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— Novel Ideas and Pilot Projects —

POLLINATOR DEPENDENCY, POLLEN LIMITATION AND POLLINATOR VISITATION RATES TO SIX VEGETABLE CROPS IN SOUTHERN INDIA

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Abstract—We investigated levels of pollinator dependency and pollinator visitation rates to flowers of six vegetable crops: brinjal (aubergine), tomato, chilli pepper (Solanaceae), okra (Malvaceae), bitter and snake gourds (Cucurbitaceae) in six small family farms in the Coimbatore region of southern India. We tested the null hypothesis that fruit set in these crops would be independent of pollinators. We assessed fruit set through self and cross pollination by pollen augmentation, by pollinator exclusion and open pollination. We evaluated pollen limitation by comparing percentage fruit set by hand outcrossed pollen with open pollination; pollinator dependency by differences in percentage fruit set by open pollination and autogamous pollination; and visitation rates to flowers by pollinating insects. Tomato, chilli and okra produced self-compatible hermaphrodite flowers, with higher levels of autogamous fruit set (32-76%) and significantly lower levels of pollinator dependency (0-37%), whereas andro-monoecious brinjal and monoecious gourds had significantly lower levels of fruit set through autogamy, and higher levels of pollinator dependency. Pollen limitation was not evident in any crop. Diverse pollinating insects visited the flowers, and the frequency of visits by different pollinator taxa differed with crop type. Native vegetation and uncultivated land may enhance pollinator diversity in small farms.

Keywords: Agro-biodiversity, Coimbatore, India, pollinator dependency, pollination services, vegetable crops

INTRODUCTION

Pollinators are critical for the reproduction of many plants, and about 94% of plant species in tropical communities and a third of global food crops are likely to rely on animal pollination (McGregor 1976; Klein et al. 2007; Ollerton et al. 2011). Aizen et al. (2009) suggested that in the absence of pollinators, reduction in crop production would range from 3-8% (Allen-Wardell et al. 1998; Kearns et al. 1998; Klein et al. 2007; Garibaldi et al. 2013). Tropical agriculture could be particularly susceptible to pollinator declines since the cultivation of pollinator dependent crops, and the use of pesticides has increased (Roubik 1995; Aizen et al. 2009). As proximity to forests has been shown to increase pollinator activity and enhance crop production (De Marco & Coelho 2004; Ricketts et al. 2004, 2008; Blanche et al. 2006), tropical deforestation could further imperil pollination services (Bradshaw et al. 2009). In the Indian subcontinent plantation crops such as cardamom and coffee and many of the vegetable and fruit crops are dependent on wild bees for pollination (Partap 1999; Chandel et al. 2004; Sinu & Shivanna 2007a, b; Davidar 2009; Krishnan et al. 2012; Davidar et al. 2015). The Indian green revolution which started in the 1960's with the introduction of high yielding varieties and the intensive use of organophosphates, carbamates, synthetic pyrethroids and organochlorine pesticides (Kumari et al. 2002; Bhanti & Taneja 2007; Roy et al. 2007), could have adversely affected pollinating insects thereby reducing pollination services (Basu et al. 2011).

The aim of this study is to document and assess levels of pollinator dependency, pollen limitation and identify major pollinating insects visiting flowers of six vegetable crops in the Coimbatore district of Tamil Nadu (Tab. 1, Fig.1), a major industrial and agricultural region in southern India. The six crops were widely used vegetables such as aubergine known in India as brinjal (*Solanum melongena* L., 1753), tomato (*Solanum lycopersicum* L., 1753), and chilli pepper (*Capsicum annuum* L., 1753) of the family Solanaceae; tropical gourds such as the bitter gourd (*Momordica charantia* L., 1753) and snake gourd (*Trichosanthes cucumerina* var. *anguina* (L.) Haines, 1922) belonging to Cucurbitaceae; and okra (*Abelmoschus esculentus* (L.) Moench, 1794), a member of the Malvaceae.

We used hand pollination experiments to assess levels of pollinator dependency and observed flowers to record visitation rates by pollinating insects. We tested the null hypothesis that fruit set in these six crops, regardless of sexual systems would be independent of pollinators.

