Individuals matter: habitat factors and plant traits shape individual-level pollinator interactions in a semi-arid landscape

Diana Michael[1], Kunjan Joshi[1], Shivani Krishna[1]*

[1]Department of Biology, Trivedi School of Biosciences, Ashoka University, Sonepat, India

*Corresponding author (shivani.krishna@ashoka.edu.in)

Running head: Individual-based network

Abstract

Background Plant-pollinator networks are vital for understanding ecological processes influencing reproductive success in plant communities. While species-level pollinator interaction networks are important for predicting community stability, it remains equally crucial to understand individual-level interactions of keystone species in the community. This study examined the role of habitat factors and floral traits in shaping individual-level pollinator interactions of *Maytenus senegalensis*, a dominant native species in the semi-arid Aravalli Hills. We measured flower production, nectar sugar concentration, flower diameter, and external factors such as percentage soil moisture, distance to habitat edge, and density of co-flowering conspecifics to assess their impact on pollinator interactions and reproductive success.

Results We found significant variation in reproductive investment in the form of flower production and a trade-off with reward quality, where plants with higher flower production were found to have a lower nectar sugar concentration. Higher flower production negatively influenced reproductive success, suggesting the likelihood of increased within-plant visitation. *Eristalinus* and *Apis* were the dominant pollinator genera, and overall, Dipterans were found

to play a critical role in maintaining the network stability. The presence of flowering conspecific plants in the neighborhood reduced the pollen deposition, suggesting competitive interactions. Moreover, individual plants were found to show some amount of specialization in their interaction niches. We predict that this could lead to further divergence of interaction niches due to pollinator-mediated competition. Any perturbation to interactions of plants with a high degree of pollinator connectance was found to disproportionately influence the network. **Conclusions** Overall findings suggest that the individual variation in reproductive investment and trade-off with reward quality had an impact on the plant-pollinator interactions and reproductive success. In semi-arid systems, which are undergoing considerable anthropogenic and climatic changes, our study provides insights into individual pollinator interaction niches and the role of microhabitat factors in species persistence within a community.

Keywords: Flower production; Individual-based network; Intraspecific variation; Resource trade-off; Soil moisture

Introduction

The stability of plant-pollinator interactions is crucial for maintaining plant communities [1, 2]. In arid and semi-arid communities, anthropogenic pressures coupled with climatic changes are impacting these interactions [3, 4]. One of the ways these interactions are being affected is via reduced reproductive investment. Montane plant communities exposed to warmer and drier conditions were found to show clear signs of drought stress, including early senescence and diminished allocation to both reproductive structures and vegetative growth [5]. Studies have demonstrated that climate warming negatively affects plant flowering times, disrupting plant-pollinator interactions and, thereby, reproductive success [6, 7].

Variations in soil moisture influenced reproductive investment directly while also modifying the microhabitat for the organisms that interact with plants [8]. Experimental studies revealed that drought-stressed plants produced significantly fewer flowers and reduced nectar per flower, while pollen quantity per flower remained unchanged. Additionally, nectar from drought-stressed plants exhibited a lower sucrose-to-total sugar ratio, although the overall sugar concentration was unaffected [9]. Plants, being sessile and highly responsive to microhabitat conditions, contrast with the mobility and predominantly generalist feeding habits of pollinators. As a result, plants are expected to exhibit greater spatial variability than pollinators. Despite apparent uniformity in the landscape, both flowers and pollinators demonstrate significant heterogeneity, creating a mosaic of distinct local communities. Therefore, examining these variations at the level of individuals is critical.

Plant-pollinator interaction studies in communities typically focus on how interaction patterns vary between species, while intraspecies interactions remain largely unexplored. Few studies have concentrated on plant-pollinator interactions at the individual plant level [10, 11].

Additionally, there is limited research that correlates both abiotic and biotic factors with pollinator interaction patterns at the individual level [12, 13]. Individual plants within populations exhibit phenotypic variation, such as differences in plant and flower size or flowering phenology, which can influence their pollination niche by attracting different pollinator guilds. Plants with similar phenotypes tend to interact with comparable pollinator assemblages [14]. Additionally, the spatial location of a plant within the population could influence its pollinator niche, as it is influenced by microhabitat conditions, local plant community dynamics, and competition, all of which shape the context-dependent outcomes of pollinator interactions [15]. Individual plants respond differently to these microhabitat variations. Hence, investigating these patterns at the individual level allows us to understand their contributions to the overall fitness of the community [16, 17].

The preferences of pollinators vary with floral traits, resulting in diverse interaction niches. For example, bee visitation was influenced by pollen production and flower height, and fly visitation was associated with flower size and number [18, 19]. Notably, bees favoured plants with higher pollen production, while flies were drawn to larger flowers with more nectar [20]. Furthermore, the neighborhood of the plant also plays an important role in pollinator behaviour and interactions. Plants near more attractive species often benefit from 'spillover' effects, where pollinators attracted to the more prominent species also visit the less attractive species [21]. A similar pattern can be expected at the population level, which could increase the visitation rates for the less attractive plants, even if their floral traits alone would not typically draw as much attention. However, when plant individuals compete for pollinator resources, the dynamics can shift. Increased plant density and abundance can also lead to competitive interactions, where plants might block pollinator access or dilute the effectiveness of visitation [22]. Such pollinator-mediated, plant-plant interactions can range from facilitative to

competitive in nature. These dynamics of pollinator behaviors contribute to variation in the deposition of pollen on stigmas, directly affecting reproductive success. Recent studies have shown that individual plant traits, such as floral position and nectar concentration, can impact pollinator foraging patterns. This emphasizes the importance of both spatial neighborhood and floral traits as key determinants of reproductive success in plant species [23, 24].

