

Plant a Rose Today to Conserve the World's Most Important Solitary Bee

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Abstract

Pollinator conservation is a global priority. Efforts are taken to restore pollinators by improving flower resources, a crucial driver of pollinator diversity and population. It gave a facelift to gardening and landscaping supply chains, which introduced lists of bee-friendly plants and bee hotels, yet, desirable results seem distant. One shortcoming of the present schemes is the lack of a cohesive planning for nesting opportunities and nesting provisions for the wild solitary bees, the crucial pollinators of crops and wild plants. We tested whether the world's most favourite ornamental plant, Rose (*Rosa chinensis* Jacq.) – a hitherto unlisted bee-friendly plant – can aid conserving leafcutter bees, which require fresh leaves for constructing nest cells. We surveyed 2,360 Rose plants in 136 sites in rural and urban places and lowlands and highlands of south (8°N – 12°N) and northeastern India (26°N-27°N) for the characteristic notches the bees leave on foraged leaves. Potted Rose plants were sprayed with the contact pesticides to study the effect of pesticide on bee foraging of leaves. Broods constructed by the Rose leaves were reared to examine the brood success rate. About a quarter of all the Roses surveyed had the notches of leafcutter bees on the leaves. However, the proportion of cut Roses varied considerably among and between sites. Bees used Roses heavily in cities and lowlands over villages and highlands. Selection of plants was negatively associated with pesticide treatment. Brood success rate was 100%. Rose flowers do not support bees, but Rose leaves do. We recommend Rose plants in pollinator conservation and restoration schemes.

Introduction

Pollinators, globally, are declining^{1,2}. Many human activities have been suggested as the reasons for this precarious global phenomenon²; land-use change and the resulting decline of flowers and nesting opportunities have been suggested as the key reasons^{2,3}. This has prompted pollinator habitat restoration efforts, at least in the biodiversity-poor and developed countries^{4,5}. However, most of the efforts to restore habitats – either agroecosystems or urban places – have been directed towards enriching flower density and flower resources^{5,6}. This has opened up a booming business of bee-friendly plants and widespread use of such plants by the citizen scientists and laymen in public places and gardens^{7,8}. For example, in the UK, Wyevale, a garden centre chain, fetched an annual revenue of about GBP 311 million in 2015 alone by selling bee- and pollinator-friendly plants and landscaping gardens and properties using such plants⁹. However, a study⁹ found that a lion's share of the forb plants recommended by the garden chains is futile for attracting pollinators. This further prompted researchers to identify promising wild herbaceous plants as forb species to use in agri-environment schemes and urban landscaping¹⁰.

Nevertheless, restoring habitats of pollinators by enhancing nesting opportunities and nesting provisions of wild pollinators received little attention^{5,11,12}. It is also unclear whether any of the poor recommendations in the 'lists of bee-friendly plants' that Garbuzov and Ratnieks⁷ and Garbuzov et al.⁹

analysed or plants that have not even been recommended as a bee-friendly plant could be suitable as a non-floral resource in pollinator habitat restoration projects.

Several promising bee pollinators of crops require non-flower parts of plants for their biological and ecological processes¹²⁻¹⁴. Leafcutter bees, for instance, require leaf fragments for constructing brood chambers¹⁵ (Fig. 1). Our previous studies¹³⁻¹⁶ suggest that the leafcutter bees have a preference for plants of certain plant lineages to forage leaf fragments. Megachilidae is a cosmopolitan solitary bee family, having over 4100 species worldwide¹⁷; the genus *Megachile*, which comprises of leafcutters, has about half of these species and is globally distributed¹⁷. A recent study suggests that they can be even found at higher altitudes above 2500 m asl¹⁸. Many of these leafcutters are key pollinators of several commercial crops, such as Alfalfa¹⁹. Some of them have been managed and introduced to countries for managing crops, such as *Megachile rotundata*¹⁹.

Leafcutters construct nest tubes in cavities in structures including man-made structures above ground¹⁵ (Fig. 1). This has prompted the widespread sale and use of bee hotels (=trap nests) for the management and conservation of leafcutter bees in Europe and North America, despite the absence of evidences for their efficiency²⁰. The study by Maclvor and Packer²⁰ suggests that they support fewer number of native leafcutter bees than that was targeted for, and many of their broods have been lost to parasitoids. Nevertheless, the bee hotels can only provide holes for constructing nest tubes. Leafcutter bees require suitable fresh leaves for collecting leaf discs to construct brood chambers inside bee hotels or other suitable cavities. A pilot study in controlled conditions recently showed that the brood success in leafcutter bees can be driven by the nesting material¹⁴. Although we have some empirical studies for the leafcutter bees' leaf foraging plants^{13,16,21}, no recommendations have so far been made for the practitioners.

