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RESEARCH ARTICLE

Floral interventions enhance flower visitor communities and pollination services in moringa plantations

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Abstract

1. Pollination is a crucial ecosystem service contributing to global food security. Moringa (*Moringa oleifera*) is an economically important tropical crop, mostly cultivated by smallholder farmers.
2. Well-established approaches of planting flower-rich patches used in temperate agroecosystems for pollination enhancement were adapted to tropical moringa systems. Based on existing evidence, we hypothesised that floral interventions would improve flower visitor diversity and abundance in the crop, thereby increasing pollination services and moringa yield and quality.
3. We used standardised methods to survey flower visitors on moringa and assess economically relevant measures of crop yield quality and quantity. We selected 24 moringa fields in Tamil Nadu, India, to compare fields with and without floral interventions. We planted red gram, *Cajanus cajan* as a border crop, and marigold, *Tagetes erecta* as an intercrop on moringa fields to enhance floral resource availability for pollinators. These interventions were co-designed with local farmers to ensure additional benefits to their community.
4. We found that flower visitor abundance and species richness were significantly (50% for abundance and 33% for species richness) greater in fields with floral interventions compared with control fields. We also found that the percentage of flowers that resulted in harvestable fruits were significantly (30%) greater in fields with floral intervention. Production benefits in yield and quality were significantly positively correlated with the abundance and species richness of flower visitors.
5. *Synthesis and applications.* Our results provide clear evidence that floral interventions in the form of intercropping and border cropping can enhance pollinator communities and services they provide in tropical smallholder systems. These findings underpin a practical management option for farmers to enhance flower visitor communities and pollination services, which can potentially also provide additional co-benefits to farmers, improving livelihoods and sustainable production.

KEYWORDS

agro-ecology, co-design, floral interventions, intercropping, moringa smallholders, pollination deficit, pollination enhancement

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1 | INTRODUCTION

Pollination is one of the most important ecosystem services provided by nature, which is crucial for global food security and human nutritional health (Ehrlich & Ehrlich, 2013; Godfray et al., 2010; IPBES, 2016; Klein et al., 2007). About 75% of the food crops around the globe benefit from pollination by animal pollinators (IPBES, 2016); this figure increases in the tropics, where ~94% of tropical crops benefit from animal pollinators (FAO, 2023). Despite the advances in agricultural technology, the increasing pressure on farming to meet human food and energy needs over the last century has resulted in a rise of intensive but environmentally detrimental farming. These intensive farming systems are associated with monocultures, resulting in the loss of natural habitats and biodiversity (Ehrlich & Ehrlich, 2013; Hansen et al., 2013). Such land-use changes are greatest in the tropics (Hansen et al., 2013), having negative impacts on pollinator communities (Newton et al., 2019). This is important, as smallholder and indigenous communities in the tropics are the most at risk of negatively impacting their livelihoods through the loss of native pollinator communities and their services (Aizen et al., 2009; IPBES, 2016).

Agricultural land use covers 40% of the terrestrial earth surface area, of which over 75% of the farmland cover are family-run (Lowder et al., 2016). Most family-run farms in the tropics are smallholder, which play a major role in livelihood sustenance and the economies of many developing countries in the tropics (Adamopoulos & Restuccia, 2014; Kuivanen et al., 2016; Lowder et al., 2016; Saadun et al., 2018; Wiggins et al., 2010). India alone has 24% of global farm holdings, with many pollinator-dependent crops (Lowder et al., 2016), most of which are under-researched. It is well documented that management interventions can enhance pollinator communities in different agricultural systems (Carvell et al., 2022; Decourtye et al., 2010; Muñoz et al., 2021). Such management interventions for pollination enhancement range from changing agro-chemical regimes, switching to organic farming or using different land-sharing or land-sparing strategies (Altieri et al., 2005; Kovács-Hostyánszki et al., 2017; Ratto et al., 2021). One of the common and straightforward land-sharing strategies is the planting of wildflower strips within a field to attract pollinators, by providing additional nesting and foraging resources (Carvell et al., 2022; Muñoz et al., 2021; Varah et al., 2020; Woodcock et al., 2014). However, such strategies are mostly practised in temperate agriculture with support from policy incentives and using approaches that may not be appropriate in tropical agriculture (Sánchez-Bayo & Wyckhuys, 2019; Steward et al., 2014).

In the tropics, where there may be a paucity of established agri-environmental schemes, it is crucial to have interventions that can provide some incentives or co-benefits to help support the livelihoods of smallholding farmers, while also enhancing biodiversity and ecosystem services in the agricultural fields. Some practices for increasing insect biodiversity that is directly under the control of the farmers are to enhance floral resources and diversify microhabitats by increasing the types of crops grown in

the field through intercropping or multiple cropping. These can have whole ecosystem benefits, including disease resistance (Boudreau, 2013), soil health (Wang et al., 2015), pollination enhancement (Kovács-Hostyánszki et al., 2017), natural pest regulation (Gurr et al., 2016; Wan et al., 2020) and greenhouse gas emission mitigation (Dhandapani et al., 2020), amongst others (Ashton-Butt et al., 2018; Brooker et al., 2015). However, there is lack of evidence on the effectiveness of floral interventions in enhancing pollination in tropical agricultural systems; this is particularly crucial for some economically and socially important crops, widely grown by smallholders in South India. Moringa (*Moringa oleifera* Moringaceae) is one such crop considered important for meeting future human nutritional needs in the face of global change. It is rich in range of vitamins, micro and macro-nutrients, in addition to being highly productive, drought resilient and versatile with many uses (Devkota & Bhusal, 2020; Gopalakrishnan et al., 2016; Mansour et al., 2020; Thurber & Fahey, 2009). It is currently underutilised globally; however, it is emerging as 'super-food' supplement in local and overseas markets owing to its rich nutritional value (Gandji et al., 2018).