Here, we examined variation in plant-pollinator interactions at individual-level, their stability, and reproductive success in the semi-arid species *Maytenus senegalensis*. We hypothesized that soil moisture would influence fruit set by affecting the resource allocation to reproduction. Additionally, we predicted that fruit set and conspecific pollen loads would depend on pollinator visitation patterns at the individual level. These patterns were expected to vary with floral rewards and floral traits that contribute to attractiveness and external factors such as the density and composition of neighboring flowering individuals. We predicted that an increase in the number of flowering conspecifics would increase the competition between plants (Fig. 1). To address these hypotheses, we quantified variation in floral investment, traits, and rewards with soil moisture and assessed how this variation impacts plant-pollinator interactions and subsequent pollen loads and fruit set. Furthermore, we analyzed individual interaction patterns to determine the degree of specialization and variability in interaction niches and evaluated their stability against perturbations, which included removing the dominant pollinator groups and individual plants.

Methods

Study area

The study was conducted in the Aravalli ranges in Manethi, located in the Rewari district of Haryana, India (76.403739° E, 28.177195° N) (Fig. 2). The Aravalli ranges are among the

oldest fold mountain systems in the world and are characterized by a semi-arid forest ecosystem. It acts as a boundary separating the desert in the west from the rich lowlands in the east. This region has an annual temperature range of 0-46°C and receives annual precipitation between 400-550 mm. There are around 300 native plant species and 120 bird species documented in the Aravallis. The area has undergone a depletion of groundwater resources, driven by intensified anthropogenic activities in recent years [25].

Study species

The study species, *Maytenus senegalensis* (family Celastraceae), is a native and dominant shrub of the Aravalli ranges. It occurs across Africa, the Arabian Peninsula, Afghanistan, Pakistan, India, Bangladesh, and Spain. The plants are usually 2-6 meters in height and produce small, creamish-white flowers (Fig. 2). *M. senegalensis* relies largely on cross-pollination for reproductive success [26]. In our study area, the flowering period generally occurs between October and November, during which they exhibit a mass flowering pattern.

Habitat factors

A total of 31 plants were randomly selected and geotagged across the study site (Fig. 2). To ensure spatial independence, a minimum distance of 20-30 meters was maintained between individual plants. A 10 × 10 m plot was established around each focal plant. Within each plot, the identity of neighboring plants and their phenological status were recorded to assess the influence of spatial neighborhood on the focal individual. Habitat factors, including soil moisture percentage and distance to the habitat edge, were quantified to assess microhabitat-level variations influencing plant traits.

Soil moisture percentage was measured using a soil moisture meter (Extech 750), a device that is equipped with a 20 cm probe that is inserted into the soil to provide moisture readings as a percentage. Four readings were taken from different directions within a 2 m radius of each focal individual, and the mean was calculated. The overall soil moisture percentage for each individual was calculated by averaging the monthly means measured from the flowering period to the fruit set stage (October to December 2023).

The distance to the habitat edge for each individual was calculated using QGIS software (version 3.34 Prizren) [27]. Co-flowered conspecific density was quantified as the proportion of flowering conspecific individuals within each plot, where a value of 0 indicates the absence of co-flowered conspecifics and values approaching 1 indicate high co-flowered conspecific density.

Floral resources

Floral traits and nectar rewards were measured for each focal individual. Seven floral morphometric traits, including petal length, petal width, flower diameter, flower height, stamen height, anther width, and stamen width, were measured using digital callipers (n = 5 flowers/individual; 25 plants). Flower production was estimated for all focal individuals by counting the number of flowers every 5-6 days using the quadrat method throughout the flowering period. The total flower production per individual was calculated by summing these counts. Nectar sugar concentration was measured in % Brix using a handheld refractometer after removing the flowers from the plant (Cole-Parmer® Brix Analog Refractometer; n = 5-10 flowers/individual; 28 plants).

Plant-pollinator observations

Observations were conducted in 15-minute intervals during the flowering period on all the focal individuals (30-120 minutes/individual over 34 days). In each 15-minute slot, the number of pollinators, the number of pollinator visits, and the identity of the pollinators were recorded. A visit was defined as a pollinator making contact with the reproductive parts of a flower. The majority of pollinators were identified to the genus level (*Apis* - 9.07% and *Eristalinus* - 17.9%). Pollinators were classified into 78 morphotypes, of which 48 were identified to the genus level, 7 to the family level, and 23 to the order level.

Assessment of fruit set and pollen loads

The reproductive success of the plants was assessed by measuring conspecific pollen loads on flower stigmas (proxy for pollination success) and calculating the percentage fruit set. To quantify the conspecific pollen loads, flowers were collected immediately after pollinator visitation observations, and only flowers visited by pollinators were selected (n = 25 flowers/individual; 18 plants). The stigma from each flower was removed and visualized using the stigma squash method with basic-fuchsin jelly [28]. To distinguish conspecific pollen from heterospecific pollen, reference pollen grains from the anthers of *M. senegalensis* were observed before analysis.

The percentage fruit set was determined by tagging mature flower buds (n = 10-15 buds/individual; 31 plants) and monitoring their development every 5-6 days to record their transition from buds to flowers and subsequently to immature fruits. For each plant, this was calculated as the ratio of immature fruits formed to the total number of tagged flowers.

Analysis

All statistical analyses and plot visualizations were performed using R software [29]. We analyzed the sampling completeness of pollinator abundance, genera richness, and pollinator visitation using the iNEXT function [30]. To investigate variation in pollinator interactions among *Maytenus* individuals, we constructed an individual-level interaction network. In this network, plant individuals of *Maytenus* were connected to pollinators, and the number of visits was considered for the connection weights. Network-level and node-level metrics were calculated using the network level () and species level () functions [31, 32]. All the analyses related to networks were conducted using the bipartite package.