MATERIALS AND METHODS

Study area

The Coimbatore district of the southern Indian state of Tamil Nadu has a dry and hot climate with annual ambient

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TABLE 1. Description of the farms where the study was conducted with geographical coordinates, area of farm, type of agriculture, irrigation mode, matrix vegetation type and crops studied.

Site name	Latitude °N	Longitude °E	Farm size (km²)	Conventional/ Organic	Type of irrigation	Matrix type	Crops studied
Edayarpalayam	11. 22	76.55	0.5	Conventional	Bore well, Municipality Piped water	Shrubbery	Bitter gourd, snake gourd
Karumathampatti	11. 07	77. 11	0.5	Conventional	Bore well	Pastures and shrubbery	Brinjal, bitter gourd, snake gourd
Madukarai	10.54	76. 55	0.04	Organic	Bore well	Grassland, coconut farms	Tomato
Nehru Nagar	11.33	77. 24	0.004	conventional	Municipality Piped water	Urban housing unit	Bitter gourd, snake gourd
Pappampatti	10. 56	77. 65	0.4	Conventional	Bore well, rain fed	Pastures, open woodland	Chili, brinjal, tomato, bitter gourd
Sirumugai	11. 22	77. 05	0.02	Organic/ conventional	River	Dry forest	Chili, okra

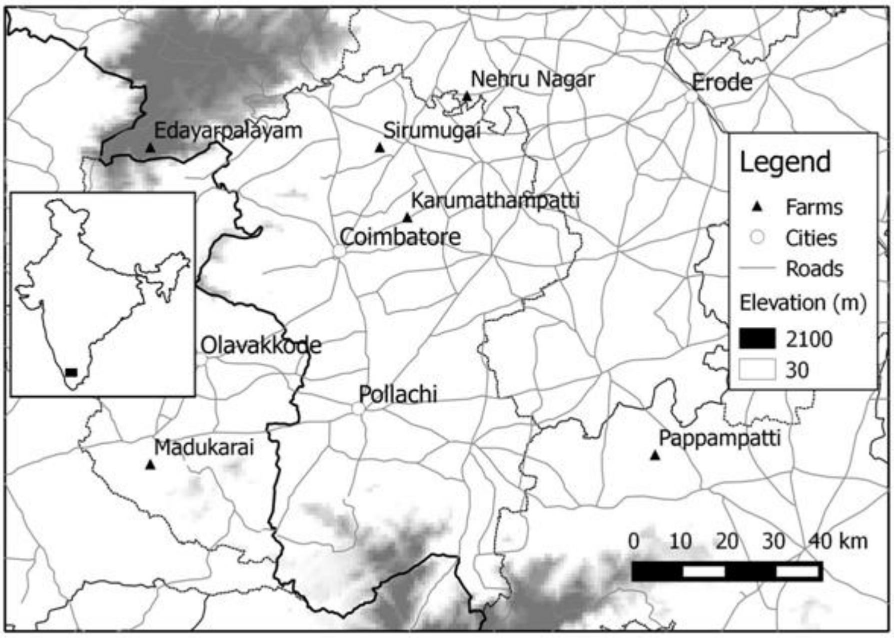

FIGURE 1. Map of the study site in Coimbatore indicating location of the farms.

temperature ranging from 18° to 35° C. Average annual rainfall is around 700 mm from the SW and NE monsoons. The farmlands have a rich fertile soil composed of mostly alfisols and vertisols where grain, pulses and vegetable crops are grown (Surendran & Murugappan, 2008).

Six small scale family farms were selected for the study in the following localities: Edyarpalayam, Karumathampatti, Nehru Nagar, Papampatti, Sirumugai, and Madukarai (Tab. 1; Fig. 1). Each farm has a different mix of crops and often the variety grown and timing of crop production differed, which made it difficult to standardise a study design. All the farms were irrigated and used pesticides except for two organic farms in Sirumugai and Madukkarai. Five of the farms had shrubbery, forests, grasslands and pastures in the surrounding matrix, whereas one farm in Nehru Nagar was located in an urban area (Tab. 1). Small scale agriculture is widely practised across India and large scale intensive agriculture is less common due to regulations on land holdings.

The study was conducted from December 2011 to June 2012, from November to December 2012, and from January to March 2013 during the main growing season for vegetables. The vegetable varieties cultivated in the farms (Tab. 2) were developed by the Tamil Nadu Agricultural University and the Sugarcane Institute at Coimbatore. We classified each crop according to its sexual system.

