0.065
F x G		1	0.22	0.635
Visitation rate	199			
Group floral display (F)		1	4.93	**0.026**
Group size (G)		1	0.07	0.795
F x G		1	0.37	0.545
Bout length	836			
Group floral display (F)		1	2.79	0.095
Group size (G)		1	4.54	**0.033**
F x G		1	0.00	0.989

Insects visited significantly more flowers and more plants in groups with larger group floral displays (Figs 3b and 3c, Table 1, Supplementary Table 2). In addition, the number of plants visited, but not the number of visited flowers per insect, marginally increased in larger groups (Table 1). The increase in flower visits within larger group floral displays was proportionally smaller than the increase in the displays themselves, resulting in lower per-flower visitation rates in groups with larger floral displays (Fig. 3d; Table 1, Supplementary Table 2). By contrast, bout length significantly decreased with group size and marginally increased with group floral display (Fig. 3e, Table 1, Supplementary Table 2).

This pattern may have arisen primarily as a by-product of the inherent variation in individual floral display among treatments. In larger group sizes, each plant had exactly half the number of flowers compared to plants in smaller groups with equivalent group floral display, hence limiting the number of flowers available per plant for a pollinator to visit. Only two groups had identical individual floral display: the group of 10 plants with 20 flowers and the group of 20 plants with 40 flowers, both with two flowers per plant. Bout length between these two groups was nearly identical (Fig. 3e), yet differences were observed in all other variables (Figs. 3a–d).

Discussion

Although pollinator visitation to *Moricandia arvensis* was largely driven by neighbourhood floral resources, group size (i.e. the number of individual plants in a group) partially modulated how the neighbourhood floral display attracted pollinators. This interaction reveals the complex role of neighbouring floral traits in shaping pollinator behaviour and highlights the importance of considering both individual floral traits and the spatial aggregation of plants when evaluating plant-pollinator interactions.

Local intraspecific neighbourhoods usually influence pollinator visitation. In *M. arvensis* we observed that as the number of flowers increased within a group, it significantly attracted more