We evaluated whether the observed network structure is a result of random processes or exhibits underlying patterns influenced by ecological factors, such as microhabitats or the availability of floral resources. To assess the randomness of the network, we employed the vaznull algorithm to generate 999 null models with constrained connectance and moderately constrained marginal totals [33]. Network-level metrics were extracted from these null models and compared to the metrics derived from the observed network. To quantify the deviation of the observed network metrics from those of the null models, z-scores were calculated, providing a measure of the variation between the observed and randomized networks. The extracted network metrics include weighted connectance, Shannon diversity, niche overlap, linkage density, interaction evenness, weighted NODF, and H2. A brief overview of these metrics is below:

a) Weighted connectance quantifies the proportion of realized interactions in a network. The values range from 0 (no realized interactions) to 1 (all possible interactions fully realized with maximum weights).
b) Shannon diversity measures interaction diversity by incorporating both richness (number of interactions) and evenness (distribution of interaction strengths).

c) Linkage density represents the average number of interactions per plant individual, weighted by interaction strengths, indicating network connectivity; values greater than 0 suggest denser, more connected networks.

d) Interaction evenness describes the uniformity of interaction strength distribution across the network, ranging from 0 (highly uneven distribution with dominant interactions) to 1 (perfectly even distribution).

e) H2 quantifies the degree of specialization in the network, with values spanning from 0 (completely generalized network with random interactions) to 1 (highly specialized network with unique, specific interactions).

f) Weighted NODF extends the understanding of nestedness in networks to account for interaction weights, with values ranging from 0 (random, unorganized interactions) to 100 (strongly nested networks where interaction presence and strength align with nested patterns).

Analyzing the modularity of a network allows us to determine whether the network is divided into distinct groups or modules, within which plants and pollinators interact more strongly with each other than with those in other modules. To analyze the modularity of the network, we utilized the Dormann Strauss algorithm in metaComputeModules() function (99 replications) [34]. To understand the variation between the modules in reproductive success, the Kruskal-Wallis test, followed by Dunn's pairwise comparisons test, was used. The stability of the network against perturbations was assessed by removing the dominant pollinator groups and comparing those network metrics with the full networks and by removal of individual plants [35]. Removal of plants was done using the second.extinct() function, which simulates species loss under two scenarios: (1) individual plants were removed in a random order, and (2) individual plants were sequentially removed based on their degree. We calculated the exponent

of the hyperbolic function curve fitted to the proportion of secondary extinctions when individual plants were removed.

Paired Differences Index (PDI), degree distribution, normalized degree, species strength, weighted closeness, and d were computed to assess interaction differences between individual plants. A brief overview of these metrics is below:-

a) PDI quantifies the degree of specialization of an individual within a network by assessing how its interaction strengths differ from those with other potential partners. It emphasizes asymmetries in interaction strengths, with values ranging from 0 to 1. A value of 0 indicates complete generalization, where interaction strengths are evenly distributed across partners, whereas a value of 1 reflects complete specialization, where a species strongly interacts with only one partner.
b) Degree distribution characterizes the frequency of plants with a given degree (number of connections) in the network.
c) Normalized degree represents the degree of a plant as a proportion of the total possible degree, scaling the plant's connectivity relative to all potential connections. Values range from 0 (no connections) to 1 (connected to all other nodes in the network).
d) Species strength measures the total interaction strength of a plant individual by summing the weights of its interactions with all partners. This metric reflects the individual plant's importance in the network, with values starting at 0 (indicating no interactions). Higher values correspond to greater total interaction strength.
e) Weighted closeness centrality measures the efficiency with which a plant can connect to other plants in the network through shared pollinators, considering both the number of connections and the interaction strengths. Plants with higher weighted closeness centrality are more centrally positioned in the network, indicating stronger and more connections to

other plants via shared pollinators. Lower values suggest fewer shared pollinator interactions between the plants.

Apart from these node-level metrics, we also calculated the interaction niche overlap between plant pairs within the network (niche.overlap function, Schoener's index, spaa package) [36]. A binary incidence matrix with the presence and absence of pollinator genera was used for the calculation of niche overlap values. Niche overlap provides insight into the extent to which a plant shares pollinator resources with other plants in the network.

In our study, binary Exponential Random Graph Models (ERGMs) were used to investigate how various predictors influence the presence and absence of pollinator visits to plant individuals (ergm package) [37]. ERGMs are similar to Generalized Linear Models (GLMs) but are specifically designed for network data. Binary ERGMs employ maximum pseudolikelihood estimation (MPLE) to estimate the effects of predictor variables on the likelihood of connections (edges) in the network. All predictor variables in this analysis were attributed as node-level covariates.

Multiple GLMs were constructed with conspecific pollen loads (median) and percentage fruit set as response variables. Flower diameter, nectar sugar concentration, flower production, soil moisture, distance to habitat edge, and co-flowered conspecific density were considered as predictors (details of model construction are outlined in the analysis section of the additional file). To ensure appropriate model fit, variables were log-transformed where necessary. The model selection process was guided by the Akaike Information Criterion (AIC), with the model that had the lowest AIC being considered the best fit. Additionally, variables were iteratively reduced based on their significance levels, determined through ANOVA (car package) [38].

Generalized Linear Mixed Models (GLMMs) were used to assess the effect of floral traits and habitat factors on conspecific pollen load receipt. Since variation within plants could contribute to some of the observed effects, we used plant identity as a random effect for the analysis. These models were fit using the lmer() function in the lmerTest package [39]. The goodness-of-fit for both GLM and GLMM was evaluated using the simulateResiduals() function from the DHARMa package [40].

