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## **Exploring the importance of floral resources and functional trait compatibility for maintaining bee fauna in tropical agricultural landscapes**

Supratim Laha<sup>1</sup>, Soumik Chatterjee<sup>1</sup>, Amlan Das<sup>2</sup>, Barbara Smith<sup>1,3</sup> and Parthiba Basu\*<sup>1</sup>

Supratim Laha: [avianlove@gmail.com](mailto:avianlove@gmail.com); Soumik Chatterjee: [soumikc83@gmail.com](mailto:soumikc83@gmail.com);

Amlan Das: [dasamlan@yahoo.co.in](mailto:dasamlan@yahoo.co.in); Barbara Smith: [barbarasmithmail@gmail.com](mailto:barbarasmithmail@gmail.com);

Parthiba Basu: [bparthib@gmail.com](mailto:bparthib@gmail.com)

<sup>1</sup>Centre for Pollination Studies, University of Calcutta, 35 Ballygunge Circular Road, Kolkata-700019, India.

<sup>2</sup>Entomology, Department of Zoology, University of Calcutta, 35 Ballygunge Circular Road, Kolkata-700019, India.

<sup>3</sup>Centre for Agroecology Water and Resilience, Coventry University, Wolston Lane, Coventry CV8 3LG, United Kingdom.

\* Corresponding author: Parthiba Basu; e-mail: [bparthib@gmail.com](mailto:bparthib@gmail.com); phone: (+91) 9831967500

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## **Abstract**

Loss of semi-natural habitats has been identified as a major driver for pollinator loss in agricultural landscapes. The challenge has been addressed in developed countries by creating flower strips and pollinator habitats in agricultural areas, but this approach has largely been overlooked in developing countries. However, even in countries that adopted pollinator-friendly measures, the complementarities between functional traits of plants and bees are not generally used as selection criteria for candidate species in floral strips. Furthermore, the combined effect of habitat variables that are likely to maximize bee visitation are also overlooked. In tropical developing countries, even the basic information to inform decision making is missing. This paper attempts to bridge this critical gap and reports how assemblages of different non-crop plants could be used to attract bees in tropical small landholdings by investigating non-crop plant identity, non-crop floral traits, bee traits and influential habitat variables at patch scale. Results showed that a combination of both non-crop flower density and diversity increased bee visitation at patch scale. Moreover, trait-based analyses revealed that bees with a larger inter-tegular distance, longer tongue frequently visited flowers with a longer corolla. This study demonstrates that both characteristics of non-crop flower patches and floral traits are important for effective management of non-crops in tropical farmland to attract pollinators with complementary functional traits. We have explored a range of non-crop plants that could be effectively sown to attract bees but recognise that more research is necessary in order to standardise their propagation, establishment and management techniques.

**Keywords:** Bee traits; Flower traits; Habitat variables; Non-crop plants; Semi-natural habitat; Tropics

## Introduction

The role of semi-natural habitat in supporting wild pollinator fauna has been well documented and has received increased attention as evidence that pollinators are threatened globally has grown. (Potts et al. 2010; Vanbergen and The Insect Pollinators Initiative, 2013). In agricultural landscapes, semi-natural habitats provide both nesting opportunities and diverse food resources to support wild pollinators outside the crop flowering period (Pywell et al. 2005; Russo et al. 2013). Resource distribution and connectivity among various semi-natural habitat patches across a landscape enable the production and survival of wild pollinators (Foley et al. 2005; Williams and Kremen, 2007).

Compared to some developed countries in temperate regions, where agricultural landscapes are more homogenous, agricultural landscapes in the tropics are heterogeneous with diverse landscape elements including patches of semi-natural vegetation closely interspersed with farmlands. Although in tropical countries, agricultural landscapes dominated by small landholdings are rich in biodiversity (Zhou et al. 2018) and thus can potentially sustain healthy communities of beneficial insects, the semi-natural habitat patches have been disappearing fast due to agricultural intensification. Disappearance of tropical habitats has accelerated over the last four decades (DeFries and Rosenzweig 2010; Basu et al. 2016), and the deteriorating state of tropical agricultural landscapes may severely threaten ecosystem services, especially pollination, in the near future.

In most tropical developing countries, creation of floral strips or suitable habitats for pollinators is not part of any agricultural land-management strategy although there is growing awareness regarding the need for such restorative measures. A list of candidate non-crop wild plant species for use in habitat creation schemes would be a useful baseline for habitat restoration projects in the tropics. This is underpinned by the fact that although there is sufficient information on the candidate species for habitat restoration exists for most temperate countries, clearly this information is not directly transferable to the tropics. This is specifically because distinctly different tropical climates and highly mosaic nature of the landscapes would impact flowering phenology, pollinator activity periods, pollinator movements and functional groups of plants and pollinators in different ways than the temperate climatic regions. However, most available information on the subject are from the temperate countries (Hipólito et al. 2018; Tangtorwongsakul et al. 2018; Cusser et al. 2019; Guenat et al. 2019; Riojas-López et al. 2019) and there are no existing prescriptions for the optimal composition of floral strips for pollinators for most tropical countries and definitely not for India. There are also no reports of pollinator-friendly semi-natural habitat creation in tropical

agricultural landscapes, including in India. Therefore, lists of candidate non-crop plants for habitat restoration, in different tropical landscapes, are urgently required before any step towards restoration of agricultural landscape are adopted therein.

Even in countries where floral strips or new habitats are created for pollinators (and bees in particular), the selection of candidate plant species is not frequently based upon functional trait complementarity between flowers and the bee species. Floral traits have been reported to influence plant-pollinator interaction (Irwin et al. 2018). Bees' preferences towards plants have been shown to be related to specific traits such as petal colour, corolla width, corolla length and nectar quality (Gumbert 2000; Gómez et al. 2008; Bauer et al. 2017; Córdoba and Cocucci 2017; Prasifka et al. 2018) or floral display (Eckhart 1991; Mitchell et al. 2004). Besides, specific bee traits (such as length of mouthparts) might have matching complementarity with various floral traits (Maad and Alexandersson, 2004; Benitez-Vieyra et al. 2006; Garibaldi et al. 2015). We suggest that the availability of diverse floral traits would ensure visitation by a diverse and more abundant bee fauna with diverse morphological traits catering to a diversity of floral types (of both crop and non-crop plants). Such complementarity can help inform strategies for the creation of floral strips that will attract a diverse bee community to agricultural fields.

The efficiency of diversified floral patches or floral strips to attract diverse bee community will not only depend on their actual composition but also on other habitat variables like floral density, plant density etc. which are little studied. Additionally, studies addressing the combined effect of different patch-scale habitat variables on pollinator visitation in non-crop floral patches are either missing or report contrasting information with respect to these variables (e.g. plant density, plant diversity or floral density of herbs and shrubs) (Hegland and Boeke 2006; Elliott and Irwin 2009). There are several other studies which showcased singular effects of various habitat variables (Tuell et al. 2008; Russo et al. 2013; Campbell et al. 2017). However, none of the above studies investigated combinations of different habitat variables and their role on bee visitation and not in the context of any tropical landscape.