Moringa is native to the foothills of the Himalayan region, but the crop is well suited for a wide range of climatic conditions, and is predominantly cultivated in South India, where it is commonly consumed (Jyothi et al., 1990). Moringa is a perennial tree crop, with most trees flowering twice a year, between February and May, and again between September and November in South India (Jyothi et al., 1990). The flowering period ranges from 39 to 71 days (Jyothi et al., 1990). Moringa leaves and pods are edible and widely consumed by humans in India. Moringa plays a major role in the rural economy with considerable amount of moringa pods traded between states in India and internationally. The moringa global market was worth USD 5.5 billion in 2018 and projected to increase to USD 10 billion by 2025 (Malhotra, 2021). India produces 80% of total worldwide consumption of moringa, and production is increasing by 30% yearly in South Indian states (Thomas, 2016). Despite the crop's importance, its pollination ecology is not well understood, though it is known that the crop's productivity depends on insect pollinators (Jyothi et al., 1990). A recent study focussing on a single moringa orchard in South India found 27 different morpho-species of insects visiting moringa flowers, with honeybees dominating floral visits and overall abundance (Sowmiya et al., 2018). Honeybees remained the dominant flower visitors of moringa in studies across all regions (Bhatnagar et al., 2018; Haran & Srinivasan, 2021; Sharma, 2019). Most studies also identified carpenter bees (*Xylocopa* spp.) as key pollinators (Bhatnagar et al., 2018; Jyothi et al., 1990; Krieg et al., 2017; Sharma, 2019).

Studies on fruit tree crops in temperate agriculture show significant pollination deficit, that is a lower yield and quality is achieved from open-pollinated branches compared with pollination achieved through hand pollination (Garratt et al., 2021). However, the effect of floral interventions on ameliorating pollination deficit in the tropical agricultural systems is not well known. To address these knowledge gaps, we aimed to assess whether floral interventions, in the form of inter and border crops, can enhance flower visitor communities and

pollination services in moringa orchards. We adapted well-established approaches from research in temperate agricultural systems (Carvell et al., 2022; Garratt et al., 2014) to tropical moringa agricultural systems to test our three hypotheses. We hypothesise that moringa fields with floral interventions have a greater abundance and diversity of flower visitors on crop compared with the moringa fields without such floral interventions. We further hypothesise that there are pollination deficits in moringa fields, and these will be greater in sites without floral interventions. Our final hypothesis is that increases in flower visitor abundance and diversity enhance pollination services, resulting in greater yield and quality of moringa pods in fields with floral interventions.

2 | MATERIALS AND METHODS

2.1 | Study sites and experimental design

The effect of floral intervention on flower visitors and pollination services in moringa (*Moringa oleifera*) fields was assessed using 24 fields, with 12 'intervention' (I) sites containing floral enhancements in the form of inter and border crops, and 12 'control' (C) sites with no floral interventions. The minimum distance between each site was at least 500 m (Figure S1; Table S1), taking into account the flight distance of different flower visitors (Hofmann et al., 2020; Nevard, 2017). The sites were selected based on geographical location, and similar landscape context, size and moringa age where applicable (Table S1). We received permission from the land owners and managers before began our work. All sites were surrounded by agricultural landscapes, dominated by fields of arable crops such as maize and cotton. All field sites had similar farming types and were under mixed management with both organic and chemical fertilisers and pesticides used. All field sites grew the same perennial variety of moringa (*Karumbu*) and were located on the foothills of Western Ghats in Dindigul district of Tamil Nadu, India. Red gram (*Cajanus cajan* Fabaceae) was used as border crop and planted on two sides of the field boundaries parallel to crop rows, while marigold (*Tagetes erecta* Asteraceae) was used as intercrop and planted in alleys between rows of moringa trees. The fields used in this study varied in size from 800 to 10,400 m² (Table S1); however, interventions and sampling area were standardised to 40 × 20 m plots within each field. The choice, establishment and management of the floral interventions were co-designed with local farmers (both male and female). Initial consultations with individual farmers were used to draw up a shortlist of potential intercrop and border crop. Following a farmer consultation workshop organised by M. S. Swaminathan Research Foundation (MSSRF) and Reddiarchatram Seed Growers Association (RSGA) in September 2020, marigold and red gram were finalised for the floral intervention. They were then grown in a nursery, and 15-day-old plants were transplanted to the field as intercrop and border crop, about 30 days before the start of moringa flowering. The intercrops were planted in the middle of the ~10 m alley between moringa rows. The width of the intervention was 0.5 and 1 m for marigold and red gram, respectively, and for each, the distance between each

plant in inter and border crop rows was 30 cm. Both marigold and red gram are annual crops and flower a few months after sowing. They were planted a month before moringa flowering in each season, and the flowering of all three crops coincided in each season.

2.2 | Pollinator surveys

Fixed-distance transects were used to sample moringa flower-visiting insects. A set of intervention and control sites were surveyed at the same time by two different surveyors, and this pattern was randomised between survey rounds to minimise surveyor bias. The field sites were visited in random order and at different times of the day for each visit. The sites were visited five times in total, twice (start and middle of the season) in the first cropping season (March–May 2021) and three times (start, middle and end of the season) in the second (August and September 2021).