Results

Intraspecific variation in floral resources

The relationships among traits such as flower diameter, petal width, petal length, flower height, stamen height, anther width, and stigma width were analysed using principal component analysis (PCA). The first two principal components (PC1 and PC2) accounted for the majority of the variation, explaining 54.8% and 14.09% of the total variance, respectively. Among these traits, flower diameter and petal width had the highest principal component (PC) scores. Given the correlation between flower diameter and petal width (Pearson correlation: cor = 0.78, $p < 0.001$), we included only flower diameter in further analyses. The estimated flower production exhibited substantial variation, ranging from 83,000 to 1,100,000 flowers (coefficient of variation, CV = 63.57%). Nectar sugar concentration levels varied between 3.0% and 6.75% Brix across individuals (CV = 20.47%), while flower diameter ranged from 3.4 to 5.82 mm (CV = 15.75%). CV values indicate that flower production exhibited the highest variability among the traits. We observed that with increasing soil moisture, flower production, flower diameter, and the concentration of nectar sugar also showed an increasing trend. However, these were not statistically significant (Additional file: Fig. S1, Table S1).

To investigate potential trade-offs in resource investment, we examined the relationships between flower production, flower diameter, and nectar sugar concentration. We observed a negative correlation between flower production and nectar concentration (Pearson correlation: cor = -0.49, $p = 0.007$). On the other hand, flower diameter was not related to changes in nectar concentration or flower production (Fig. 3a, Additional file: Table S2).

Plant-pollinator interaction structures

Sampling completeness values for the abundance of pollinators and the interactions were found to be greater than 98%, indicating sufficient sampling of the individuals (Additional file: Fig. S2). A total of 7,458 pollinator visits were recorded for the focal plants, with visits dominantly from the pollinator orders Diptera and Hymenoptera. The most dominant visitors were from the genera *Apis* (Hymenoptera) and *Eristalinus* (Diptera), accounting for 35.36% and 22.45% of the total recorded visitation, respectively (Fig. 3b). When comparing the observed networks to random assemblages, all the null model metrics differed considerably from the observed network (Additional file: Fig. S3, Table S3). All network metrics, except for H2, exhibited negative z-scores, indicating that their observed values were lower than the predicted averages. In contrast, H2 displayed a positive z-score, suggesting that its observed value exceeded the expected value from the null models. This non-random assemblage pattern was further analysed using ERGMs to examine the attributes that contribute to it. Binary ERGMs suggest that flower production, distance to the habitat edge, and flower diameter negatively influenced the presence of a connection with a pollinator genera, while soil moisture had a positive effect. Nectar sugar concentration and co-flowered conspecific density were not found to have an effect (Table 1).

To evaluate the impact of the dominant insect orders on network structure, we also constructed networks excluding each of them individually (Additional file: Fig. S4, Fig. S5, Table S4). The specialization index (H2), weighted NODF, and linkage density exhibited substantial variation between the full network and the network without Diptera, with differences exceeding 20%. The removal of Diptera increased specialization and lowered linkage density and weighted NODF. In contrast, these metrics remained comparable between the full network and the network without Hymenoptera. Weighted connectance was 25% higher in the absence of Hymenoptera compared to the full network. The PDI values indicated that individual plants exhibited a high degree of specialization, with values ranging between 0.92 and 0.98. The mean degree distribution was 7.35, and the normalized degree value was 0.23. Species strength range varied from 0.12 to 3.28. 5 individual plants were identified as key contributors to the network's structure (values higher than 2). The mean weighted closeness centrality value of plants was 0.03. The niche overlap values of plants differed significantly, with a few individuals exhibiting low niche overlap (< 45%), indicating minimal sharing of pollinators (One-sample Wilcoxon test: V= 59, p = 0.02, Fig. 4; Additional file: Table S5). We assessed the correlations between species strength and floral traits, as well as niche overlap and floral traits, and found no relationship (Additional file: Fig. S6, Table S6).

The analysis of the observed network revealed a low modularity value of 0.227, with one large module containing most plant individuals and two smaller modules (Additional file: Fig. S7a, Fig. S7b). The robustness values were 0.737 for random removal and 0.612 for degree-based removal of individual plants. The exponent values were 3.72 for random removal and 1.83 for degree-based removal. Overall, the results show that the network is moderately resilient to individual plant removal, and the removal of plants with the highest interactions might influence the stability of the network (Additional file: Fig. S7c, Fig. S7d).

Intraspecific variation in reproductive success

The median conspecific pollen loads across individuals ranged from 13 to 431 (SD = 99.21). GLM analysis showed that median conspecific pollen loads were not affected by floral traits such as flower diameter, flower production, nectar sugar concentration and habitat factors (Fig. 5, Table 2). The standard deviation of intra-individual pollen loads exhibited considerable variability, with certain individuals displaying minimal variation in pollen load while others showed greater intra-individual variation. Generalized Linear Mixed Model (GLMM) analysis indicated that co-flowered conspecific density had a marginally negative effect on conspecific pollen loads. The other floral traits and extrinsic factors did not affect the conspecific pollen loads within individual plants. However, the random effect of individual plants accounted for a substantial proportion of the variability in conspecific pollen loads than the fixed variables (Additional file: Fig. S8, Table S7).

Fruit set percentages ranged from 0% to 100% (SD = 33.24), with most plants exhibiting low fruit sets. Flower production was found to have a significant negative influence on the percentage fruit set, and soil moisture showed a marginally negative effect (Fig. 5, Table 2). The number of pollinator visits positively affected the percentage fruit set, while pollinator abundance showed a marginally negative influence on conspecific pollen loads (Additional file: Fig. S9, Table S8). There was considerable variation in the percentage of fruit set between the network modules ($\chi^2 = 33.81$, df = 2, $p < 0.001$). Post-hoc Dunn's tests revealed differences in reproductive success between Module 1 and Module 2 ($p < 0.001$) and between Module 2 and Module 3 ($p < 0.001$). However, no differences were found between Module 1 and Module 3 (p = 0.33).