In the present research, we assess the potential of Rose plants as bee-friendly plants in the urban landscaping and agri-environment schemes. By surveying the Rose plants of seven latitudinal points – 8°N to 12°N in south India and 26°N to 27°N in northeast India, two altitudinal ranges along the Western Ghats biodiversity hotspot and the central Himalayas, and two types of landscapes – urban and rural, the study asked the following questions. First, are the Rose plants used by the leafcutter bees for foraging leaves? Second, is the use of Roses by the leafcutter bees limited by landscape, latitude, altitude, and pesticide use? Third, is the plant selection by the bees driven by plant traits, such as leaf size, plant height, and variety of Rose? Fourth, what is the rate of brood success for the broods sheathed by the leaf fragments of Roses?

Roses that belong to Rosaceae in the Rosid clade has 150 species and are cultivated worldwide²². However, China Rose (*Rosa chinensis* Jacq.) and its breeds, such as tea roses, have been brought to most of the countries in the world as ornamental plants²³. Today over 30% of the total ornamental plant market is accounted by the Rose plants. They hold great symbolic and cultural value, and are used for culinary and scent production purposes²⁴. Leafcutter bees are often considered as major pests of

Rose²⁵⁻²⁷. They can severely defoliate plants as they return to the same leaves for more leaf cuttings (Supplementary Video S1). Often, pesticides have been recommended for managing them²⁷. On the other hand, evidences suggest that leafcutter bees are more susceptible to pesticide exposure as they lack enzymes to detoxify the chemical²⁸.

Results

Out of the 2360 Roses surveyed, 610 plants (26%) had the notches of leafcutter bees. However, the proportion of cut plants in sites varied tremendously by landscape type, altitude type, and latitude type. The proportion of cut plants of northeast ($22\pm 30\%$; $N=406$ roses in 10 sites) and south India ($29\pm 30\%$; $N=1954$ roses in 108 sites) was not different (0.13 ± 0.12 , $Z=0.99$, $P=0.3$), despite a greater variability was found among sites of these two regions. It suggests that the Roses are perceived similarly by the bees in these two regions.

When an average of 15% of the Roses ($N=362$) had cuts in high altitude sites, an average of 35% of the surveyed Roses ($N=1827$) in low altitude sites had cuts; Roses of very high-altitude sites (>1100 m asl) had hardly any cuts ($N=171$). The difference in the proportion of cut Roses in three altitude types was significant ($F_{2,2357}=72.8$; $P<0.005$). When an average of 18% ($\pm 38\%$; $N=1331$) of the Roses in rural sites was used by the bees, an average of 36% ($\pm 38\%$) of the Roses in urban sites ($N=1029$) was used by the bees (0.93 ± 0.09 , $Z=9.71$, $P<0.005$). Plants that have a history of pesticide treatment were less preferred ($9\pm 15\%$) over the plants that had never been exposed to pesticides anytime in the past ($27\pm 26\%$; -0.69 ± 0.24 , $Z=-2.95$, $p<0.005$).

Drivers of plant selection by the leafcutter bees

Leaf length of the Roses was different for the sites of seven latitudinal points ($F_{5,2353}=30.48$, $P<0.005$) and six altitudinal bands ($F_{5,2354}=68.94$, $P<0.005$). The difference was primarily due to the Roses of highest latitudinal points (27°N) and highest altitude (above 1100 m asl.), where, the Rose leaves were larger and broader (Fig. 2).

Our predictive Models suggest that the probability for Roses being used for foraging leaves was driven by pesticide application, altitude, landscape type, sites (represented by latitude), leaf size, and plant height (Table 1). The Model with the interaction has accumulated for only three percent variation on the Model that had the factors represented by single effects. The final single-effect Model predicted 89% of the total variation encountered in the study ($R^2_{\text{marginal}}=0.89$). The selection of plants was negatively affected by pesticide application on Rose leaves and increasing altitude. In south India, bee activity on Roses was lower above 800 m asl. In northeast India, the bee activity was present up to an altitude of about 1100 m asl. The bee activity was higher on urban landscapes than on rural landscapes. Leaf length was not a driver of leafcutter bee's selection of Rose plants. In fact, the leaf length was negatively associated to plant selection (Table 1).