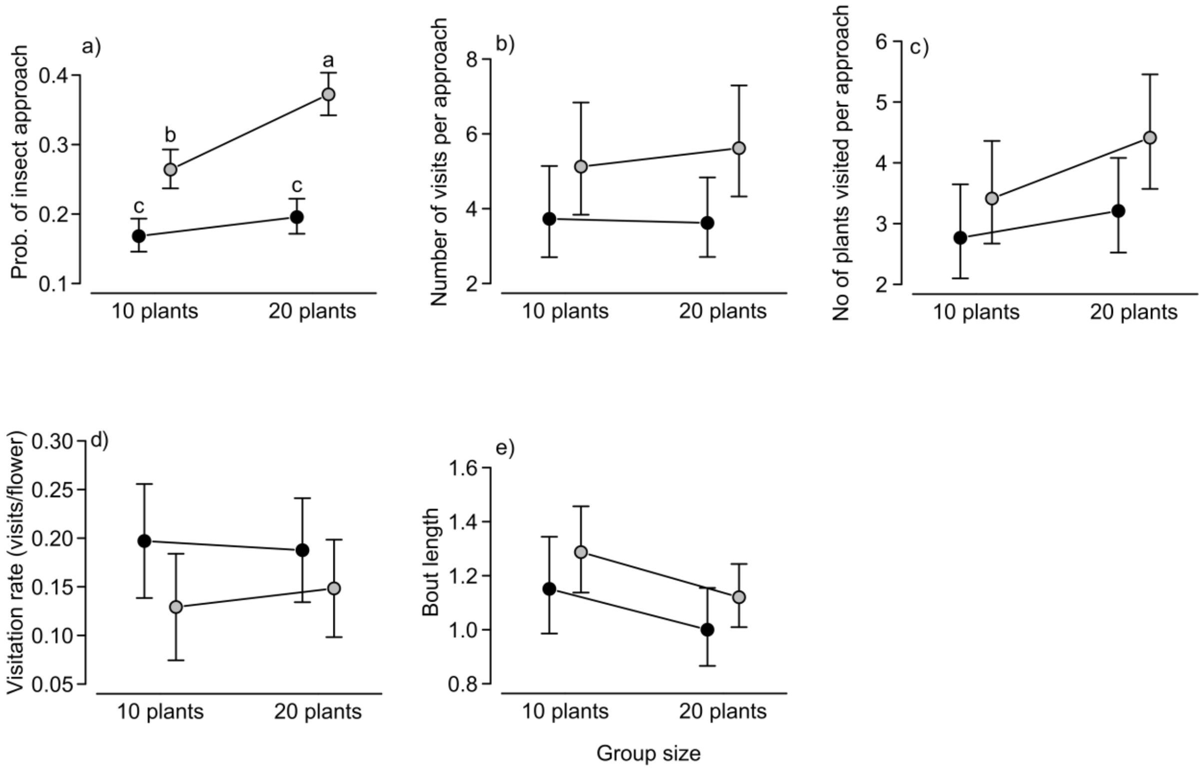

Figure 3. Effect of floral display and group size on floral visitors. Least-square means (± 95% CI) of (a) the probability of insect approach to a group, (b) the number of flowers visited within the group per each approach, (c) the number of plants visited per each insect approach, (d) visitation rate in terms of the number of flowers visited per total number of flowers in the group per hour, and (e) the bout length. Groups had 20 flowers (closed dots) or 40 flowers (grey dots). Different letters indicate significant differences between groups ($P < 0.05$, all P-values were corrected for multiple comparisons using Holm's adjustment, Supplementary Table 4).

potential pollinators. However, the increase in floral visitation rate in groups with larger displays was lower than the increase in group floral display itself, resulting in a significant decrease in the probability of a flower of being visited in groups with larger displays compared to groups with smaller displays. Pollinators may leave a plant when the cost of revisiting previously visited flowers exceeds the cost of moving to another plant (Ohashi & Yahara 2002), leading to a decrease in per-flower visitation rate under high flower density. This pattern aligns with predictions from optimal foraging theory, which suggests that despite an increase in pollinator approaches to a patch, individual flower visitation may decline (Essenberg 2012). Understanding this trade-off between group-level attraction and individual visitation efficiency could be key to predicting pollinator-mediated selection in natural populations.

Although the impact of floral resource accumulation on pollinator foraging behaviour is well documented (Ghazoul 2005; Underwood et al. 2020), the potential for plant aggregations to exhibit other emergent properties that influence pollinator activity remains to be clarified. Previous studies have typically quantified either local floral abundance (e.g. Hegland 2014) or plant density (e.g. Grindeland et al. 2005; Fieldman 2006), often under the reasonable—though sometimes untested—assumption that plant and flower abundance are correlated, and that the effects of plant density on pollinator behaviour is primarily mediated by flower abundance. However, our experiment provided a novel insight into the potential emergent properties of plant group configurations, which go beyond local plant density or floral abundance. We found that increasing the number of flowers in a patch enhanced the probability of pollinator approaches, but this effect was significantly stronger when the patch comprised more individual plants, even when the total number of flowers remained constant. Interestingly, this interaction was limited to the probability of approach and did not extend to per-flower visitation rates or the number of plants visited per approach. The influence of plant groups on plant–pollinator interactions may not be limited to simple metrics of individual or floral abundance, such as those used in our experiment. For instance, pollinator constancy towards specific floral phenotypes was found to be higher in those phenotypes showing a patchier spatial structure (Takagi & Ohashi 2025). Disentangling whether the emergent properties of group aggregations are modulated by the magnitude of individual traits—such as floral display size—could provide valuable insights into how plant spatial structure influences the outcomes of plant–pollinator interactions.