Discussion

Our study investigated the relationships between floral traits, habitat factors, and plant-pollinator interactions in a semi-arid region, revealing substantial inter-individual variation in flower production and a trade-off between flower production and nectar sugar concentration. Soil moisture levels did not have a direct effect on floral traits or fruit set. Flower production negatively influenced pollinator interactions, thereby reducing reproductive success. While flower diameter, soil moisture, and co-flowered conspecific density influenced the structure of pollinator interactions, these factors did not affect conspecific pollen loads or fruit set. Additionally, while individual plants occupied overlapping pollinator niches, network analyses indicated a degree of specialization likely driven by competition avoidance. Furthermore, stability analyses showed that Dipterans were critical for network structure, and simulated plant removals revealed that the loss of highly connected plant individuals had a greater impact on individual-level network resilience.

Resource allocation patterns are largely genetically determined within plant species but can be influenced by environmental conditions [41]. Specifically, plants in resource-limited environments were often found to exhibit selective resource allocation strategies that enhance reproductive success [42, 43]. However, the extent to which microhabitat variations impact plants and their flower visitors was variable [12, 15, 17]. In this study, conducted in a semi-arid region, we hypothesized that *Maytenus senegalensis* individuals would exhibit a reduction in floral traits with decreasing soil moisture levels. However, we found that soil moisture variation had little impact on floral traits, but there was considerable intraspecific variation in floral traits. Individuals with higher flower production tended to have lower nectar sugar concentration, while those with fewer flowers exhibited higher nectar sugar concentration. Flower production varied negatively with nectar sugar concentration, suggesting a trade-off in

421 the allocation of resources between these traits [44, 45]. This could be expected when the
422 energetic costs involved in the production of nectar sugars are higher than the costs of
423 producing flowers [46, 47]. Such trade-offs that are indicative of quality (reward) and quantity
424 (number of flowers) allow the maintenance of the combined attraction of the plant for the
425 pollinators [48, 49]. Overall, we also found that there was higher variation at the individual
426 level in flower production, suggesting higher plasticity in this trait [50, 51].
427
428 Pollinators that are abundant in the local habitat and visit multiple plants are known to be
429 important for the stability of the network [52]. In our study, the exclusion of pollinators from
430 Diptera resulted in a more specialized network with lower nestedness values and linkage
431 density, indicating a reduction in generalization and connectivity. Such a pattern suggests that
432 Dipterans are critical for *M. senegalensis* in maintaining network generalization. On the other
433 hand, weighted connectance exhibited significant increases following the removal of
434 Hymenoptera and was relatively unaffected by the removal of Diptera. In a network without
435 Hymenopterans, pollinator interactions were found to increase, this could potentially be driven
436 by reduced interspecific competition between pollinators and niche displacement by other
437 pollinator groups. These findings indicate that the functional role of Hymenoptera within the
438 network can be partially compensated by other pollinators.
439
440 Our observed network differed from the randomly generated networks and was found to exhibit
441 a higher degree of specialization. The higher specialization is likely driven by ecological factors
442 such as pollinator preferences and resource partitioning [53]. ERGM analyses suggest that traits
443 such as flower production and flower size are critical in determining the likelihood of a
444 particular type of pollinator visiting the plant. A couple of broad patterns in pollinator visitation
445 were seen in our data. Plants visited by pollinators from multiple genera were found to have

flower production or nectar sugar concentration that is slightly higher than others, whereas plants visited by pollinators from fewer genera showed intermediate levels of both traits. These observations suggest a possible relationship between genera richness and floral traits, which requires further consideration.

In our study, individual plants were found to exhibit a high degree of specialization (high PDI values). The analysis showed that not all plants were connected within the network through shared pollinators. Some plants exhibited higher species strength values, and these individuals were found to have slightly higher nectar sugar concentrations, low flower diameter, and flower production than other plants. However, these trends are only indicative, as there were no statistically significant relationships with floral traits. Ten plant individuals within the network were found to have a low niche overlap (<45% overlap), pointing towards resource partitioning, possibly reducing competition between the plants [54]. The exponent values from the random simulation scenario indicate that the extent of redundancy in pollinator interactions was higher during initial removals, hence, the network remained stable, which was then followed by an abrupt collapse. On the contrary, the lower exponent values of degree-based removal suggest a collapsing trend from the first few removals itself. These patterns are similar to previous findings, where the loss of highly connected plants accelerated network collapse [10, 16]. Together, these results highlight the interconnectedness between individual-level variation in reproductive traits and network-level stability. Conserving highly connected plants is essential not only for maintaining network robustness but also for preserving the ecological processes that support reproductive success within the system.

The floral traits of plants are known to influence the modularity of plant-pollinator networks at the species level [55, 56]; however, this may not always hold at the individual level. The

network in our study resulted in three modules. Within these modules, plants in one of the smaller modules (module 3) were found to be from higher soil moisture levels and were visited by Dipterans. This may be linked to higher flower production in plants found in areas with elevated soil moisture. However, previous studies reported that Dipterans preferentially selected flowers based on size or nectar availability rather than flower production [18, 20]. Plants in the other smaller module (module 2) were surrounded by fewer flowering conspecifics, and their visits were largely from Hymenopterans. This pattern could be due to the change in foraging preferences of pollinators with the change in spatial distribution of floral resources and also to possibly avoid competition [57, 58]. Previous studies have demonstrated that modules dominated by abundant and common species tend to exhibit higher reproductive success [16, 59]. Our study revealed variation in reproductive success among the modules, where one of the smaller modules (module 2) had a significantly higher percentage of fruit set compared to the other two modules in the network.