TABLE 2. Results of the pollination experiments indicating the fruit set [in % with number of investigated flowers in brackets] by hand augmented cross (CP) and self pollination (SP), open pollination (OP) and autogamy (AUT). Levels of pollinator dependency (PD), index of self incompatibility (ISI) and pollinator limitation (PL) in six crops. The decimal values have been rounded to the nearest whole number. Abbreviations of site names: Edyarpalayam (E), Karumathampatti (K), Madukarai (M), Nehru Nagar (N), Papampatti (P), Sirumugai (S).

Name of crop	Farm	Month-Year	Variety	CP	SP	OP	AUT	% PD (%OP-%AUT)	ISI	% PL
Brinjal (*Solanum melongena*)	E	Nov-12	Shiva	30 (23)	25 (24)	39 (31)	9 (43)	29	I	0.8
	N	Dec-12	Aruki25	9 (11)	0 (9)	27 (15)	6 (17)	21	0	0.3
	P	Dec-12	Shiva	20 (15)	0 (11)	33 (21)	7 (14)	26	0	0.6
	P	Feb-13	Shiva	50 (34)	50 (22)	48 (50)	6 (17)	42	I	1.0
	K	Mar-13	Kathri25	38 (29)	23 (31)	42 (43)	10 (51)	32	I	0.9
	Total			35 (112)	25 (97)	41 (160)	8 (142)	30		
Tomato – (*Solanum lycopersicum*)	P	Jan-12	Lakshmi 5005	68 (22)	60 (20)	58 (24)	76 (34)	0	I	1.2
	M*	Feb-12	NS 25	67 (24)	88 (24)	27 (26)	32 (57)	0	I	2.5
	Total			67 (46)	75 (44)	42 (50)	48 (91)	0		
Chili - (*Capsicum annuum*)	P	Nov-11	S7	86 (14)	-	86 (14)	-	-	I	1.0
	S*	Mar-12	Sannam	50 (20)	50 (28)	60 (15)	36 (28)	24	I	0.8
	Total			65 (34)	50 (28)	72 (29)	36 (28)	36		
Bitter gourd – (*Momordica charantia*)	N	Nov-12	Neelam105	13 (16)	23 (13)	11 (9)	0 (11)	11	I	1.1
	P	Nov-12	Neelam105	0 (7)	11 (9)	8 (12)	0 (9)	8	0	0.6
	N	Jan-13	Neelam105	44 (25)	57 (21)	76 (17)	0 (20)	76	I	0.8
	P	Jan-13	Neelam105	26 (34)	29 (38)	33 (43)	0 (51)	33	I	0.8
	K	Mar-13	Raja	34 (56)	29 (55)	43 (44)	0 (54)	43	I	1.1
	Total			30 (138)	32 (136)	38 (125)	0 (145)	38		
Snake gourd – (*Trichosanthes cucumerina var. anguina*)	N	Nov-12	Lakshmi7	30 (27)	38 (24)	41 (32)	11 (19)	30	I	0.7
	P	Nov-12	S25	17 (12)	14 (14)	11 (9)	0 (10)	11	I	1.5
	P	Jan-13	S25	41 (41)	38 (37)	50 (46)	0 (32)	50	I	0.8
	K	Mar-13	Bhuvan	23 (40)	30 (37)	36 (55)	3 (33)	33	I	0.6
	Total			30 (120)	32 (112)	40 (142)	3 (94)	37		
Okra – (*Abelmoschus esculentus*)	S	Mar-12	Shakthi	38 (40)	32 (34)	55 (40)	35 (20)	20	I	0.68

* organic

Pollination treatments

We evaluated the breeding systems of the plants, levels of autogamy and pollinator dependency using hand pollination experiments. Plants were randomly selected in a field, and 1-3 flowers were selected for hand pollinations on target plants. Usually just one flower was used for the pollination treatment.However, in some cases based on the size of the plant, 2-3 flowers were used for different treatments, one of which was to document fruit set through open pollination (OP). The mode of collection of pollen varied for each crop type. For tomatoes, brinjal and okra, the stamens are fused into a cylinder around the pistil, and therefore a razor blade was used to slit the cylinder on one side and around the base, and remove it using tweezers. For chilli, the stamens were separated and removed using curved scissors and tweezers. The pollen was collected using a fine brush or forceps for deposition onto the target stigma. Cotton mosquito mesh cloth bags of 15 cm in length and 7.5 cm in width were used to exclude pollinators after treatment of the flowers and tagged. Fruit set was monitored until maturity.