Within each moringa field, four parallel transects—two near field borders and two near field centres were marked out to ensure coverage of the whole field, including areas close to the border and intercrops (Figure S2). The distance between the different transects was minimum 10 m.

All flower visitor surveys were carried out under fair weather conditions with temperature range 23–29°C, clear sky and wind-speed under Beaufort scale 1. The surveys took place before 11:00 or after 15:00 h to avoid high temperatures when pollinator activity was relatively low.

Transects involved walking 20 m at a steady pace for 10 min recording all flower-visiting insects observed down one side of one row of moringa. Moringa trees were pruned and maintained at the maximum height of 4 m as a common management practice in the region, and hence, the whole tree is observable during the walking transect. Data were collected in two 5-min observation periods (subtransects) from one end of the transect to the other. The moringa flower visitors were recorded in a moving window of 1 m width along the row on which the transects were walked. Moringa flower visitors were recorded to species or morpho-species level based on the taxonomic expertise available. As most of the flower visitors were recorded to species level, hereafter the identified insects are referred to as species. The specimens that could not be identified on the wing were caught and identified later at the field station. We did not require ethics approval for our work.

2.3 | Pollination experiments and yield and quality measures

Pollination service measures were taken from three trees from each transect, totalling 12 trees from each orchard, one at the beginning, middle and the end of each 20 m transect.

Just prior to flowering (March 2021 and July 2021), each tree was randomly assigned two treatments (open-pollinated and hand-pollinated) in two different branches. The number of flower clusters

and flowers on each branch was counted on every visit for the next 4 days, covering the whole period the flowers stayed open.

- Open-pollinated: No manipulations were undertaken to assess open pollination.
- Hand-pollinated: During each visit and on the same day as pollinator surveys, all open flowers on this study branch received hand pollination using a paint brush following the methods in Garratt et al. (2014). Donor pollen was collected from another tree in the field. The total number of flowers receiving supplementary pollination per branch was recorded.

On each study branch, the number of fruits was counted initially at the fruit set stage (roughly a week after flowering) and then again just prior to harvest (roughly a month after flowering) to calculate percentage of fruit set at both fruit set and harvest stage. During or close to the harvest, three moringa pods were collected from each branch. The crop quality parameters were recorded, including number of seeds per pod (seed set), length, diameter and weight of moringa pods. The pollination deficit was identified by a significant difference in quantity (percentage of flowers that set to fruit and harvest) and quality (length, weight, diameter and seed set of moringa pods) between pollination treatments, with greater percentage/quality metric in Hand pollination treatment to that of Open pollination indicating a significant pollination deficit (Garratt et al., 2021).

2.4 | Statistical analyses

All statistical analyses were carried out using R version 4.2.2. For all models, p -value < 0.05 was deemed significant. Data were tested for normality using the Shapiro–Wilk test.

2.4.1 | Impact of interventions on flower visitor abundance and species richness

As flower visitor abundance data were overdispersed, generalised linear mixed models (GLMMs) fitted with negative binomial distribution were used to identify the impact of the interventions on flower visitors. Flower visitor abundance and species richness were used as response variables with site type (control vs. intervention) and temperature ($^{\circ}\text{C}$) as fixed effects, and transects nested within sites, and visits as random effects.

2.4.2 | Impact of interventions on moringa yield and quality

Linear mixed models (LMMs) were used to test for effects of floral interventions on percentage of flowers that set to fruit (pod), percentage of flowers that resulted in harvestable fruits and yield characteristics, including moringa pod's length, diameter and fresh

weight. A GLMM fitted with Poisson distribution was used to test for effects on seed set. Site type (control vs. intervention), pollination type (Hand vs. Open) and the interactions between site type and pollination type were used as fixed effects, with transects nested in sites used as random effects. Differences in pollination types (Hand vs. Open) were used to test for pollination deficits in both yield and quality. Post hoc Bonferroni multiple comparison test was used to compare the means of yield and quality parameters for individual site types and pollination types.

2.4.3 | Influence of flower visitor abundance and diversity on moringa yield and quality

LMMs were used to test the influence of flower visitor abundance and species richness on percentage of flowers that set to fruit and percentage of flowers that resulted in harvestable fruit. LMMs were also used to model the influence of flower visitor abundance and species richness on the yield quality parameters including length, weight and diameter as response variables, while GLMMs fitted with Poisson distribution were used for models with seed set as response variable. Abundance and species richness of all flower visitors were used as fixed effects in two separate models, and transects nested within sites were used as random effects for all mixed models involving moringa yield and quality.

3 | RESULTS

3.1 | Flower visitor abundance and species richness

A total of 6450 flower visitors were observed across visits covering two fruit-growing seasons, with 2585 flower visitors observed in control sites and 3865 observed in sites with floral intervention. A total of 30 species of flower visitors were observed in the moringa fields, with nine species of bees, five species of wasps, seven species of flies and nine species of butterflies and moths (Table 1). Bees were the most dominant group of flower visitors, constituting 1410 observations (54.6% of flower visitors) in control sites and 2035 observations (52.7% of flower visitors) in sites with floral intervention (Table 1).

The number of flower visitors observed was significantly greater in sites with floral interventions (abundance per transect: 16.1 ; standard error: ± 0.4) than in the control sites (10.8 ± 0.4 ; Figure 1; Table 2; site means provided in Table S2). Bees (I : 8.48 ± 0.23 ; C : 5.88 ± 0.17) were the group with the greatest abundance per transect, followed by flies (I : 3.89 ± 0.13 ; C : 2.41 ± 0.1), butterflies and moths (I : 1.85 ± 0.1 ; C : 1.27 ± 0.09), and wasps (I : 1.88 ± 0.09 ; C : 1.21 ± 0.06 ; Figure 1; Table S3; Site means provided in Table S2).