In tropical countries including India, importance of bees and other insects in pollination of important crops and several non-crops including forest trees have been recorded (Hanh et al. 2014; Chakraborty et al. 2018; Saunders and Rader 2019; Barth et al. 2020). However, decline in pollinator populations in tropical heterogeneous landscapes are also evidenced from different studies (Basu et al. 2016; Potts et al. 2016). The vegetation in Indian landscape is

highly diverse ranging from alpine and sub-alpine to arid and semi-arid to tropical evergreen, semi-evergreen or deciduous plant species interspersed with small to medium scale agricultural landholdings and other anthropogenic structures. Over the last four and a half decades, India has undergone large-scale agricultural intensification that involved land conversion to agriculture and consequent landscape simplification through loss of semi-natural habitats (Basu et al. 2011). There is an urgent need to establish an appropriate evidence base to help develop pollinator habitat restoration strategies for the country. To challenge this exploration, this study was conducted in a region of eastern India where the farming landscapes are facing rapid agricultural intensification and urbanization.

This study, therefore, attempted to answer: (1) Which habitat variables are important in maximising bee visitation at patches of non-crop plants? (2) Which non-crop floral traits attract maximum bee visits? (3) If bee–non-crop floral traits compatibility influence bee visitation.

## **Methods**

### Study sites

The study area was situated in Balasore, Odisha, an Eastern Indian state. Balasore is a coastal district which is broadly divided into three geographical regions- coastal belt, inner alluvial plain and North-Western hills (Chakraborty 2011; Mahapatra et al. 2012). Our study region falls in the Nilagiri block of the district which is situated in the North-Western hilly region (Chakraborty 2011; Mahapatra et al. 2012). The landscape is a mosaic of agricultural fields, unmanaged hedgerows, semi-natural habitats and sparse deciduous and evergreen tree patches. The soil is mostly red and yellow lateritic type, mixed with gravels. The annual average temperature is 32°C and annual average rainfall is around 1300 mm (Mahapatra et al. 2012). Study region is broadly mosaic of farmlands, man-made structures as well as several randomly situated semi-natural habitat patches. In the overall hot and dry climate of study region, non-crop plant flowering peaks during monsoon to post-monsoon and then gradually declines through winter. Hence, the study was conducted between July 2014 and January 2015 (monsoon to winter).

A total of 20 study sites were selected randomly within all the available semi-natural habitats across a broad landscape covering an area of about 728 km<sup>2</sup> (from 21°35'6.89"N, 86°32'6.86"E to 21°21'17.06" N, 86°48'35.34" E) (Online Resource 1). These semi-natural habitats are more or less surrounded by agricultural fields

where a variety of crops (for example, eggplant (*Solanum melongena*), cucumber (*Cucumis sativus*), pumpkin (*Cucurbita maxima*), chilli (*Capsicum frutescens*) and rice (*Oryza sativa*)) are cultivated throughout the year. The average distance between the sites was 10.68 km (SE  $\pm$  0.39). All the study sites were situated on plain lands having more or less uniform inclination and altitude (74.3 m; SE  $\pm$  6.06).

#### Bee visit observation

The study sites varied in size and vegetation composition. At each study site, one 50 m  $\times$  50 m permanent plot was established in which three permanent 10 m  $\times$  10 m plots were located randomly. All observations were taken within those 50 m  $\times$  50 m established plots. In each 10m  $\times$  10m plot, three permanent 1m  $\times$  1m quadrats were randomly selected to carry out focal observation of bee visitation and estimation of habitat variables. To minimize the temporal variation in observation among the sites, sampling was repeated three times through the study period in each study site with an interval of average 22 days. At each study site, observation of bee visitation was carried out for 10 min session in each 1m  $\times$  1m plot from 0700 h to 1500 h (i.e. total 24 hours of observation per study site). A 15 min interval was taken between two consecutive focal observations. During each focal observation, all the bees visiting and touching the reproductive parts of the non-crop flowers present in 1m  $\times$  1m quadrats were recorded and respective flower species were noted down for further analysis. Bees were collected by sweep net and were put into a killing jar (with ethyl acetate). Collected bee specimens were dried and pinned for preservation (Gullan and Cranston 2014) and taxonomic identification. Observations were only carried out on sunny dry days.

#### Measurement of habitat variables

The number of non-crop plants (herbs and shrubs) and their species identity were recorded within each 1m  $\times$  1m quadrat in each study site. To minimize the effect of temporal variation in non-crop plant density within each site, vegetation sampling was performed twice during the first and third day of focal observation. Number of open flowers (for an estimation of flower density) for each non-crop species was also recorded (Hamblin et al. 2018) once during each day of focal observation. Plants with GBH (Girth at breast height)  $>$  10 cm and height  $\geq$  5 m were considered to be trees (Gomes et al. 2008). Trees were not included in the bee visitation survey. However, to take into account the probable effect of flowering trees on bee abundance, the total number of trees in flower (NOTF) and total number of tree species in flower (NOTSF) were counted on each day of focal observation within each 10m  $\times$  10m quadrat at each site. Non-crop plant species and leaves of each tree species were collected and preserved in a

herbarium for further taxonomic identification. Trees were also photographed during blooming (if they bloomed at all during the study period) and further classification was done at lowest possible taxonomic category.

#### Bee trait measurements

We conducted morphological measurements on all bee individuals collected during focal observations. For each bee species, 1 to 10 individuals (depending on availability) were measured in the laboratory after preservation. Bee body length (BOL) (from the front of the head to the tip of the abdomen), inter-tegular distance (ITD; the length between the two originating points (tegulae) of wings) and lengths of foreleg (FLL) and midleg (MLL) (from base of femur to tip of tarsal claws) were measured. For estimation of tongue (proboscis) length (TOL), we measured length from the basal part of the tongue (i.e., from labiomaxillary tube, where it attaches to the head) to the tip of the glossa after the tongue was fully stretched. When necessary, bee's head was dissected for tongue measurement. All the traits were measured with a stereomicroscope (Olympus SZ61) and ocular micrometer scale. Finally, all the measurements in ocular divisions were converted to micrometer and subsequently to millimetre (Online Resource 2).

#### Non-crop (herbs and shrubs) floral trait measurements

Flowers of non-crops were collected for the measurements of floral traits from same 1m × 1m quadrats where the bee visitation study was conducted. Flower traits were measured for 15 individual flowers of each species. Corolla length (LEN), corolla opening diameter (DIA) and sugar content (SUG) in the nectar were measured for each non-crop flower species visited by bees. Corolla length and diameter were measured by Vernier callipers. Corolla length was measured as the length from the base of the calyx to the longest end of the petal (Engel and Irwin 2003). Corolla diameter was measured as the longest width of the corolla opening (Engel and Irwin 2003). For Asteraceae flowers, we measured floret cluster diameter as corolla diameter and floret length as corolla length. Corolla colour was also noted for every bee visited plant species and further categorised into following categories: blue-violet flower; reddish flower; white flower; white combination flower; yellow flower. These colour categories were made based on the human colour perception and may further include other colours that are easily distinguished by the bees (for example, yellow coloured corolla with or without UV reflecting property). Nectar was extracted following standard protocols using glass capillary tubes (size 1µl microcaps®, Drummond Scientific) (Corbet 2003; Phillips et al. 2018) and its sugar percentage was measured using a regular hand-held graduated refractometer (ERMA Inc.) (Phillips et



al. 2018). For each non-crop species, nectar was extracted from individual flowers until 5 µl nectar was collected. It was then mixed well with 100 µl distilled water. The solution was then placed on the refractometer and the Brix % value was recorded. This process was repeated 15 times for each non-crop species to minimize uncertainty in measuring error; mean value was used for analysis. The refractometer was calibrated with distilled water at the field weather condition to minimize the error prior to the sampling.