Co-flowered conspecific density and pollinator abundance affected conspecific pollen loads negatively. This finding supports our hypothesis that an increase in conspecific density intensifies competition among individuals. Contrary to our predictions, floral traits and habitat factors did not influence the conspecific pollen loads considerably. This lack of effect may be due to pollinator saturation or stigma saturation. A study on *Medicago sativa* in the dry grasslands of Gansu Province, China, found that pollen limitation was the major reason for the lowered reproductive success of the plant [60]. Flower production exhibited a significant negative effect on the percentage fruit set, likely due to resource allocation trade-offs, where increased flower production reduced the flower quality [61, 62]. A study on *Senita cacti* in Arizona showed that higher flower production lowered the pollinators-to-flower ratio and caused fruit abortion [61]. Soil moisture percentage exhibited a marginally significant negative

effect on the fruit set. We predict that this is linked to the observed resource trade-off between flower production and nectar concentration. Beyond moisture, soil nutrients generate considerable spatial heterogeneity within habitats [63, 64], and incorporating the combined effects of nutrients and water availability would be crucial for future studies. Given the limited water resources in our study area, we focused on the impacts of variations in soil moisture. Furthermore, examining seasonal transience in individuals' pollinator niches would be critical to understanding variations in plant-pollinator interactions.

Conclusions

Our study shows the intricate links between floral traits, habitat factors, and plant-pollinator interactions in shaping the structure and resilience of ecological networks. Key findings include the critical role of Diptera in maintaining network robustness for *M. senegalensis* and the significant trade-offs between flower production and nectar sugar concentration. Flower production and conspecific flowering neighborhood negatively influenced the reproductive outcomes, suggesting the role of pollinator-mediated competition. Future studies could test if such competition could lead to further diversification of the existing interaction niches. Overall, these findings provide valuable insights into the mechanisms driving individual-level plant-pollinator interactions and the importance of preserving keystone individuals to support ecosystem resilience in resource-limited environments.

Figures and Tables

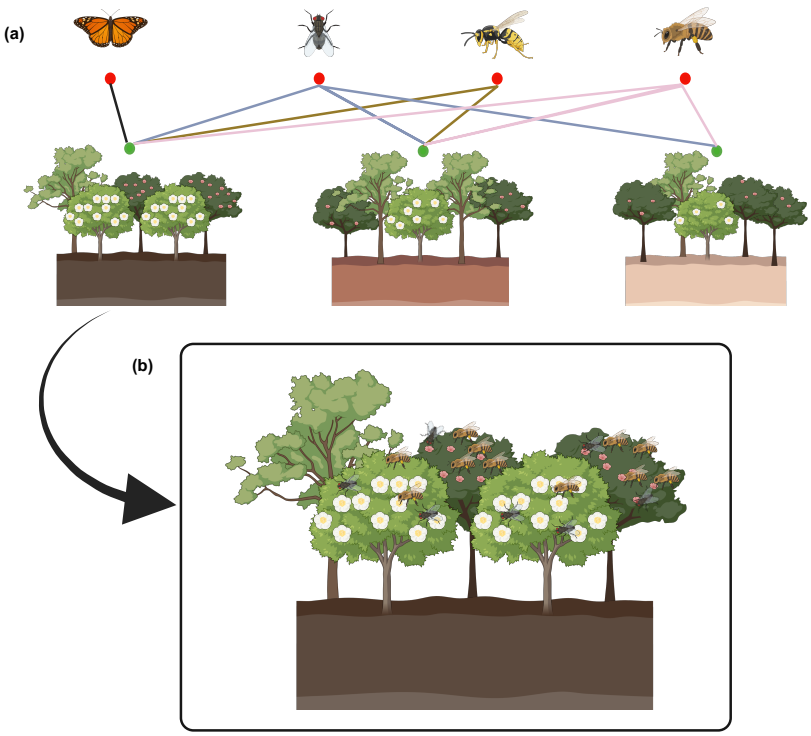


Fig. 1 Conceptual diagram providing an overview of our study. (a) The potential influence of microhabitat-level variation (represented as different colored soil: darker coloration indicating relatively higher moisture region) on variation in floral traits, species diversity, and reproductive investment. The subsequent effects of such variations on the pollinator-mediated interactions (Bipartite network: red nodes indicating pollinators, green nodes indicating individual plants). (b) Within each microhabitat, plants may experience facilitation or competition for pollinators. The diagram illustrates a microhabitat containing both conspecifics and heterospecifics, highlighting the possible role of competition between plants for pollinator access.

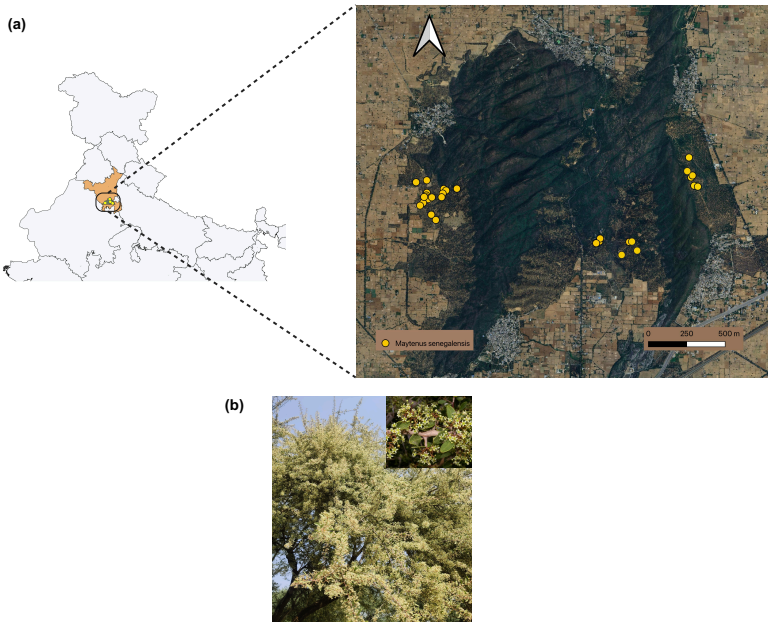


Fig. 2 (a) Study location: Aravalli Hills, Manethi, Haryana, along with a satellite image of the Aravalli Hills in Manethi, where *Maytenus* individuals are marked as yellow dots according to their respective locations. (b) Image of a *Maytenus senegalensis* plant, with an inset showing the flower.