The number of flower visitor species observed was also significantly greater in sites with floral interventions (11.0 ± 0.2) than in the control sites (8.29 ± 0.21 ; Figure 2; Table 2; site means provided in Table S2). Bees (I : 5.27 ± 0.11 ; C : 4.33 ± 0.11) were the group with the

TABLE 1 Overview of total flower visitor abundance and community composition in control sites and sites with floral intervention including the different species observed.

Common name	Scientific name	Control sites		Intervention sites	
		Abundance	Community composition, %	Abundance	Community composition, %
Carpenter bee	<i>Xylocopa</i> spp. ^a	175	6.77	243	6.29
Asiatic honeybee	<i>Apis cerana indica</i>	326	12.61	440	11.38
Giant honeybee	<i>Apis dorsata</i>	175	6.77	282	7.30
Dwarf honeybee	<i>Apis florea</i>	183	7.08	215	5.56
Blue banded bee	<i>Amegilla zonata</i>	213	8.24	307	7.94
White banded bee	<i>Amegilla quadrifasciata</i>	37	1.43	63	1.63
Stingless bee	<i>Melipona irridipennis</i>	229	8.86	339	8.77
Sweat bee	<i>Halictus</i> spp. ^a	66	2.55	124	3.21
Leaf cutter bee	<i>Megachile rotundata</i>	6	0.23	22	0.57
Paper wasps	<i>Polistes</i> spp. ^a	43	1.66	79	2.04
Oriental hornet	<i>Vespa orientalis</i>	89	3.44	132	3.42
Wasps	<i>Scolia</i> spp. ^a	124	4.80	171	4.42
Digger wasps	<i>Sphex</i> spp. ^a	29	1.12	64	1.66
Spider wasps	<i>Pepsis</i> spp. ^a	6	0.23	6	0.16
Hoverfly	<i>Eristalinus arvorum</i>	93	3.60	147	3.80
Hoverfly	<i>Episyrphus</i> spp. ^a	128	4.95	207	5.36
Flesh fly	<i>Sarcophaga</i> spp. ^a	111	4.29	197	5.10
House fly	<i>Musca domestica</i>	212	8.20	278	7.19
Asian long-leg fly	<i>Condylostylus</i> spp. ^a	11	0.43	31	0.80
Green bottle fly	<i>Lucilia papuensis</i>	19	0.74	60	1.55
Blue bottle fly	<i>Chrysomya megacephala</i>	5	0.19	13	0.34
Common mormon butterfly	<i>Papilio polytes</i>	48	1.86	63	1.63
Cabbage white butterfly	<i>Pieris rapae</i>	8	0.31	3	0.08
Blue moon butterfly	<i>Hypolimnas bolina</i>	0	0.00	3	0.08
Blue tiger butterfly	<i>Tirumala limniace</i>	7	0.27	5	0.13
Ceylon darlet butterfly	<i>Oriens goloides</i>	21	0.81	46	1.19
Plain tiger butterfly	<i>Danaus chrysippus</i>	30	1.16	40	1.04
Spotted rustic butterfly	<i>Phalanta phalantha</i>	8	0.31	15	0.39
Blue butterfly	<i>Lampides boeticus</i>	70	2.71	95	2.46
Moths	<i>Sphinx</i> spp. ^a	113	4.37	175	4.53

^aThese were the groups that could not be identified down to individual species level, and hence, they were grouped into their respective genera.

greatest average number of species per transect, followed by flies (I: 2.74 ± 0.08 ; C: 1.82 ± 0.07), wasps (1.52 ± 0.07 ; 1.07 ± 0.05), and butterflies and moths (I: 1.48 ± 0.08 ; C: 1.07 ± 0.07), with all groups exhibiting a significantly greater number of species in sites with floral intervention than in control sites (Figure 2; Table S3; site means provided in Table S2). Abundance and species richness of all flower visitors also showed significant decrease with increased temperature (Table 1).

3.2 | Impact of floral interventions on moringa yield, quality and pollination deficit

The percentage of flowers that set to fruit during the fruit set stage in both the control sites and sites with floral intervention were significantly affected by pollination type, with significantly greater percentage of moringa pods in hand pollination than open pollination (Figure 3a; Table 3). There was also a significant interaction between

site type and pollination type. This taken together with Bonferroni multiple comparison results indicates a significant reduction in pollination deficit in sites with floral intervention compared with control sites during the fruit set stage (Figure 3a). The pollination deficit for control sites was 33%, and it was 18% for sites with floral intervention (Figure 3b).

The percentage of flowers that resulted in harvestable fruit was significantly greater in sites with floral interventions than in the

control sites and significantly greater under hand pollination than open pollination for control sites. However, the percentage of flowers that resulted in harvestable fruit did not significantly vary between open and hand pollination for sites with floral intervention, as indicated by a significant interaction between site type and pollination type (Figure 3c; Table 3). There was no significant difference