The following pollen augmentation treatments were used to assess the extent of selfing and outcrossing. For the self pollination treatment (SP), pollen from the dehisced anthers of a freshly opened flower was transferred onto the receptive stigma of the same flower in the case of hermaphrodites and andro-monoecious crops, or onto the stigma of another isolated flower on the same plant in monoecious crops, and the flowers were re-bagged. For augmented hand cross pollination treatment (CP), the flower buds were teased opened the previous evening and the anthers excised to prevent self pollination. The buds were enclosed and tagged. The next morning fresh pollen from flowers of a different plant was collected and deposited on the stigma. To test for parthenocarpy or autogamous self pollination (AUT), a tagged flower bud was enclosed in a mosquito mesh bag. For open pollination, fresh flowers were tagged and fruit set noted.

Breeding system, pollinator dependency and pollen limitation

The breeding system of the crop varieties was assessed using the index of self-incompatibility (ISI) which is the ratio between % fruit set from augmented hand self pollination over augmented hand cross pollination (Zapata & Arroyo 1978). Crops with ratios < 0.25 were considered self incompatible and those > 0.25 as self compatible (Bawa 1974).

Pollinator dependency (PD) was estimated by subtracting the % fruit set by autogamous pollination from % fruit set by open pollination (PD = OP - AUT, Tur et al. 2013). PD ranges from 0 for plants that are not dependent on pollinators to 100 for plants that completely rely on pollinators for fruit production. Negative values were represented by 0 = no pollinator dependency.

Pollen limitation was assessed as the ratio of % fruit set from augmented hand cross pollination by open pollination (Larson and Barrett 2000; Rathcke 2000). The scale was from 0 to 100 with 0 indicating no pollen limitation and 100 indicating complete pollen limitation. Negative values resulted where in some cases % fruit set from OP was higher than that of % from CP and was represented as 0 which indicated no pollen limitation.

Pollinator Visitation Rates

Usually the study crop was grown in only one field. Flowering plants were selected for observation in different areas of the field to be representative of site conditions. One or two freshly opened flowers in a plant were observed continuously for 5-minute blocks separated by intervals of 5-minutes, for a total of 30 minutes and all flower visitors were recorded. Then the observations were continued on a different plant. Observations were carried out from dawn (0700 hours) till dusk (1800 hours), except for okra flowers that closed at around 1500 hours. All insects visiting the flowers and touching the reproductive parts were noted; however, it was not possible to definitively ascertain whether pollen was transferred. The visitation data was summed for that field in a farm totalling minutes of observation and converting to hours of observation. The visitation rate (mean ± standard deviation) was estimated by dividing the number of visits by each pollinator group by the total hours of observation in that field.

The pollinators were grouped into the following categories: *Apis* honeybees, Meliponine bees such as *Heterotrigona*, solitary bees of the genus *Xylocopa* and *Amegilla,* Lepidoptera which included butterflies and moths, and wasps of different families. The overall average visitation rate for a crop was also calculated using the data from individual farms.

Data analysis

We used non parametric statistical analysis to test for differences between fruit set from the pollination treatments between crops, and visitation rates of different pollinator taxa. All analyses were conducted using SYSTAT (SPSS 2000).

RESULTS

The flowers of all the crops opened in the morning hours and closed in the late afternoon, except in okra which closed earlier in mid afternoon. Tomato, chilli and okra were hermaphroditic with both male and female sexual parts in the same flower, the brinjals were andro-monoecious with male and hermaphrodite flowers on the same plant and the gourds were monoecious with male and female flowers on the same plant. Pollen was the major reward for all the 6-crops and only okra produced nectar.

Fruit set, breeding systems and pollinator limitation

All crops were self-compatible except for two cases in brinjal and one in bitter gourd (Tab. 2). In many cases the fruit set through CP was lower than that resulting from OP, which could be due to damage to floral parts while emasculation, or poor quality pollen. Pollinator dependency was 26 ± 21 on average, except for tomato where it was 0. PD ranged from 8-76% across all crop varieties except tomato (Tab. 2).