#### Data analyses

For each of the 20 sites, number of open non-crop flowers and number of non-crop plants, recorded from nine 1m × 1m quadrats, were averaged to estimate non-crop flower density (FD) and non-crop plant density (NCD) which were included in the model. For each study site, the bee visitation rate (VR) was estimated by averaging the number of individual bees visiting each 1m × 1m quadrat across all observation sessions across all observational days. Total number of trees in flower (NOTF), total number of tree species in flower (NOTSF), non-crop flower diversity (FDIV), and non-crop flower colour diversity (CDIV, number of flowers present in each colour category) were also calculated for each site. NOTF and NOTSF were calculated by summing up the total number of individual trees having flowers and the total number of tree species having flowers in three 10 m × 10 m plots in each site, respectively. FDIV and CDIV were estimated using the Shanon and Weiners' (1949) equation-

$$FDIV = - \sum_{i=1}^S p_i \cdot \ln p_i$$

where, 'S' was the number of non-crop plant species and 'p<sub>i</sub>', the proportion of flowers in each 'i<sup>th</sup>' non-crop species.

Effects of non-crop flower density (FD), non-crop flower diversity (FDIV), non-crop flower colour diversity (CDIV), total number of trees in flower (NOTF), total number of tree species in flower (NOTSF) and non-crop plant density (NCD) on bee visitation rate (VR) were analysed using a generalized linear model (GLM) where FD, FDIV, CDIV, NOTF, NOTSF, NCD were predictor variables and VR the response. We fitted our model with different error functions e.g. 'inverse.gaussian', 'gaussian' and 'Gamma' with appropriate link function e.g. 'log', 'identity' and 'inverse'. All the combinations of predictor variables were used in the model. Models were first ranked according to their respective AICc (Akaike's information criterion corrected for small sample size) value and respective AICc weight (w<sub>i</sub>). Generally, models with 'ΔAICc > 2' were considered to be less supportive models

(Burnham and Anderson 2002). The best approximating models were determined after creating a 95% confidence interval according to the 'Information-theoretic approaches' proposed by Burnham and Anderson (2002). Model averaging was also conducted to visualize the effect of different predictor variables in the model (Burnham and Anderson 2002).

Relations between corolla length (LEN), corolla diameter (DIA) and nectar sugar percentage (SUG) with bee visitation rate (VR) were also explored by generalized linear regression (GLM) method where LEN, DIA and SUG were predictor variables and the VR was response. Residual errors for these three separate regressions were different and therefore, the combination effect of predictor variables could not be explored through 'Information-theoretic approaches' proposed by Burnham and Anderson (2002).

Morphological trait data (ITD and TOL) of those bee species that made visits to the non-crop flowers were arranged sequentially according to the data of floral traits (LEN and DIA) of those non-crop species which were visited by the bees. Relations between bee traits (ITD and TOL as response variables) and floral traits (LEN, DIA and SUG as predictor variables) were, then, explored by generalized linear regressions (GLM). Bee traits that were multicollinear with each other were not included in the regression (Online Resource 3).

All the plots were created from GLM analyses, where a sequence of length values was first set up for predictor variable and fitted values (for response variable) were, then, predicted within the sequence of length values from respective GLM analyses.

Normality and heteroscedasticity were checked by normal Q-Q plots and standardized residuals against fitted value plots (Crawly, 2007). Variance inflation factor (VIF) tests were performed to check the multicollinearity among the predictor variables. 'VIF' value  $> 5$  was considered as multicollinear (Craney and Surles 2002; Akinwande et al. 2015; Vu et al. 2015) (Online Resource 3 and 4). Non-parametric tests were performed in all the cases as our data did not meet normality even with transformation. All the analyses were performed in 'R' statistical software (version 3.4.3) (R Core Team 2013) with MuMIn (Barton 2017), AICcmodavg (Mazerolle 2017), and 'fmsb' (Nakazawa 2015) packages.

## Results

About 15,000 non-crop plant individuals (herbs and shrubs together) were recorded across all of the 20 study sites. These belonged to a total of 78 species from 32 families and 59 genera. Six non-crop species could not be identified at any taxonomic level (Table 1). Family Asteraceae had 7 representative species which is the highest in number in a single-family followed by Acanthaceae (6 species), Fabaceae (6 species), Rubiaceae (6 species), Lamiaceae (5 species), Caesalpiniaceae (4 species), Euphorbiaceae (4 species) and Malvaceae (4 species). The rest of plant families were represented by one or two plant species.

Among this wide range of non-crop plant species, only a total of 25 species (32.05%) belonging to 12 genera were observed being visited by bees during our study (Table 1). Total number of bee-visited non-crop species under each plant family was shown in Fig. 1. Although non-crops belonging to Fabaceae, Lamiaceae, Acanthaceae and Caesalpiniaceae attracted higher number of bees, there was no significant difference in bee visitation across non-crop plant families (Kruskal-Wallis test,  $df=12$ ,  $p > 0.05$ ).

A total of 146 individuals belonging to 26 different tree species (Online Resource 5 and 6) were also recorded at the study sites.

A total of 293 bee individuals, from 3 families and 22 species, were recorded during the period of our study. Of the 22 species, 82.9% of individuals belonging to 20 species touched the floral reproductive parts during visit.

#### Effects of habitat variables on bee visitation

Variation in wild bee visitation rate was explained by five best candidate models which were within 95% confidence interval (Table 2). Out of these candidate models, 'FD + FDIV' (non-crop flower density + non-crop flower diversity) and 'FD + FDIV + NOTF' (non-crop flower density + non-crop flower diversity + total number of trees in flower) were the best parsimonious models which determined bee visitation. However, 'FD + FDIV' had greater 'Akaike weight' (' $w_i$ ' = 0.50) than 'FD + FDIV + NOTF' (' $w_i$ ' = 0.22). All the combination models are listed in Online Resource 7. FD was the most important factor in the models followed by FDIV as ascertained by "Model-averaging of parameters" (Table 3). Although, NOTF was one of the variables selected in the best parsimonious models, it had negligible 'Relative Importance' compared to the other two variables in the models (Table 3).

#### Relationship between floral traits and bee visitation

Bee visitation rate (VR) was significantly determined by nectar sugar content, corolla length and corolla diameter. Visitation rate significantly increased with increase in nectar sugar content ( $t = 11.14, p < 0.0001$ ) and corolla length ( $t = 4.13, p < 0.001$ ) (Fig. 2a–b). However, visitation rate dropped with increase in corolla diameter ( $t = -2.25, p = 0.03$ ) (Fig. 2c). Although corolla diameter had significant negative relationship with nectar sugar content ( $t = -3.735, p < 0.01$ ) (Fig. 3).