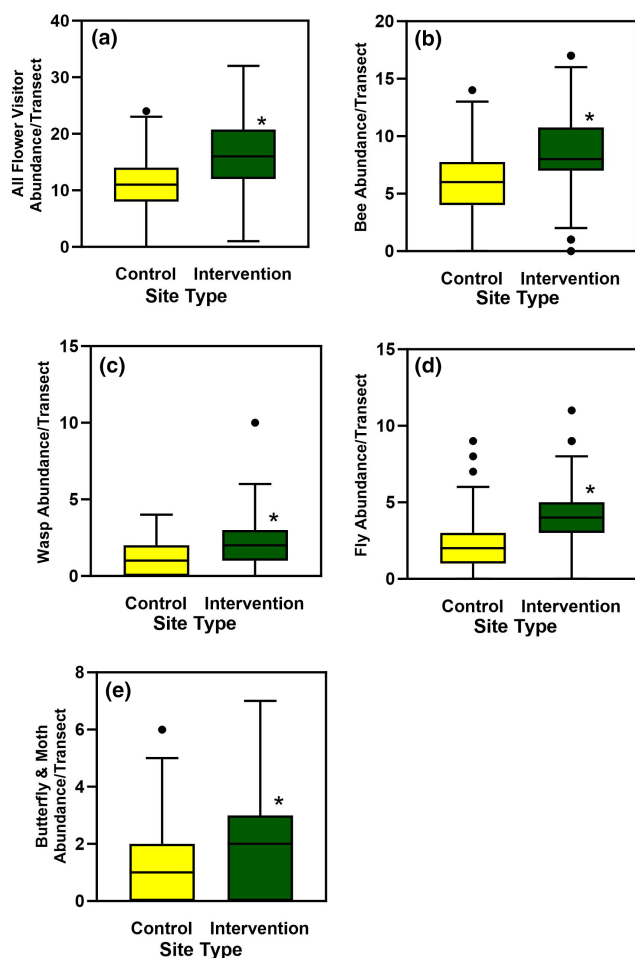


FIGURE 1 Box plots showing comparison of flower visitors abundance per transect in control sites and sites with floral interventions for (a) all flower visitors (b) bees, (c) wasps, (d) flies, (e) butterflies and moths. Statistically significant treatment effects were indicated by '*' above box plots.

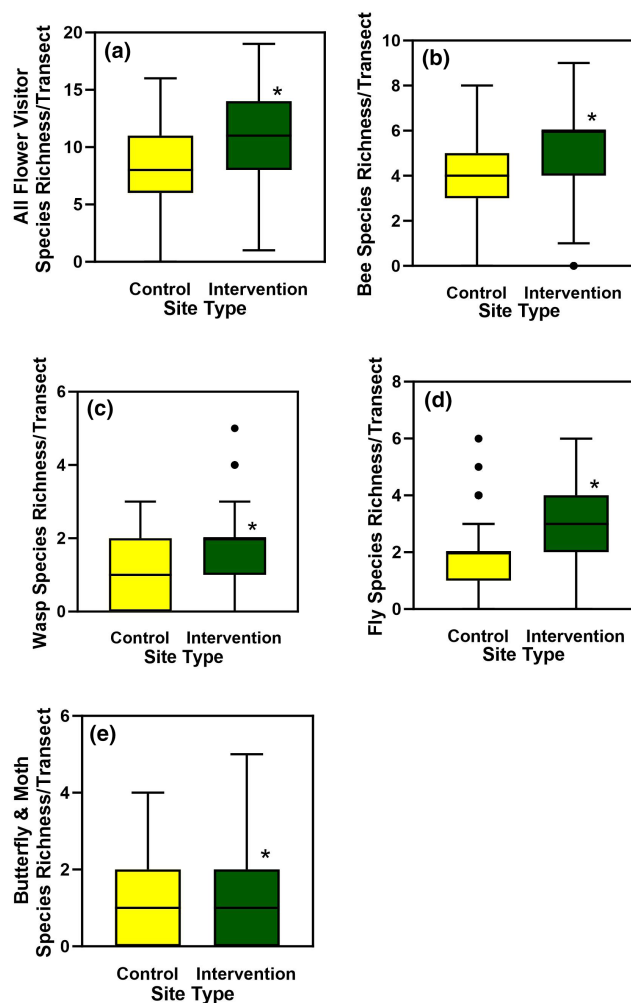


FIGURE 2 Comparison of species richness of flower visitors in control sites and sites with floral interventions for (a) all flower visitors, (b) bees, (c) wasps, (d) flies and (e) butterflies and moths. Statistically significant treatment effects were indicated by '*' sign above box plots.

TABLE 2 Summary table of generalised linear mixed model (fitted with negative binomial distribution) showing effects of site type (intervention vs. control) and temperature on abundance and species richness of all flower visitors. Transects nested in sites were used as random effects.

Response variable	R^2	Residual degrees of freedom	Fixed effects	Estimate	\pm SE	z-Value	p-Value
Abundance of all flower visitors	Marginal $R^2=0.24$	473	Site type	0.401	0.0436	9.20	<0.001
	Conditional $R^2=0.50$		Temperature	-0.097	0.0191	-5.09	<0.001
Species richness of all flower visitors	Marginal $R^2=0.17$	474	Site type	0.280	0.0304	9.22	<0.001
	Conditional $R^2=0.29$		Temperature	-0.078	0.0182	-4.29	<0.001

between the percentage of flowers that resulted in harvestable fruit between open and hand pollination within intervention sites, indicating the lack of pollination deficit in the intervention sites. The pollination deficit in the control sites at the harvest stage was at 12% (Figure 3d).

All the measured moringa quality parameters were significantly greater in hand pollination than in open pollination, both within control and within sites with floral interventions, indicating significant pollination deficit in moringa quality across all sites (Figure 4; Table 3). All measured quality parameters except moringa diameter were significantly greater in hand-pollinated branches of control sites than in the hand-pollinated branches of sites with floral interventions, while moringa diameter did not show significant difference between the two site types within hand pollination (Figure 4). However, all measured quality parameters were significantly greater in open-pollinated branches of sites with floral interventions than in the open-pollinated branches of control sites, suggesting that the pollination deficit is reduced in sites with floral interventions, as indicated by a significant interaction between site type and pollination type, and Bonferroni multiple comparison tests (Figure 4; Table 3).