The number of cuts per leaf (range=1-7) on cut plants was independent of the leaf length (0.02 ± 0.03 , $t=0.43$, $P=0.6$). The number of cuts per leaf was used as the proxy for the level of dependence, which, however, was not driven by most of the fixed variables included in the study, but latitude. Only about 6% of the total variation in the number of cuts on the leaves was explained by the final model (Table 1).

Table 1

Parameter estimates from generalised linear models testing responses of Rose plant usage and number of cuts on leaves. The intercept is the estimate of non-pesticide plants of rural landscape, altitude below 100 m asl, and latitude 8°N. Leaf length and plant height were covariates in the model. * Indicates $p < 0.05$. ** Indicates $p < 0.005$. *** Indicates $p < 0.0005$.

Fixed effect	Cut plants		Number of cuts/ leaf	
	β [SE]	Z-value	β [SE]	Z-value
Intercept	-0.61 [0.38]	1.6	0.12 [0.26]	0.46
Pesticide usage (used)	-1.32 [0.29]	-4.43**	-	-
leaf length	-0.20 [0.06]	-3.18**	0.03 [0.03]	0.68
Landscape (urban)	0.93 [0.17]	5.38***	0.11 [0.08]	1.27
Plant height	1.11 [0.13]	8.51***	-	-
altitude (100-300 m asl)	-0.42 [0.47]	-0.88	0.26 [0.30]	0.87
altitude (300-600 m asl)	-1.24 [0.41]	-2.98**	-0.23 [0.34]	-0.66
altitude (600-800 m asl)	-1.35 [0.39]	-3.45***	0.10 [0.19]	0.5
altitude (800-1100 m asl)	-5.61 [1.17]	-4.79***	-0.24 [0.28]	-0.83
altitude (>1100 m asl)	-	-	-	-
latitude (9°N)	-1.34 [0.38]	-3.51***	0.25 [0.25]	0.96
latitude (10°N)	-1.55 [0.27]	-5.71***	0.39 [0.16]	2.43*
latitude (11°N)	-1.40 [0.25]	-5.57***	-0.04 [0.13]	-0.31
latitude (12°N)	-0.68 [0.55]	-1.22	0.10 [0.15]	0.61
latitude (26°N)	0.65 [0.56]	1.15	0.10 [0.34]	0.3
latitude (27°N)	6.42 [1.22]	5.27***	0.82 [0.35]	2.34*

Effect of Rose variety on plant selection

In Guwahati city, about 73% of the total sampled Roses (N=55) had the notches of leafcutter bees on the leaves. While the proportion of cut Roses for magenta (80%), pink (81%), and red (88%) were very high, only about 30% of the white roses were used by the bees ($F_{3,51}=4.44$, $P<0.01$), despite the fact that the lengths ($F_{3,51}=0.12$, $P=0.9$) and widths ($F_{3,51}=0.009$, $P=0.9$) of the leaves of these four varieties were not different.

Brood Success

Brood success for all seventeen cells was high. They took 20 to 27 days to complete the development, but all emerged into the leafcutter bees. Although our methodology does not allow us to relate high brood success to the plausible parasitism by the parasitoids, allow us to relate it to the leaf type. Rose leaves have not hampered brood success.

Effect of pesticide application on plant and leaf selection

Megachile lanata was responsible for cutting the leaves for the Roses that we used to study the effect of pesticide on plant and leaf selection. The bee foraged leaves only from control leaves of three control plants. The bee visited control plants for four straight days after pesticide treatment. Neither the pesticide-treated leaves of control plants nor the pesticide-treated leaves of treated plants were used by the bees.

Discussion

We tested whether the world's favourite ornamental plant, Rose (*Rosa chinensis* Jacq.), can help conserve the world's most important and propagated solitary bee pollinators, leafcutter bees, in the present investigation. The answer to this is that, yes, but with an epilogue, do not spray pesticides on the plants! This well-replicated study in various parts of India suggests that a range of plant-specific, landscape-related, and management factors predict the bees' use of Rose plants as a leaf-forage resource. For instance, the bees used Roses well in lowlands and urban places than in very high lands and rural places. The pesticide use negatively affects the bee's use of Rose leaves. Leaf size or plant variety are not important drivers of plant selection by the bees.