Fruit set through OP ranged from 40-72% and did not differ with crop type (Kruskal-Wallis One Way ANOVA: $F = 0.52$, $N = 18$, $P = 0.72$ excluding chilli due to inadequate data), although levels of autogamy significantly differed (Kruskal-Wallis One Way ANOVA: $F = 13.99$, $N = 18$, $P = 0.0001$). Monoecious/andromonoecious crops had significantly lower autogamous fruit set than hermaphrodite crops (MWU test: $Z = 6$, $N = 19$, $P = 0.009$), higher levels of pollinator dependency (MWU test: $Z = 70$, $N = 18$, $P = 0.001$), and marginally higher levels of fruit set through hand augmented self pollination (MWU test: $Z = 56.5$, $N = 19$, $P = 0.05$) indicating potential for geitonogamous pollination (Tab. 2). Pollen limitation was not evident in most crops except for brinjal in one site (Tab. 2).

Pollinators

The study identified five major flower visiting taxa: Social bees of the family Apidae: *Apis cerana* Fabricius 1793,

TABLE 3. Visitation rates (total visits/hour) of different pollinator taxa to each crop in farms in the Coimbatore region. The decimal values have been rounded to the nearest whole number. Abbreviations of site names: Edyarpalayam (E), Karumathampatti (K), Madukarai (M), Nehru Nagar (N), Papampatti (P), Sirumugai (S).

Name of crop	Farm	Month-Year	Sample sizes			Visits per hour (mean ± SD)				
			No of hours	No of plants	No of flowers	Apis spp	Stingless bees	Solitary bees	Butterflies Moths	Wasps
Brinjal (*Solanum melongena*)	E	Nov-12	13	23	57	0.5 ± 0.7	0	3	1.5 ± 0.7	0
	N	Dec-12	20	74	198	2.7 (0.6)	1 ± 1	3 ± 2	2.7 ± 0.6	0
	P	Feb-13	21	364	916	1± 1	1.3 ± 1.2	8 ± 1	6 ± 2.6	1
	K	Mar-13	15	54	135	3 ± 4	0.5 ± 0.7	2.5 ± 0.7	9 ± 7	2.5 ± 0.7
	Total		69	515	1306	1.8	0.7	4.1	4.8	0.9
Tomato (*Solanum lycopersicum*)	P	Jan-12	78	212	532	2.2 ± 0.9	1.3 ± 1.2	2 ± 1.1	6.5 ± 2.2	1.5 ± 1.8
	M*	Mar-Jun-12	53	106	537	9.3 ± 7.4	0.9 ± 1.5	1.1 ± 1.2	5.3 ± 2.4	0.2 ± 0.4
	Total		131	318	1069	5.8	1.1	1.6	5.9	0.9
Chili (*Capsicum annuum*)	P	Dec-11	53	206	516	8.4 ± 3.4	0	0	5.9 ± 2	0.6 ± 0.8
	S*	Feb-12	29	91	217	15 ± 4	0	0	4.8 ± 2.3	0
	Total		82	297	733	11.7	0.00	0.00	5.4	0.3
Bitter gourd (*Momordica charantia*)	N	Nov-12	19	45	199	5.3 ± 1.5	4 ± 1	0	9 ± 2	0.3 ± 0.6
	P	Dec-12	12	506	1256	7 ± 2.7	1 ± 1	3.3 ± 1.2	12.3 ± 3.5	0.3 ± 0.6
	K	Mar-13	18	64	168	10.3 ± 1.5	1.3 ± 0.6	0	12 ± 1	0.3 ± 0.6
	Total		49	615	1623	7.5	2.1	1.1	11.1	0.3
Snake gourd (*Trichosanthes cucumerina* var. *anguina*)	P	Jan-13	16	76	266	12.5 ± 0.7	2.5 ± 0.7	5.5 ± 0.7	15.5 ± 3.5	3.5 ± 0.7
	K	Mar-13	29	58	297	7 ± 2.6	2.3 ± 1.3	3 ± 0.8	20.3 ± 3.9	0
	N	Nov-12	21	42	213	1 ± 0.1	0.5 ± 0.2	0	1.8 ± 0.2	0.2 ± 0.2
	Total		66	176	776	6.8	1.8	2.8	12.5	1.2
Okra (*Abelmoschus* esculentus)	S	Aug-Oct-12	47	193	496	10.1 ± 3.5	0.1 ± 1.4	3.4 ± 1.8	± 1.5	0