The percentage of flowers that set to fruit were significantly positively affected by both flower visitor abundance and species richness (Table 4; Figures S3 and S4). The percentage of flowers that resulted in harvestable fruit was significantly positively related to the abundance of all flower visitors (Table 4).

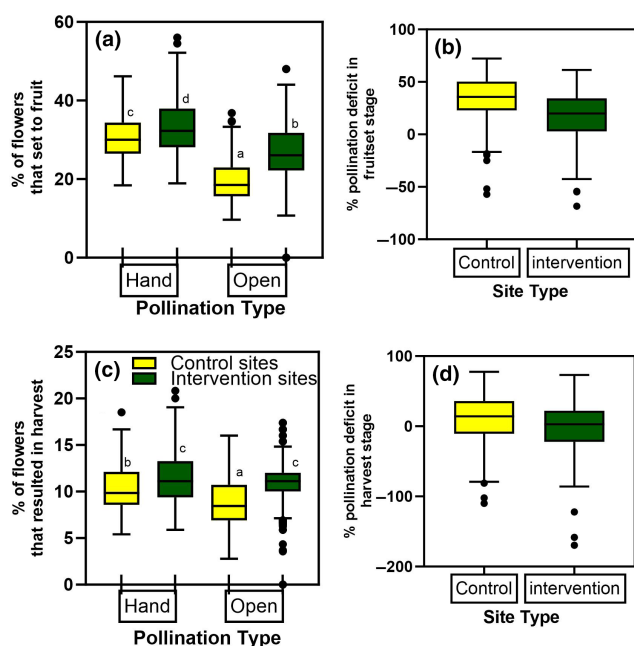


FIGURE 3 Comparison of control sites and sites with floral interventions in terms of (a) percentage of flowers that set to fruit under hand and open pollination, and (c) percentage of flowers that resulted in harvest under hand and open pollination. Pollination deficit between control and sites with floral intervention at (b) fruit set stage and (d) harvest stage. For (a, c), the bars that do not share a letter are significantly different from each other based on Bonferroni multiple comparisons test.

The abundance of all flower visitors was significantly correlated with weight and diameter of moringa pods (Table 4). Species richness of all flower visitors was also significantly positively related to weight and diameter of moringa pods (Table 4). Moringa length and seed set did not show any significant relationship with abundance or species richness of flower visitors.

4 | DISCUSSION

Our study tests the potential for floral interventions to influence flower visitor communities and reduce pollination deficit in small moringa fields and, to the best of our knowledge, is the first study to do so. Our findings indicate that fields with floral interventions experienced greater abundance and species richness of all flower visitors to moringa flowers. Furthermore, the lack of pollination deficit in yield quantity across seasons in the sites with floral interventions provides strong evidence that floral interventions can be used as an effective measure to enhance flower visitor communities and pollination services in tropical agricultural systems.

The greater abundance of flower visitor in site with floral interventions may be due to the increased availability of food and other parameters that are not assessed in this study such as nesting resources and improved microclimatic conditions as a result of increased diversity of crops through interventions (Carvell et al., 2022; Lucas et al., 2017; Nicholls & Altieri, 2013). It is known that the planting of native co-flowering crops with the main crop can enhance wild pollinator communities in a wide range of contexts (Carvell et al., 2022; Griffiths-Lee et al., 2020; Muñoz et al., 2021). However, it has been previously reported that the cost of adding such native flower patches in their fields may discourage farmers from practising such interventions for pollination enhancement (Kleijn et al., 2019). Due to the absence of agri-environment type schemes, and a high degree of livelihood dependence of farmers on smallholding farms in developing countries, it is critical that any interventions provide additional benefits (e.g. economic and nutritional) for smallholder farmers. Red gram is known to attract a wide range of pollinators and is a commercially important crop with high nutritional value (Kambrekar et al., 2019). Marigold is known to be an effective companion crop that helps in attracting pollinators and also deterring pests (GuishuaXie et al., 2017), while also providing commercially valuable flowers (Singh et al., 2013; Verma et al., 2019). Our findings provide evidence that floral interventions that are co-created with farmers can provide context-specific ecological intensification that benefits biodiversity and crop production. Furthermore, this approach can provide a foundation for work towards wide-scale practical adaptation of floral interventions in tropical agricultural systems.

Bees were the dominant group of flower visitors on moringa in our study sites constituting more than half of the observed fauna, consistent with previous observations in the moringa fields in the region (Jyothi et al., 1990; Sowmiya et al., 2018). The findings

TABLE 3 Summary table of linear mixed models for percentage of flowers that set fruit, percentage of flowers that resulted in harvestable fruit, length, diameter and weight; and generalised linear mixed model (fitted with Poisson distribution) for seed set, showing effects of site type, pollination type and their interactions.