#### Relationship between floral traits and bee traits

All the measured floral traits are listed in Online Resource 8. Bees with larger ITD visited flowers having larger corolla diameter ( $t = -2.157, p = 0.0348$ ) and longer corolla length ( $t = -3.139, p = 0.00256$ ) significantly more frequently (Fig. 4a–b). Also, we found significant relationship between bee tongue length (TOL) and corolla length of flowers ( $t = -3.698, p = 0.000454$ ) (Fig. 4d). However, tongue length and corolla diameter did not show any significant relationship ( $t = -1.838, p = 0.0707$ ) (Fig. 4c). Also, there were no significant relationships among tongue length (TOL) ( $t = 0.011, p = 0.992$ ) and ITD ( $t = 0.012, p = 0.991$ ) with nectar sugar percentage (SUG) found in our study.

## Discussion

Carefully designed non-crop flower mixtures for flowering strips/margins can help improve the capacity of intensively managed landscapes to maintain bee diversity (Kremen et al. 2004; Morandin and Kremen 2013). For effective delivery of pollination services in order to enhance crop yield, it is important to maximize flower visits by attracting the optimum number of bees (Geslin et al. 2017). Given the limited space available for creation of bee attracting plant habitat patches in a tropical agricultural landscape, it is especially crucial to select appropriate plant species that maximise bee visits. Only about one-third of the non-crop plant species recorded from the studied agricultural landscape attracted bees and these belonged to a restricted subset of 13 plant families. This shows the narrow choice available for selection of candidate non-crop plants that have potential to create bee-friendly habitats in our study area.

In our study, non-crop plant species belonging to family Fabaceae and Lamiaceae received higher number of bees than other families. Fabaceae flower morphology has evolved to maximize bee pollination (Aronne et al.

2012). The aestivation of Fabaceae flowers is vexillary type (closed type flower) where a vexillum or banner petal protrudes from the base of the calyx while the other petals cover the reproductive parts (Aronne et al. 2012). Banner petals generally have nectar guides that attract pollinators (Aronne et al. 2012) and guide them to the nectar source. The second most important group in our study was Lamiaceae which consists of 16% of the total plant species visited by bees. Aestivation of Lamiaceae flowers are, generally, imbricate or valvate (open type flower) where both pollen and nectar are easily accessible to pollinators (Harley et al. 2004). Although, several species of Lamiaceae, due to their morphological constraints, can be restrictive for different insect flower visitors, the Lamiaceae flowers in our study region had smaller corolla tubes with exposed reproductive parts and therefore did not pose any constraints for the visitors. Lamiaceae flowers generally consist of five petals where three petal lobes are fused to form the largest petal structure (Elpel 2000). The petals also consist of nectar guides which attract pollinators to the flower (Harley et al. 2004). Our study suggests that Fabaceae and Lamiaceae should be essential components of seed mixtures for creation of flower-rich patches in the agricultural landscape in our study region to attract bees. Nevertheless, further studies are required to identify more bee attracting non-crop plant species and their phenotypic traits in other unexplored parts of India and other tropical agricultural landscapes.

Patch characteristics (or variables) of the local habitats are also important ~~too~~ in attracting bee species for pollination (Williams and Winfree 2013). Whether density or diversity of non-crop flowers is more important in attracting a higher number of bees has been a matter of debate (Basu et al. 2016; Rollin et al. 2019). As the study shows, among all the combinations, the combined effect of both non-crop flower density and diversity is more important in attracting a higher number of bees. Flower density in our study was found to be the most important habitat variable and has been previously reported as being a crucial one for increasing bee visitation (Hegland and Boeke 2006). High flower density acts as a visual signal of resource availability to the bees (Dafni et al. 1997). Therefore, in a fragmented landscape, at patch scale, non-crop habitats with high flower density are an attractive foraging ground for pollinators, and subsequently, non-crops and nearby crops might involve in competition for pollinator visitation. However, presence of non-crops was observed to increase the probability of pollination in nearby pollinator-dependent crops (Morandin and Kremen 2013), and this facilitation may be sufficient to minimize the effect of competition for pollinator visitation between non-crops and crops. Flower diversity was the second most important factor that influenced bee visitation to the flowers in our studied non-crop habitat patches. The presence of diversified flowering species increases the resource diversity for the pollinators, thereby attracting a

diverse pollinator assemblage (MacArthur 1972; Russo et al. 2013). Flowers of different species of plants contain different nutritional ingredients, including sugars (Nicolson 2011). Different bee species display differential preferences towards nectar sugar (Wykes 1952; Waller 1972; Nicolson 2011) and therefore diverse flower patches with associated differential sugar content, may attract a diverse bee community regulated by their nutritional preferences. Most of the information regarding nectar nutritional ingredients has been studied in the *Apis* species and there remains a considerable knowledge gap regarding nutritional composition and nectar preferences for wild bees.

Diversified flower patches can also increase trait-based compatibility for attracting or sustaining a diversified bee community (Pontin et al. 2006; Campbell et al. 2012). This, in turn, may increase overall bee visitation. Our study revealed the existence of a close relationship between bee visitation and flower traits. A patch with high species diversity may be assumed to have a high trait diversity as well. Availability of diverse floral traits may help to sustain a higher diversity of floral visitors with diverse morphological traits. This explains higher bee visitation towards patches with increasing flower diversity in our study area. As our results reveal, specific floral traits attracted a higher number of bees. For example, visitation seemed to be influenced by corolla length, and corolla diameter as more tubular flowers attracted a higher number of bees. This means in our study area, presence of tubular flowers should be an essential component of floral strips. Again, while certain bees with compatible morphology and size can access and explore rewards in tubular flowers, visitation from bees that cannot access floral rewards in such flowers would also require availability of non-tubular flowers. Smaller bee species may explore the resource easily by entering the corolla tube and generally provide more visitation to the flowers (Sahli and Conner 2007; Mallinger and Prasifka 2017). Sometimes, body size does not permit larger bees completely/partly to enter the corolla tube and as a consequence, their proboscis cannot reach the nectary. Our results also showed that bee visitation increased with increasing sugar concentration of the nectar. Bees' preference towards higher sugar concentration also have been observed in studies comparing different flower species (Roubik and Buchmann 1984; Bailes et al. 2018; Masierowska et al. 2018). A previous study has shown that sugar type may vary with floral structure and tubular flowers contain more sucrose in nectar (Southwick et al. 1981). This may be the reason for higher bee visitation in tubular flowers since bees have a distinct preference for sucrose compared to fructose and hexose (Biesmeijer et al. 1999).

The positive association of inter-tegular distance and tongue length of foraging bees with corolla length of flowers found in our study is also supported by earlier studies (Bommarco et al. 2012; Klumpers et al. 2019). This also goes with the concept that flower structures seem to have co-evolved with specialized pollinators to increase pollination success by providing structural compatibility to the latter (Herrera 1996; Jauker et al. 2016; Pauw et al. 2017; Woźniak and Sicard 2018). Specialised pollination syndromes can also promote flower constancy, reduce interspecific pollen transfer and therefore provide better reproductive fitness for the plants (Krishna and Keasar 2018). This concept can be applied for the preparation of bee-friendly habitats to enhance insect-flower interactions.