*organic

A. florea Fabricius 1787, and *A. dorsata* Fabricius 1793; the stingless bee *Heterotrigona iridipennis* Smith 1854 (Meliponinae); solitary bees, *Xylocopa* Latreille, 1802, *Ceratina* Latreille, 1802 and *Amegilla* Friese, 1897 (Anthophorini); Lepidoptera which included butterflies and moths; and wasps of the families Sphecidae, Braconidae, Chalcididae and Vespidae (Ollerton et al. 2014) (Tab. 3). The sweat bees of the family Halictidae represented by *Nomia* Latreille, 1804, and Syrphid flies (Syrphidae) were minor visitors (Carr 2012).

Average rates of visitation to crops differed significantly between pollinator taxa (Friedman's two way nonparametric ANOVA: F = 25.53, df = 3, $P < 0.0001$). *Apis* honeybees (mean visits hr-1 6.4 ± 4.6) and butterflies (mean visits hr-1 7.8 ± 5.3) were major visitors and visited the flowers of all six crops. *Apis* honeybees and butterflies had higher visitation rates to tomato and chilli; butterflies and *Apis* honeybees to gourds; solitary bees and butterflies to brinjal, and *Apis* honeybees to okra (Tab. 3).

DISCUSSION

Our study shows that levels of pollinator dependency ranged from 0% in tomato to 76% in bitter gourd, and pollinators are required for fruit set in five of the six crops. Monoecious and andromonoecious crops were more reliant on pollinators than hermaphrodite crops. There was considerable variation in levels of pollinator dependency which could be due to effects of site, varieties of crops grown and inputs, which we could not test because of limitations of study design.

Our results did not support many cases in literature: For example brinjal and chilli, listed as having low levels of reliance on pollinators for crop production (Klein et al. 2007) showed significant levels of pollinator dependency in our study (32% and 37%); okra, described as having moderate levels of pollinator dependence (Klein et al. 2007) was lower in our assessment (20%). The tropical monoecious gourds which were not assessed earlier, showed significant levels of pollinator dependency because pollinators are needed to move pollen within and between plants. Tomato that has been demonstrated to have enhanced fruit set with wild pollinators (Greenleaf & Kremen 2006; Hogendoorn et al. 2006) showed no pollinator dependency in our study. Therefore, more data from different sites are required to get a realistic picture of pollinator dependence of tropical crops.

However, the good news is that there was minimal pollen limitation and diverse pollinator assemblages visiting flowers in this study. This could be due to small scale farms having adequate shrubbery and weedy vegetation that could provide foraging and nesting habitats for pollinators despite the extensive use of pesticides. Uncultivated areas and shrubbery around farms are an important refuge for insects and buffer the effects of insecticides (Lee et al. 2001).

The visitation rates of pollinator taxa differed with crop type although we could not evaluate their effectiveness. Brinjal like many of the Solanaceae is buzz pollinated, and buzzing bees such as *Xylocopa* and *Amegilla*, are probably the major pollinators (Davidar et al. 2015). Our study also identifies butterflies as a possible major pollinator group. Bees, particularly honeybees have rightly been given the key role of pollinating crops worldwide (Potts et al. 2010); however, butterflies visited flowers as frequently and were common visitors to five of the six crops. Butterflies could be important as pollinators because Carr (2012) recorded more species of butterflies and at greater size ranges than the other pollinator taxa. Wing span ranged from about 20-30 mm in the lycaenids to 90-100 mm in the papilionids (Kehimkar 2008). This diverse butterfly assemblage requires host plants for reproduction which are probably available in unmanaged hedges and fallow land with shrubbery and native plants that provide food, shelter and breeding habitats for pollinators. Indian small family farms have been recognized to promote biodiversity by incorporating forest and fallow lands with non domesticated plant species that are used by people for wood, fodder and medicine (Robbins 2001). The overall importance of the landscape for supporting diverse pollinator fauna should not be underestimated.

Conclusion

Our study demonstrates that overall levels of pollinator dependency among the six crops were significant in small family farms across the Coimbatore region in southern India. We did not find any evidence of pollen limitation, and the diverse pollinator assemblage probably enhances pollination services to crops.

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