Response variable	R ²	Residual degrees of freedom	Fixed effects	Estimate	±SE	t-Value (z-Value for seed set)	p-Value
Percentage of flowers that set fruit	Marginal R ² = 0.37 Conditional R ² = 0.39	1145	Site type	2.754	0.6522	4.22	<0.001
			Pollination type	-10.577	0.5341	-19.80	<0.001
			Site type × pollination type	4.018	0.7553	5.32	<0.001
Percentage of flowers that resulted in harvest	Marginal R ² = 0.15 Conditional R ² = 0.17	1145	Site type	1.205	0.2453	4.91	<0.001
			Pollination type	-1.671	0.2143	-7.80	<0.001
			Site type × pollination type	1.215	0.3030	4.01	<0.001
Length (cm)	Marginal R ² = 0.19 Conditional R ² = 0.32	1721	Site type	-1.596	0.8177	-1.95	0.06
			Pollination	-5.825	0.2929	-19.89	<0.001
			Site type × pollination type	6.690	0.4142	16.15	<0.001
Weight (cm)	Marginal R ² = 0.17 Conditional R ² = 0.27	1721	Site type	-4.098	1.3373	3.065	0.005
			Pollination type	-11.104	0.5795	-19.16	<0.001
			Site type × pollination type	12.471	0.8196	15.22	<0.001
Diameter (cm)	Marginal R ² = 0.10 Conditional R ² = 0.18	1721	Site type	-0.145	0.0593	-2.44	0.020
			Pollination type	-0.436	0.0307	14.21	<0.001
			Site type × pollination type	0.432	0.4317	9.94	<0.001
Seed set (count)	Marginal R ² = 0.33 Conditional R ² = 0.33	1722	Site type	-0.046	0.0137	-3.37	<0.001
			Pollination type	-0.104	0.0139	-7.46	<0.001
			Site type × pollination type	0.117	0.0196	5.97	<0.001

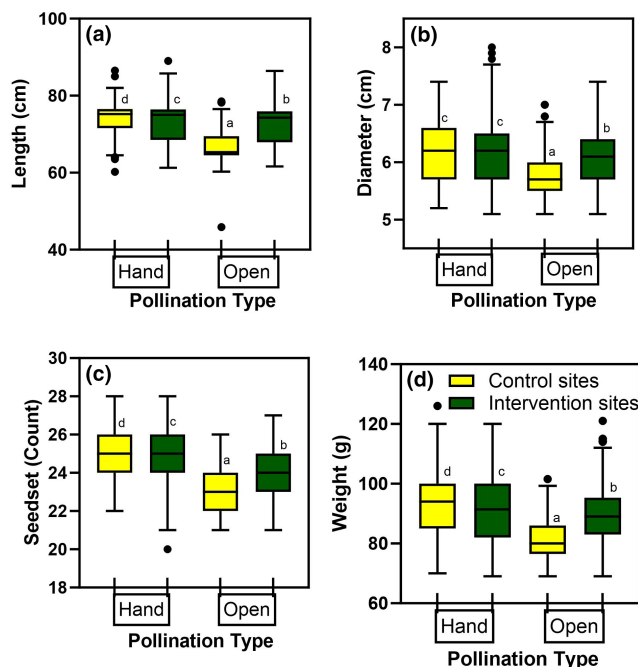


FIGURE 4 Comparison of moringa yield quality parameters in control and sites with floral interventions in terms of, (a) length, (b) diameter, (c) seed set and (d) weight. The boxes that do not share a letter are significantly different from each other based on Bonferroni multiple comparison test.

TABLE 4 Summary table of linear mixed models for percentage of flowers that set fruit, percentage of flowers that resulted in harvest, length, diameter and weight, and generalised linear mixed model (with Poisson distribution) for seed set showing effects of abundance and species richness of all flower visitors.

Response variable	R^2	Residual degrees of freedom	Estimate	\pm SE	t-Value	p-Value
Abundance model						
Percentage of flowers that set fruit	Marginal $R^2=0.52$ Conditional $R^2=0.64$	187	0.97	0.676	14.34	<0.001
Percentage of flowers that resulted in harvest	Marginal $R^2=0.02$ Conditional $R^2=0.60$	187	8.994	0.3958	22.72	<0.001
Length (cm)	Marginal $R^2=0$ Conditional $R^2=0.73$	187	0.01	0.0329	0.29	0.769
Weight (g)	Marginal $R^2=0.07$ Conditional $R^2=0.64$	187	0.273	0.0574	4.76	<0.001
Diameter (cm)	Marginal $R^2=0.15$ Conditional $R^2=0.44$	187	0.018	0.0031	5.9	<0.001
Seed set (count)	Marginal $R^2=0$ Conditional $R^2=0.77$	187	0.002	0.0095	0.23	0.815
Species richness model						
Percentage of flowers that set fruit	Marginal $R^2=0.37$ Conditional $R^2=0.58$	187	1.189	0.1016	11.7	<0.001
Percentage of flowers that resulted in harvest	Marginal $R^2=0.01$ Conditional $R^2=0.62$	187	0.049	0.0315	1.55	0.123
Length (cm)	Marginal $R^2=0$ Conditional $R^2=0.73$	187	-0.003	0.0439	-0.06	0.951
Weight (g)	Marginal $R^2=0.038$ Conditional $R^2=0.66$	187	0.315	0.0775	4.07	<0.001
Diameter (cm)	Marginal $R^2=0.11$ Conditional $R^2=0.46$	187	0.023	0.0042	5.46	<0.001
Seed set (count)	Marginal $R^2=0$ Conditional $R^2=0.77$	187	-0.001	0.0126	-0.09	0.927