As our study shows, an ideal seed mix for creation of floral strips in our study area that can attract bees in good numbers has to have a bias for species with flowers having long and tubular corolla, preferably belonging to families Fabaceae and Lamiaceae. Further, our study also indicates that such floral strips have to have high plant species diversity with synchronous flowering. However, the trait matching was based on the bee species assemblage available in our study area and the pattern might be different in other areas where different floral traits may emerge as important. Therefore, we argue that similar studies need to be carried out in other areas of the tropics. Moreover, seasonal studies would also be necessary for understanding the temporal fluctuations of plant-pollinator interactions in semi-natural habitats and therefore, selection of seed mixtures to support pollinator throughout the years will be more appropriate. Our study at this moment is a pioneering attempt (as far as we are aware) to select candidate plant species using a trait-based approach for creating pollinator habitats in the tropics. Hopefully, this study would be a possible starting point that will inspire others to explore more information for conserving or creating such habitats in the tropics.

## Conclusions

Small and fragmented land holdings in the tropics, including India, pose a major constraint in sparing land for creation of pollinator habitat. In most cases, the only land available for such purpose is the meagre area of bunds that divide the landholdings. Creation of pollinator-attracting vegetation in this limited available space would, therefore, entail careful selection of non-crop plants with traits appropriate for maximising bee visits with matching functional traits. Knowledge of non-crop plants that can qualitatively improve the agricultural landscape is a major pre-requisite; the present work is an important contribution towards that in the context of Indian agriculture. However, given the situations in some developed countries where traditionally managed semi-natural habitats have been

completely destroyed, our primary goal should be beyond mere creation of floral strips and focussed more towards conservation of natural/semi-natural areas across agricultural landscapes before it is too late.

## Compliance with ethical standards

### Conflict of interest

The authors declare no conflict of interest.

## References

- Ågren J (1996) Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. *Ecology* 77:1779–1790.
- Akinwande MO, Dikko HG, Samson A (2015) Variance inflation factor: as a condition for the inclusion of suppressor variable (s) in regression analysis. *Open J Stat* 5:754.
- Aronne G, Giovanetti M, De Micco V (2012) Morphofunctional traits and pollination mechanisms of *Coronilla emerus* L. flowers (Fabaceae). *Sci World J* 2012:1–8.
- Bailes EJ, Patrick JG, Glover BJ (2018) An analysis of the energetic reward offered by field bean (*Vicia faba*) flowers: Nectar, pollen, and operative force. *Ecol Evol* 8:3161–3171.
- Barth OM, de Freitas ADS, Vanderborcht B (2020) Pollen preference of stingless bees (*Melipona rufiventris* and *M. quadrifasciata anthidioides*) inside an urban tropical forest at Rio de Janeiro city. *J Apic Res.* <https://doi.org/10.1080/00218839.2020.1714863>.
- Barton K (2017) MuMIn: Multi-model inference. R Package Version 1.42.1. <https://cran.r-project.org/web/packages/MuMIn/>. Accessed 20 August 2018.
- Basu P, Parui AK, Chatterjee S, Dutta A, Chakraborty P, Roberts S, Smith B (2016) Scale dependent drivers of wild bee diversity in tropical heterogeneous agricultural landscapes. *Ecol Evol* 6:6983–6992.



- Bauer AA, Clayton MK, Brunet J (2017) Floral traits influencing plant attractiveness to three bee species: Consequences for plant reproductive success. *Am J Bot* 104:772–781.
- Benitez-Vieyra S, Medina AM, Glinos E, Cocucci AA (2006) Pollinator-mediated selection on floral traits and size of floral display in *Cyclopogon elatus*, a sweat bee-pollinated orchid. *Funct Ecol* 20:948–957.
- Biesmeijer JC, Richter JAP, Smeets MAJP, Sommeijer MJ (1999) Niche differentiation in nectar-collecting stingless bees: the influence of morphology, floral choice and interference competition. *Ecol Entomol* 24:380–388.
- Bommarco R, Lundin O, Smith HG, Rundlöf M (2012) Drastic historic shifts in bumble-bee community composition in Sweden. *Proc R Soc B Biol Sci* 279:309–315.
- Brosi BJ, Daily GC, Shih TM, Oviedo F, Durán G (2008) The effects of forest fragmentation on bee communities in tropical countryside. *J Appl Ecol* 45:773–783.
- Burnham KP, Anderson DR (2003) Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.
- Campbell AJ, Biesmeijer JC, Varma V, Wäckers FL (2012) Realising multiple ecosystem services based on the response of three beneficial insect groups to floral traits and trait diversity. *Basic Appl Ecol* 13:363–370.
- Campbell AJ, Wilby A, Sutton P, Wäckers FL (2017) Do sown flower strips boost wild pollinator abundance and pollination services in a spring flowering crop? A case study from UK cider apple orchards. *Agric Ecosyst Environ* 239:20–29.
- Chakraborty A (2011) Scope of tourism development in a socio-economically backward area: a case study of Shyamsundarpur mouza, Baleshwar, Odisha. *Geo-Analyst* 1:78–81.
- Chakraborty P, Smith B, Basu P (2018) Pollen Transport in the Dark: Hawkmoths Prefer Non Crop Plants to Crop Plants in an Agricultural Landscape. *Proc Zool Soc* 71:299–303.
- Corbet SA (2003) Nectar sugar content: estimating standing crop and secretion rate in the field. *Apidologie* 34:1–10.

- Córdoba SA, Cocucci AA (2017) Does hardness make flower love less promiscuous? Effect of biomechanical floral traits on visitation rates and pollination assemblages. *Arthropod Plant Interact* 11:299–305.
- Craney TA, Surlles JG (2002) Model-dependent variance inflation factor cutoff values. *Qual Eng* 14:391–403.
- Crawley MJ (2007) *The R Book*. John Wiley & Sons, Ltd, UK.
- Cusser S, Grando C, Zucchi MI, López-Urbe MM, Pope NS, Ballare K, Luna-Lucena D, Almeida EA, Neff JL, Young K, Jha S (2019) Small but critical: semi-natural habitat fragments promote bee abundance in cotton agroecosystems across both Brazil and the United States. *Landsc Ecol* 34:1825–1836.
- Dafni A, Lehrer M, Kevan P (1997) Spatial flower parameters and insect spatial vision. *Biol Rev* 72:239–282.
- DeFries R, Rosenzweig C (2010) Toward a whole-landscape approach for sustainable land use in the tropics. *Proc Natl Acad Sci* 107:19627–19632.
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carrè G, Marquèz JRG, Gruber B, Lafourcade B, Leitão PJ, Münkemüller T (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 35:27–46.
- Eckhart VM (1991) The effects of floral display on pollinator visitation vary among populations of *Phacelia linearis* (Hydrophyllaceae). *Evol Ecol* 5:370–384.
- Elliott SE, Irwin RE (2009) Effects of flowering plant density on pollinator visitation, pollen receipt, and seed production in *Delphinium barbeyi* (Ranunculaceae). *Am J Bot* 96:912–919.
- Elpel TJ (2000) *Botany in a Day: Thomas J. Elpel's Herbal Field Guide to Plant Families*. HOPS Press, Montana.
- Engel EC, Irwin RE (2003) Linking pollinator visitation rate and pollen receipt. *Am J Bot* 90:1612–1618.
- Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH (2005) Global consequences of land use. *Science* 309:570–574.
- Garibaldi LA, Bartomeus I, Bommarco R, Klein AM, Cunningham SA, Aizen MA, Boreux V, Garratt MPD, Carvalheiro LG, Kremen C, Morales CL, Schüepp C, Chacoff NP, Freitas BM, Gagic V, Holzschuh A, Klatt BK, Krewenka KM, Krishnan S, Mayfield MM, Motzke I, Otieno M, Petersen J, Potts SG, Ricketts