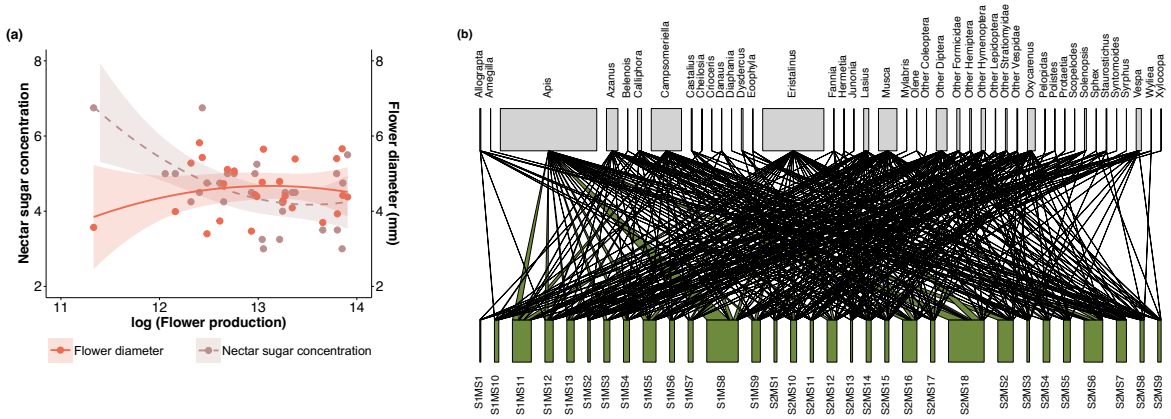


Fig. 3 (a) Scatter plots depicting the variability in nectar sugar concentration (% Brix) and flower diameter with increasing flower production in *M. senegalensis* individuals. Each dot represents an individual plant, and the dashed line indicates the significant relationship. (b) Weighted bipartite network showing the interactions between pollinator species (grey) and

Maytenus senegalensis individuals (green). The links between nodes represent flower visitation interactions, with the width of the links corresponding to the number of visits recorded. The pollinators mentioned as 'Other' are the morphotypes that could not be identified until the genus level (e.g., Other Coleoptera).

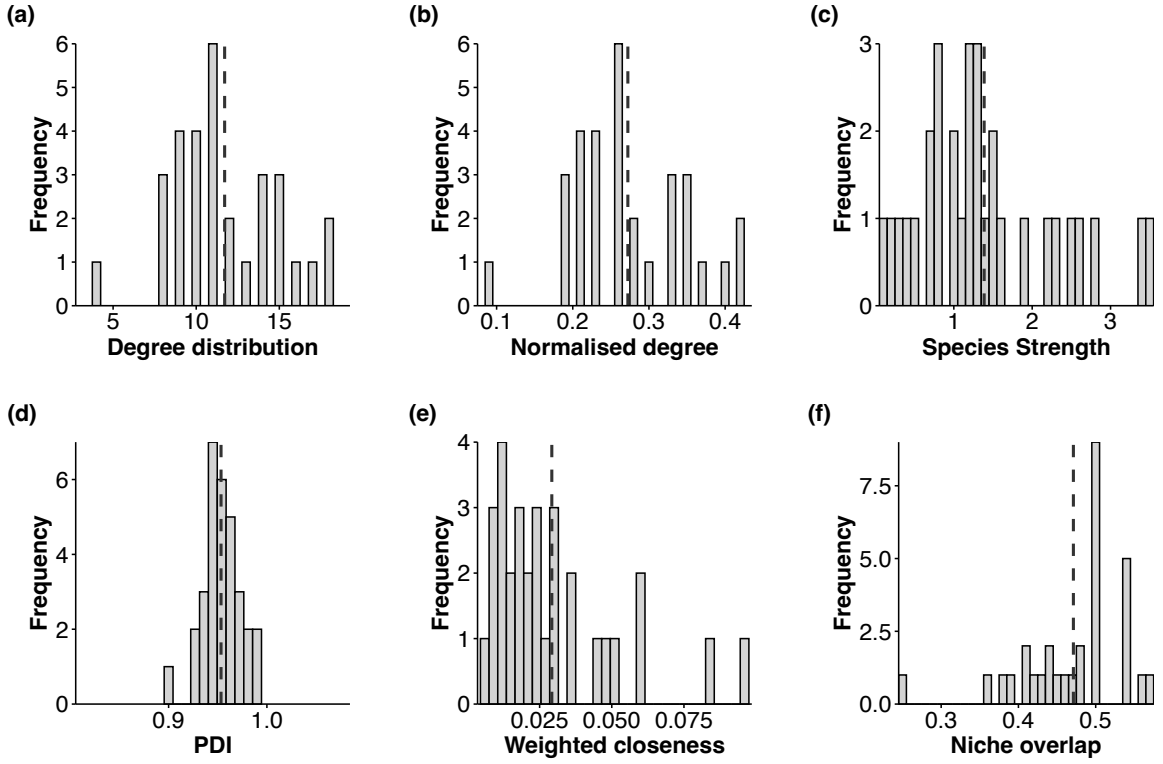
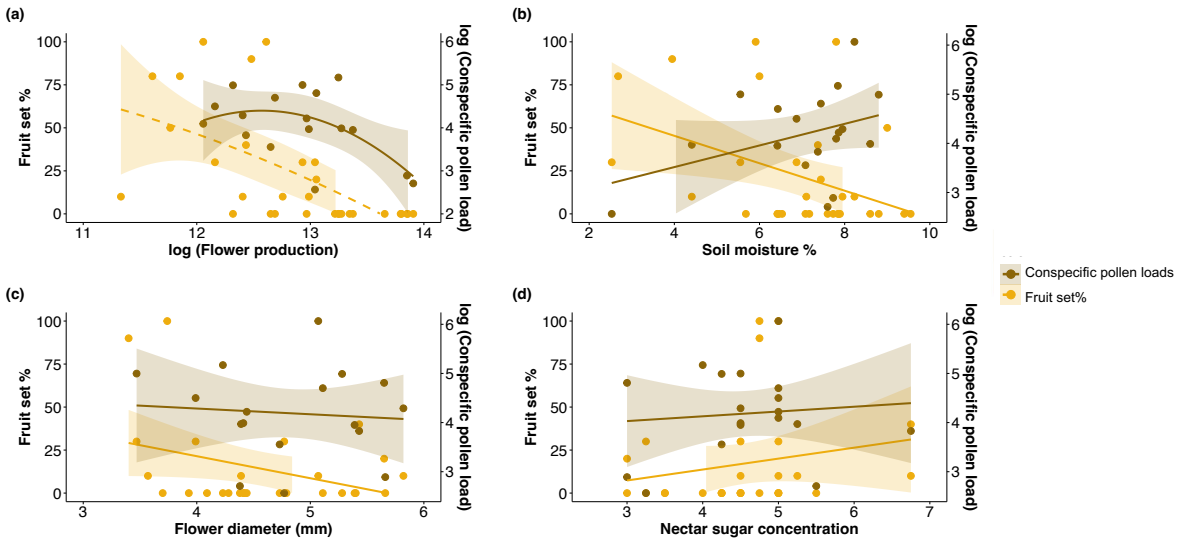