A relevant feature of plant neighbourhoods is that their ecological effects result from the aggregation of individual traits. The abundance of flowers in a given place depends on the number of flowers displayed by the individual plants inhabiting that place. It is well known that flower number per plant is under positive selection in many species (Worley & Barrett 2000; Gómez et al. 2009; Parachnowitsch & Kessler 2010; Sletvold et al. 2010; Barbot et al. 2022). However, the floral investment of a single plant not only influences its own reproductive success but also will affect the mating dynamics of neighbouring conspecifics, ultimately modulating the efficiency of its investment in floral display. In our study, we aimed to isolate the effects of group size and its potential interaction with floral display by limiting the between-plant variation in floral display. However, it is reasonable to expect that, in natural conditions, plants will vary in size and floral output. Plant or floral group size might not have the same impact on all group members. Previous research supports this idea and indicates that the group effects might be dependent on individual traits. For instance, Ohashi & Yahara (2002) reported that the number of flowers visited per plant increased less than proportionally with display size, and that this increase was weaker at higher plant densities. Similarly, Grindeland et al. (2005) found that the proportion of flowers visited decreased with display size, and that this decline was more pronounced in high-density patches. Consequently, small displays received more visits in dense patches, while larger displays were favoured in sparse ones. Given the broad influence of intraspecific neighbourhood structure on plant–pollinator interactions and its potential consequences for pollination success, understanding the evolution of floral traits under pollinator-mediated selection requires considering both individual traits and those of neighbouring plants.

Thus, the intraspecific local configuration will not only influence pollinator attraction to the group but also the efficiency of advertising traits of individual plants. Plants able to adjust their advertising traits to their neighbouring environment in order to maximize matings may invade their population. The observed visitation patterns in *M. arvensis* are consistent with the hypothesis that the increased floral display of *M. moricandioides* when growing with kin may be a consequence of kin selection on plant male success (Torices et al. 2018; Sun et al. 2021). Assuming that *M. moricandioides* aggregations may have similar pollinator responses, since they share the same pollinator niche (Gómez et al. 2016; 2022), it can be expected that a group of kin will attract more pollinators to their patch, as they will produce larger group floral displays enhancing thus pollen export and siring success. However, this increased group display and pollen export will be at the expense of a reduction in the per flower visitation rate and likely on female fertility. To understand the consequences of neighbouring effects on the evolution of floral traits, it is necessary to quantify the direct fitness consequences on individual plants, as well as the indirect fitness consequences through the reproduction of relatives that coexist in the same neighbourhood.

Our small manipulative study has important advantages, but it is also important to note that there are some relevant caveats. We used an artificial population of cultivated plants that made them very uniform. This proved very useful to assess group traits such as group size and floral group display, but it did not allow us to evaluate the specific contributions of genetic and individual plants to pollinator decisions. Moreover, we did not separate different pollinators species. As Makino et al. (2007) describe, group characteristics can have different consequences for different types of pollinators, so additional efforts should be made to characterize the local population of pollinators. Although, the limitations of any manipulative approach are always relevant, as the experimental conditions constrain the resulting phenomena limiting the extent of the conclusions, they also provide a robust approach for testing hypotheses about the manipulated factors. Our approach proved very useful for assessing group traits such as group size and floral group display, which can be very difficult to test in natural populations. With this approach, we were able to demonstrate that group size has relevant implications for the plant-pollinator interaction. From the plant's point of view, a *M. arvensis* plant that grows within a large group might have a higher probability of being approached by a higher number of visitors, but it might record a lower visitation rate per flower. Future research should not control by neighbourhood effects, but rather measure and quantify their effects and interactions with individual traits. Given the particularities of plant neighbourhoods and plant-pollinator interactions, phenotypic selection studies of floral traits should follow multilevel selection approaches capable of disentangling individual- and group-level effects on mating patterns and plant fitness.

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AUTHOR CONTRIBUTION

Concept and design RT, AGM & JMG, data collection RT, AGM & JMG, data analysis RT, writing RT, edits and approval for publication RT, AGM & JMG.

DISCLOSURE STATEMENT

The authors declare no conflicts of interest related to this manuscript.

DATA AVAILABILITY STATEMENT

The datasets used in this manuscript are available on ZENODO:
Torices, R., Gómez, J. M., & Gonzalez Megias, A. (2025). Influence of Group Size and Floral Display on Pollinator Behaviour in *Moricandia arvensis* [Data set]. Zenodo. https://doi.org/10.5281/zenodo.15722571

APPENDICES

Additional supporting information may be found in the online version of this article:

Table S1. Effect of plant group size on pollinator foraging behaviour.

Table S2. Pairwise comparisons between the effects of plant group size levels.

Table S3. Effect of group floral display and plant group size.

Table S4. Pairwise comparisons between all treatment levels of group floral display and plant group size.

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