- TH, Rundlöf M, Sciligo A, Sinu PA, Steffan-Dewenter I, Taki H, Tschamtker T, Vergara CH, Viana BF, Woyciechowski M (2015) Trait matching of flower visitors and crops predicts fruit set better than trait diversity. *J Appl Ecol* 52:1436–1444.
- Geslin B, Aizen MA, Garcia N, Pereira AJ, Vaissière BE, Garibaldi LA (2017) The impact of honey bee colony quality on crop yield and farmers' profit in apples and pears. *Agric Ecosyst Environ* 248:153–161.
- Gibbs HK, Ruesch AS, Achard F, Clayton MK, Holmgren P, Ramankutty N, Foley JA (2010) Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proc Natl Acad Sci* 107:16732–16737.
- Gomes LGL, Oostra V, Nijman V, Cleef AM, Kappelle M (2008) Tolerance of frugivorous birds to habitat disturbance in a tropical cloud forest. *Biol Conserv* 141:860–871.
- Gómez JM, Bosch J, Perfectti F, Fernández JD, Abdelaziz M, Camacho JPM (2008) Association between floral traits and rewards in *Erysimum mediohispanicum* (Brassicaceae). *Ann Bot* 101:1413–1420.
- Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. *Oecologia* 153:589–596.
- Groom MJ (1998) Allee effects limit population viability of an annual plant. *Am Nat* 151:487–496.
- Guenat S, Kunin WE, Dougill AJ, Dallimer M (2019) Effects of urbanisation and management practices on pollinators in tropical Africa. *J Appl Ecol* 56:214–224.
- Gullan PJ, Cranston PS (2014) *The insects: an outline of entomology*. John Wiley & Sons, Ltd, UK.
- Gumbert A (2000) Color choices by bumble bees (*Bombus terrestris*): innate preferences and generalization after learning. *Behav Ecol Sociobiol* 48:36–43.
- Hamblin AL, Youngsteadt E, Frank SD (2018) Wild bee abundance declines with urban warming, regardless of floral density. *Urban Ecosyst* 21:419–428.
- Hanh TTM, Sharma SK, Rana MK (2014) Pollination efficiency of native bee pollinators of cucumber (*Cucumis sativus* L.) in India. *J Apic* 29:199–205.

- Harley RM, Atkins S, Budantsev AL, Cantino PD, Conn BJ, Grayer R, Harley MM, De Kok RD, Krestovskaja TD, Morales R, Paton AJ (2004) Labiatae. In: Kadereit JW (ed) Flowering Plants · Dicotyledons. The Families and Genera of Vascular Plants, vol 7. Springer, Heidelberg, Berlin, pp 167–275.
- Hegland SJ, Boeke L (2006) Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecol Entomol* 31:532–538.
- Herrera CM (1996) Floral traits and plant adaptation to insect pollinators: a devil’s advocate approach. In: Lloyd DG, Barrett SCH (eds) *Floral Biology: Studies on Floral Evolution in Animal-Pollinated Plants*. Chapman and Hall, New York, pp 65–87.
- Hipólito J, Boscolo D, Viana BF (2018) Landscape and crop management strategies to conserve pollination services and increase yields in tropical coffee farms. *Agric Ecosyst Environ* 256:218–225.
- Irwin RE, Warren PS, Adler LS (2018) Phenotypic selection on floral traits in an urban landscape. *Proc R Soc B Biol Sci* 285:20181239.
- Jauker F, Speckmann M, Wolters V (2016) Intra-specific body size determines pollination effectiveness. *Basic Appl Ecol* 17:714–719.
- Klumpers SGT, Stang M, Klinkhamer PGL (2019) Foraging efficiency and size matching in a plant-pollinator community: the importance of sugar content and tongue length. *Ecol Lett* 22:469–479.
- Kremen C, Williams NM, Bugg RL, Fay JP, Thorp RW (2004) The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol Lett* 7:1109–1119.
- Krishna S, Keasar T (2018) Morphological complexity as a floral signal: from perception by insect pollinators to co-evolutionary implications. *Int j Mol Sci* 19:1681–1695.
- Kutner MH, Nachtsheim CJ, Neter J, Li W (2004) *Applied Linear Statistical Models*. McGraw Hill Higher Education, New York.
- Maad J, Alexandersson R (2004) Variable selection in *Platanthera bifolia* (Orchidaceae): phenotypic selection differed between sex functions in a drought year. *J Evol Biol* 17:642–650.

- MacArthur RH (1972) *Geographical ecology: patterns in the distribution of species*. Harper and Row, New York.
- Mahapatra N, Marai N, Dhal K, Nayak RN, Panigrahi BK, Mallick G, Ranjit M, Kar SK, Kerketta AS (2012) Malaria outbreak in a non endemic tribal block of Balasore district, Orissa, India during summer season. *Trop Biomed* 29:277–285.
- Mallinger RE, Prasifka JR (2017) Bee visitation rates to cultivated sunflowers increase with the amount and accessibility of nectar sugars. *J Appl Entomol* 141:561–573.
- Masierowska M, Stawiarz E, Rozwałka R (2018) Perennial ground cover plants as floral resources for urban pollinators: A case of Geranium species. *Urban For Urban Green* 32:185–194.
- Mazerolle MJ (2017) AICcmodavg: model selection and multimodal inference based on (Q)AIC(c). R package version 2.1-1. <http://CRAN.R-project.org/package=AICcmodavg>. Accessed 20 August 2018.
- Mitchell RJ, Flanagan RJ, Brown BJ, Waser NM, Karron JD (2009) New frontiers in competition for pollination. *Ann Bot* 103:1403–1413.
- Morandin LA, Kremen C (2013) Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecol Appl* 23:829–839.
- Nakazawa M (2017) fmsb: functions for Medical Statistics Book with some Demographic Data. R package version 0.6.3. <https://CRAN.R-project.org/package=fmsb>. Accessed 20 August 2018.
- Newbold T, Scharlemann JPW, Butchart SHM, Sekercioglu CH, Joppa L, Alkemade R, Purves DW (2014) Functional traits, land-use change and the structure of present and future bird communities in tropical forests. *Global Ecol Biogeog* 23:1073–1084.
- Nicolson SW (2011) Bee food: the chemistry and nutritional value of nectar, pollen and mixtures of the two. *Afr Zool* 46:197–204.
- Pauw A, Kahnt B, Kuhlmann M, Michez D, Montgomery GA, Murray E, Danforth BN (2017) Long-legged bees make adaptive leaps: linking adaptation to coevolution in a plant–pollinator network. *Proc R Soc B Biol Sci* 284:20171707.