also showcase a great diversity of insects that visit moringa flowers, with 30 different species observed. These include all the 27 species observed by Sowmiya et al. (2018). High diversity of flower visitors may contribute to a high degree of resilience and stability of flower-visiting invertebrate communities (Senapathi et al., 2021) and is therefore a promising finding for smallholder moringa systems in our study. Asiatic honeybees were the most abundant species in both control and site with floral interventions, in agreement with previous observations in moringa fields in the region (Sowmiya et al., 2018). However, the relatively less abundant carpenter bees in our study were previously found to have the greater pollination efficacy index on moringa compared with more abundant Asiatic honeybees, giant honeybees and blue banded bees (Sowmiya et al., 2018). Flies were the second most abundant group of flower visitors in moringa fields, in contrast to the findings of Haran and Srinivasan (2021) that flies were the least abundant group of moringa pollinators in Southern Tamil Nadu. Flies were the only group of flower visitors that showed no temperature effect while other groups decreased in abundance and species richness with increased temperature, indicating that the flower visitor groups may be sensitive to environmental and seasonal change, and their response may vary from each other. However, further research is needed on environmental changes, to fully understand the interactions between different flower visitor

groups and changes in environmental conditions. Nevertheless, the findings clearly show that floral interventions were effective in enhancing overall flower visitor communities across seasons, validating our first hypothesis.

The significant increase in flower visitor abundance and species richness also translated into increased productivity and quality. This is consistent with other findings indicating pollination limitation on yield, and the impacts of pollination enhancement on different crops worldwide (Muñoz et al., 2021). The pollination deficit of 33% in control sites during fruit set stage, shows a considerable pollination limitation on yield in these moringa fields. However, this deficit is significantly reduced in the sites with floral interventions, and the deficit is fully closed in the harvest stage for sites with floral interventions, showing the effectiveness of floral interventions in enhancing the pollinator communities and yield, validating our second hypothesis. Similarly, the moringa quality parameters such as diameter, length, weight and seed set also indicated pollination deficits. All such deficits in quality were also significantly reduced in the sites with floral interventions, with the increase in weight and diameter showing significant correlations with both flower visitor abundance and species richness. These results taken together show that pollination enhancement through floral interventions has improved pollination services, reflected in positive change in all relevant measurable yield and quality metrics, validating our third hypothesis. The reduction in pollination deficits from the fruit set stage to the harvest stage shows that there may be resource limitations within the plant, or other limiting factors such as plant health, soil nutrients and pests that are limiting the moringa plants from sustaining the fruit sets from maximum pollination (through hand pollination) to harvest stage. Nevertheless, the difference in the number of fruits between the fruit set and harvest stage indicates further potential for increase in yield, with the improvement in other factors complementing pollination enhancement (Garratt et al., 2018; Tamburini et al., 2019).

The moringa quality parameters measured in this study were commonly used to set price in local wholesale markets where smallholding farmers sell most of their produce. In addition to the extra income from the produce from the intercrop (marigold) and border crop (red gram), this increase in moringa yield and quality may provide additional economic benefits. These combined economic uplifts from floral interventions may very well overcome any economic cost incurred for additional irrigation and field management needed for intervention establishment, even in the absence of agri-environmental type incentive schemes. There is some preliminary evidence from other low- and middle-income countries that the increase in economic income with pollinator protection/enhancement, with greater awareness of the benefits within farming communities, can help in widescale adoption in countries with no agri-environmental type schemes for pollinator protection (Christmann et al., 2022). However, further focussed research is needed on the economic costs and gains from floral interventions to fully understand and assess the economic benefits

of practising intercropping and border cropping for pollination enhancement in moringa plantations.

5 | CONCLUSIONS

Floral interventions, in the form of intercropping and border cropping, that are co-designed with the farmers, can be effective in enhancing flower visitor abundance and diversity in smallholder moringa fields. This increase in flower visitor abundance and diversity can also effectively close pollination deficits in moringa yield and quality. The provision of additional immediate benefits by the companion crops for smallholder livelihood is a crucial incentive in the absence of agri-environmental type incentive schemes, or other policy support, in tropical agricultural systems. The success of co-designed floral interventions is an encouraging result and provides a roadmap towards enhancing functional biodiversity and related ecosystem services in other tropical agroecosystems. Our findings further provide empirical evidence that the general principles of ecological intensification can be successfully translated from temperate to tropical systems, by taking into account local agronomic and ecological contexts. However, further research is needed to identify additional socio-economic incentives and barriers for wider practical adoption of ecological interventions in tropical smallholder agriculture.

AUTHOR CONTRIBUTIONS

Deepa Senapathi, Rengalakshmi Raj, Michael P. D. Garratt and Simon G. Potts originated and acquired funding for this research. Ranjith Rajaraman and Manikandan Pakkirisamy collected data in the field. Selva Dhandapani arranged the data, carried out initial statistical analyses, wrote the first draft and carried out subsequent editing. Deepa Senapathi finalised the statistical analyses and directed the editing of the manuscript. Malarvannan Subramanian and all the authors contributed to the methodology, critically reviewed and edited the manuscript and approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available via University of Reading Research Data Archive <https://researchdata.reading.ac.uk/id/eprint/508> (Dhandapani et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Location of moringa fields with (intervention sites) and without (control) floral interventions in Tamil Nadu, India.

Figure S2. Survey design including location of pollinator transects, open and hand pollination assessment (Service measure) and the location of floral interventions.

Figure S3. Relationship between flower visitor abundance and (a) % of flowers that set to fruit, (b) % of flowers that resulted in harvest, (c) moringa weight, and moringa diameter.

Figure S4. Relationship between flower visitor species richness and (a) % of flowers that set to fruit, (b) moringa length, and (c) moringa weight.

Table S1. Location and dimensions of moringa field fields.

Table S2. Site means and standard errors for abundance and species richness of flower visitor groups.

Table S3. Summary table showing the impact of floral interventions and temperature on the abundance and richness of different groups of flower visitors.

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