Fig. 4 Bar graphs depicting the plant-level metrics from the network. Each bar represents the frequency of plants with the corresponding metric, with the dashed line indicating the mean value of the metric. Network metrics include: (a) Degree distribution, (b) Normalized degree, (c) Species strength, (d) Paired Differences Index (PDI), (e) Weighted closeness, and (f) Niche overlap (Schoener's index).



550 **Fig. 5** Scatter plots illustrating the variability in reproductive success (conspecific pollen loads
551 and fruit set%) of individual plants, explained by (a) flower production, (b) soil moisture%, (c)
552 flower diameter, and (d) nectar sugar concentration (% Brix). Each point represents an
553 individual plant, and the dashed line indicates the significant relationship.

554

555 **Table 1** Summary of the binary exponential random graph models (ERGM) showing the effects
556 of individual plant floral traits and extrinsic factors on the structure of the bipartite plant-
557 pollinator network. Estimates of predictor variables with significant effects indicate the
558 expected change in the presence of plant-pollinator interactions given a one-unit change in that
559 predictor variable. Significant values ($p < 0.05$) appear in boldface.

	Predictor variables	Estimate	Std.Error	z value	p-value
Edges	Nectar concentration	0.01	0.04	0.39	0.68
	Flower diameter	-0.14	0.04	-3.04	**0.002**
	Soil moisture	0.29	0.05	5.62	**<0.001**
	Flower production	-0.22	0.05	-4.27	**<0.001**
	Co-flowered conspecific density	0.03	0.04	0.69	0.48
	Distance to habitat edge	-0.24	0.04	-4.96	**<0.001**

Table 2 GLM of percentage fruit set and median conspecific pollen loads in response to floral traits (flower production, nectar sugar concentration, flower diameter) and extrinsic factors (soil moisture%, co-flowered conspecific density and distance to habitat edge) of *M. senegalensis* plants. Significant values ($p < 0.05$) appear in boldface.

Response variables	Models	Predictor variables	Estimate	Std. Error	t value	p-value
Fruit set%	Model 1	Nectar Concentration	-0.08	0.29	-0.3	0.76
		Flower diameter	-0.31	0.33	-0.95	0.35
		log (Flower production)	-1.29	0.44	-2.9	**0.007**
	Model 2	Soil moisture	-0.31	0.16	-1.97	**0.05**
		Distance to habitat edge	0.002	0.001	1.36	0.18
	Model 3	Co-flowered conspecific density	-1.55	1.17	-1.32	0.19
Conspecific pollen load	Model 4	log (Flower production)	-0.95	0.47	-1.98	0.06
		Nectar Concentration	-0.08	0.25	-0.31	0.75
		Flower diameter	-0.17	0.34	-0.49	0.62
	Model 5	Soil moisture	0.22	0.14	1.57	0.13
		Distance to habitat edge	0.0002	0.001	0.16	0.87
	Model 6	Co-flowered conspecific density	-1.57	0.72	-2.16	**0.04**

Declarations

Ethics approval and consent to participate

This work did not require ethical approval.

Consent for publication

Not applicable.

Availability of data and materials

Datasets will be available from the corresponding author on request.

Competing Interests

The authors have no conflict of interest.

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Author contributions

D.M.: Methodology, Data curation, Formal analysis, Investigation, Visualisation, Writing-Original draft, Writing-review & editing. K.J.: Investigation, Writing-review & editing. S.K.: Methodology, Conceptualization, Formal analysis, Funding acquisition, Investigation, Supervision, Writing-review & editing.

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