- Phillips BB, Shaw RF, Holland MJ, Fry EL, Bardgett RD, Bullock JM, Osborne JL (2018) Drought reduces floral resources for pollinators. *Glob Chang Biol* 24:3226–3235.
- Pontin DR, Wade MR, Kehrl P, Wratten SD (2006) Attractiveness of single and multiple species flower patches to beneficial insects in agroecosystems. *Ann Appl Biol* 148:39–47.
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. *Trends Ecol Evol* 25:345-353.
- Potts SG, Imperatriz-Fonseca V, Ngo HT, Aizen MA, Biesmeijer JC, Breeze TD, Dicks LV, Garibaldi LA, Hill R, Settele J, Vanbergen AJ (2016) Safeguarding pollinators and their values to human well-being. *Nature* 540:220–229.
- Prasifka JR, Mallinger RE, Portlas ZM, Hulke BS, Fugate KK, Paradis T, Hampton ME, Carter CJ (2018) Using nectar-related traits to enhance crop-pollinator interactions. *Front Plant Sci* 9:812–819.
- Pywell RF, Warman EA, Carvell C, Sparks TH, Dicks LV, Bennett D, Wright A, Critchley CNR, Sherwood A (2005) Providing foraging resources for bumblebees in intensively farmed landscapes. *Biol Conserv* 121:479-494.
- R development core team 2013. R: A Language and Environment for Statistical Computing. <http://www.r-project.org/>.
- Ricketts TH, Daily GC, Ehrlich PR, Fay JP (2001) Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conserv Biol* 15:378-388.
- Ricketts TH, Regetz J, Steffan-Dewenter I, Cunningham SA, Kremen C, Bogdanski A, Gemmill-Herren B, Greenleaf SS, Klein AM, Mayfield MM, Morandin LA (2008) Landscape effects on crop pollination services: are there general patterns? *Ecol Lett* 11:499–515.
- Riojas-López ME, Díaz-Herrera IA, Fierros-López HE, Mellink E (2019) The effect of adjacent habitat on native bee assemblages in a perennial low-input agroecosystem in a semiarid anthropized landscape. *Agric Ecosyst Environ* 272:199–205.

- Rollin O, Pérez-Méndez N, Bretagnolle V, Henry M (2019) Preserving habitat quality at local and landscape scales increases wild bee diversity in intensive farming systems. *Agric Ecosyst Environ* 275:73–80.
- Roubik DW, Buchmann SL (1984) Nectar selection by *Melipona* and *Apis mellifera* (Hymenoptera: Apidae) and the ecology of nectar intake by bee colonies in a tropical forest. *Oecologia* 61:1–10.
- Russo L, Debarros N, Yang S, Shea K, Mortensen D (2013) Supporting crop pollinators with floral resources: network-based phenological matching. *Ecol Evol* 3:3125–3140.
- Sahli HF, Conner JK (2007) Visitation, effectiveness, and efficiency of 15 genera of visitors to wild radish, *Raphanus raphanistrum* (Brassicaceae). *Am J Bot* 94:203–209.
- Saunders ME, Rader R (2019) Network modularity influences plant reproduction in a mosaic tropical agroecosystem. *Proc R Soc Lond B Biol Sci* 286:20190296.
- Shannon CE, Weaver W (1949) *The Mathematical Theory of Communication*. University of Illinois Press, Urbana.
- Southwick EE, Loper GM, Sadwick SE (1981) Nectar production, composition, energetics and pollinator attractiveness in spring flowers of Western New York. *Am J Bot* 68:994–1002.
- Tangtorwongsakul P, Warrit N, Gale GA (2018) Effects of landscape cover and local habitat characteristics on visiting bees in tropical orchards. *Agric Ecosyst Environ* 20:28–40.
- Taubert F, Fischer R, Groeneveld J, Lehmann S, Müller MS, Rödiger E, Wiegand T, Huth A (2018) Global patterns of tropical forest fragmentation. *Nature* 554:519–522.
- Tuell JK, Fiedler AK, Landis D, Isaacs R (2008) Visitation by Wild and Managed Bees (Hymenoptera: Apoidea) to Eastern U.S. Native Plants for Use in Conservation Programs. *Environ Entomol* 37:707–718.
- Tylianakis JM, Klein AM, Tscharntke T (2005) Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. *Ecology* 86:3296–3302.
- Vanbergen AJ, Initiative TIP (2013) Threats to an ecosystem service: pressures on pollinators. *Front Ecol Environ* 11:251–259.

- Vu DH, Muttaqi KM, Agalgaonkar AP (2015) A variance inflation factor and backward elimination based robust regression model for forecasting monthly electricity demand using climatic variables. *Appl Energy* 140:385–394.
- Waller GD (1972) Evaluating responses of honey bees to sugar solutions using an artificial-flower feeder. *Ann Entomol Soc Am* 65:857–862.
- Williams NM, Kremen C (2007) Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecol Appl* 17:910–921.
- Williams NM, Winfree R (2013) Local habitat characteristics but not landscape urbanization drive pollinator visitation and native plant pollination in forest remnants. *Biol Conserv* 160:10–18.
- Woźniak NJ, Sicard A (2018) Evolvability of flower geometry: Convergence in pollinator-driven morphological evolution of flowers. *Semin Cell Dev Biol* 79:3–15.
- Wu X, Lv M, Jin Z, Michishita R, Chen J, Tian H, Tu X, Zhao H, Niu Z, Chen X, Yue T (2014) Normalized difference vegetation index dynamic and spatiotemporal distribution of migratory birds in the Poyang Lake wetland, China. *Ecol Indic* 47:219–230.
- Wykes GR (1952) The preferences of honeybees for solutions of various sugars which occur in nectar. *J Exp Biol* 29:511–518.
- Zhou W, Lee M-B, Goodale E (2018) The relationship between crop cover, crop heterogeneity and the diversity of herbaceous plants in uncultivated areas of a tropical agricultural landscape of southern China. *Glob Ecol Conserv* 14:e00399.



**Table 1** List of herb and shrub species encountered during focal observation in the study sites. Asterisk (\*) indicates species which received bee visits during focal observation.

Serial no.	Binomial name	Family
1	* <i>Rungia parviflora</i>	Acanthaceae
2	<i>Clerodendrum viscosum</i> (= <i>C. infortunatum</i> )	Lamiaceae
3	<i>Holarrhena pubescens</i>	Apocynaceae
4	* <i>Sida veronicaefolia</i> (= <i>S. humilis</i> )	Malvaceae
5	<i>Croton oblongifolius</i>	Euphorbiaceae
6	* <i>Desmodium triflorum</i>	Fabaceae
7	<i>Meyna spinosa</i> ( <i>Xeromphis</i> )	Rubiaceae
8	<i>Emilia sonchifolia</i>	Asteraceae
9	<i>Phyllanthus simplex</i>	Phyllanthaceae
10	<i>Spermacoce hispida</i>	Rubiaceae
11	<i>Evolvulus nummularius</i>	Convolvulaceae
12	<i>Hybanthus enneaspermus</i> (= <i>Ionidium suffruticosum</i> )	Violaceae
13	* <i>Sida acuta</i>	Malvaceae
14	<i>Ludwigia parviflora</i>	Onagraceae
15	<i>Sida rhombifolia</i> var. <i>rhomboidea</i>	Malvaceae
16	<i>Melochia corchorifolia</i>	Sterculiaceae
17	<i>Corchorus aestuans</i>	Tiliaceae
18	* <i>Hyptis suaveolens</i>	Lamiaceae
19	<i>Didelacanthus prostratus</i> (= <i>Ruellia prostrata</i> )	Acanthaceae
20	<i>Elephantopus scaber</i>	Asteraceae
21	<i>Hedyotis pinifolia</i>	Rubiaceae
22	Unidentified plant 1	-----
23	<i>Bonnaya brachiata</i> (= <i>Lindernia ciliata</i> )	Linderniaceae
24	<i>Evolvulus alsinoides</i>	Convolvulaceae

25	* <i>Glycosmis pentaphylla</i>	Rutaceae
26	<i>Dicliptera</i> sp.	Acanthaceae
27	<i>Vernonia cinerea</i>	Asteraceae
28	<i>Oldenlandia corymbosa</i>	Rubiaceae
29	<i>Alternanthera sessilis</i>	Amaranthaceae
30	<i>Lobelia</i> sp.	Campanulaceae
31	<i>Spermacoce ocymoides</i>	Rubiaceae
32	<i>Scoparia dulcis</i>	Plantaginaceae
33	Unidentified plant 2	-----
34	* <i>Anisochilus carnosus</i>	Lamiaceae
35	Unidentified plant 3	-----
36	Unidentified plant 4	-----
37	<i>Tarannus labialis</i>	Fabaceae
38	<i>Biophytum sensitivum</i>	Oxalidaceae
39	* <i>Limnophila repens</i>	Scrophulariaceae
40	<i>Hydrolea zeylanica</i>	Hydroleaceae
41	<i>Oldenlandia</i> sp.	Rubiaceae
42	<i>Erythraea roxburghii</i>	Gentianaceae
43	<i>Drosera burmannii</i>	Droseraceae
44	<i>Eranthemum</i> sp.	Acanthaceae
45	<i>Barleria prionitis</i>	Acanthaceae
46	<i>Ageratum conyzoides</i>	Asteraceae
47	<i>Boerhavia repens</i>	Nyctaginaceae
48	<i>Crotalaria prostrata</i>	Fabaceae
49	* <i>Lindernia crustacea</i>	Linderniaceae
50	Unidentified plant 5	-----
51	* <i>Phyllanthus rheedei</i>	Phyllanthaceae
52	<i>Allophylus cobbe</i>	Sapindaceae

53	<i>Cleome viscosa</i>	Cleomaceae
54	* <i>Ocimum canum</i>	Lamiaceae
55	* <i>Ocimum basilicum</i>	Lamiaceae
56	<i>Mollugo stricta</i>	Molluginaceae
57	Unidentified plant 6	-----
58	* <i>Crotalaria pallida</i>	Fabaceae
59	* <i>Cipadessa baccifera</i>	Meliaceae
60	<i>Adenosma indianum</i>	Scrophulariaceae
61	<i>Urena lobata</i>	Malvaceae
62	<i>Spilanthes paniculata</i>	Asteraceae
63	<i>Achyranthes bidentata</i>	Amaranthaceae
64	<i>Jatropha curcas</i>	Euphorbiaceae
65	* <i>Stylosanthes hamata</i>	Fabaceae
66	* <i>Cassia occidentalis</i>	Caesalpiaceae
67	* <i>Cassia tora</i>	Caesalpiaceae
68	* <i>Cassia alata</i>	Caesalpiaceae
69	* <i>Tephrosia purpurea</i>	Fabaceae
70	* <i>Tridax procumbens</i>	Asteraceae
71	<i>Mimosa pudica</i>	Mimosaceae
72	* <i>Chromolaena odorata</i> (= <i>Eupatorium odoratum</i> )	Asteraceae
73	* <i>Jatropha gossypifolia</i>	Euphorbiaceae
74	<i>Bryophyllum</i> sp.	Crassulaceae
75	* <i>Andrographis paniculata</i>	Acanthaceae
76	<i>Cassia hirsuta</i>	Caesalpiaceae
77	* <i>Croton bonplandianus</i>	Euphorbiaceae
78	* <i>Martynia annua</i>	Martyniaceae

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**Table 2** Best candidate models (according to 95% confidence interval) showing effects of different habitat variables (FD= non-crop flower density, FDIV= non-crop flower diversity, NCD= non-crop plant density, NOTF= total number of trees in flower and NOTSF= total number of tree species in flower) on bee visitation rate (VR). The best models are shown in bold.

Response	Predictor	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	wi
VR	<b>FD + FDIV</b>	<b>-46.75</b>	<b>0</b>	<b>0.50</b>
	<b>FD + FDIV + NOTF</b>	<b>-45.14</b>	<b>1.61</b>	<b>0.22</b>
	FD	-44.30	2.46	0.15
	FD + FDIV + NCD	-43.15	3.61	0.08
	FD + NCD	-41.78	4.97	0.04

NOTSF was multicollinear with NOTF and therefore not included in the analysis.

**Table 3** Summary of model averaging (GLM) analysis and relative importance of each habitat variable (FD= non-crop flower density, FDIV= non-crop flower diversity, NCD= non-crop plant density and NOTF= total number of trees in flower) while response variable was bee visitation rate (VR).

Response	Habitat variables	Model-averaged Coefficients	Standard error (adjusted)	<i>z</i>	<i>p</i>	Relative importance
VR	FD	0.0028877	0.0006040	4.781	<0.001	1
	FDIV	0.0598033	0.0271557	2.202	<0.05	0.81
	NOTF	0.0015741	0.0013755	1.144	0.25	0.22
	NCD	0.0003819	0.0013614	0.281	0.78	0.12

The relative Importance =  $\sum w_i$ .

**Fig.1** Family wise number of plant species visited by bees. Horizontal axis represents number of plant families which were observed to be visited by bees. Height of the column represents number of plant species (under each respective family) that were visited by bees during the study period

**Fig.2** Relationships between bee visitation rate (VR) and (a) nectar sugar content (SUG), (b) corolla length (LEN) and (c) corolla diameter (DIA). Regression lines were plotted after GLM fitting

**Fig.3** Relationship between nectar sugar content (SUG) and corolla diameter (DIA). Regression line was plotted after GLM fitting

**Fig.4** Relationships between bee inter-tegular distance (ITD) and tongue length (TOL) with (a, c) corolla diameter (DIA) and (b, d) corolla length (LEN). Regression lines were plotted after GLM fitting