There are reports that pesticides have a negative effect on bees^{3,29}. It is postulated that the solitary wild bees are worst affected than the honey bees^{30,31}. However, little evidence has come from studies for the routes other than the flowers the bees exposed to pesticides³². Our findings report that the Rose plants subjected to periodical pesticide treatment are less preferred by the bees, and this strongly suggest that the leafcutter bees can experience and expose to pesticides through the leaves. Albeit a pilot study, we report the first experimental proof that the bees avoid pesticide-treated foliage for foraging leaf fragments. The bees abandoned our experimental plants after four days of visits and foraging leaves from control plants. We limited our pilot study with a contact pesticide, which degrades faster in the environment. A targeted study should explore the response of the bees to a range of new-generation

pesticides, neonicotinoids, biopesticides, and systemic pesticides to make recommendations for safer pesticides for the ornamental plant industry, which perceive leafcutter bee as a major defoliator and “pest”^{25–27}. Moreover, it is shown that *Megachile rotundata*, the first successfully propagated managed solitary bee, has no mechanism to detoxify pesticides and therefore is highly sensitive to pesticide exposure^{28,33}.

The bees explored the Roses in urban environment more than rural environment. Urbanization is considered as a threat to biodiversity and certain biotic functions³⁴. However, the response of bees to urbanization has been often depicted positive by recent studies^{35–38}, and our findings support it. Leafcutter bees are cavity nesters and use almost all unpredictable sites for constructing nest tubes^{39,40}. Since they are above-ground nesters, they are less affected by the soil, which is often polluted and compacted in urban places and agricultural landscapes^{11,41}. Urban places are likely to provide better nesting and foraging opportunities for the bees^{35,42,43}. Plants belong to Rosaceae, and *Rosa* in particular predominate in the list of ornamentals in global cities^{44–47}. This suggests that urban places might be a heaven for the leafcutter bees. They use plants in Rosid clade for both foraging and leaf resources^{13,16,21}.

Leafcutter bees hardly used Roses cultivated above 1000 m asl. This suggests that their distribution might be driven by the altitude in India, if not everywhere¹⁸. In northern Arizona, a greater diversity of Megachilidae and *Megachile* spp is reported above 2000 m asl¹⁸. Southwestern USA is a heaven for the *Megachile* spp⁴⁸. In northeast India (Darjeeling), the senior author of the present study had surveyed Roses for three years in altitudinal bands ranging from 150 m asl to about 2000 m asl in 2018, 2019, and 2021, in which Roses had notches on leaves for about 1000 m asl in all the surveys. In south India, Roses were surveyed in 2018 and 2020 at certain places at 12°N (Kasaragod district). In both sites, the Roses that had leaf cuts had cuts every year of sampling (pers. observ.). As part of another investigation, the senior author of the present study (PAS) was monitoring flower visitors of wild, crop, and ornamental flowering plants in the Darjeeling hills for over three years. However, species belonging to Megachilidae were totally a miss on the flowers above 1100 m sl. In *Amomum subulatum* (large cardamom) – a cash crop and a major nectar source for the bees and birds in Darjeeling and Sikkim Himalayas – *Megachile* sp was a visitor to the flowers up to an elevation of about 800 m asl⁴⁹. It is therefore likely that leafcutter bees are underrepresented in high altitudes of India, rather than to hypothesize that they might be using plants other than Roses for foraging leaves at these sites.

Use of Roses – at least the proportion of plants received cuts – varied considerably among sites. The number of cuts on leaves – another measure used to study bee’s level of dependence on the plants – did not vary much on the cut plants. We took latitude as a measure of the site at a broader scale as the study was well replicated at a higher spatial scale. At each latitude, we had a good number of Roses in several sites. Overall, Roses at 8°N and 12°N are highly used by the bees in south India. Sites within each of the latitudinal points have different proportions of cut Roses (Fig. 2). There could be at least three important drivers that can explain this variation. They are availability of foraging material (pollen and nectar), number of female breeding bees, and nesting places in sites. In the present investigation, we did not

quantify them. Natural nesting sites of leafcutter bees can be any unpredictable cavities or crevices in any artificial or natural materials^{39,40}. Two of the authors' (PAS and AK) observations (N=21) in parts of southwestern USA (PAS) and south India (PAS & AK) are that the nesting places of leafcutter bees are between 0.8 m and 17 m from the leaf sources (PAS & AK, Unpublished). The location of Roses in the gardens, therefore, might play a crucial role in plant use. However, it may be important to note here that out of the 114 Rose plants belonging to *Rosa chinensis* and its breeds, and *Rosa banksiae* (N=18) surveyed in the arboretum of the University of Arizona, 101 had the notches of leafcutter bees (PAS, Unpublished). Southwestern USA is a paradise for the bees and *Megachile* spp in particular. The system offers plenty of pollen resources, such as Mesquites and cacti (PAS: pers. observ.). Leafcutter bees normally return to the preferred plant and even to the selected leaf for more cuttings and until the leaf exhausts^{13,16} (Supplementary Video S1). Therefore, we are not surprised by the finding that the number of cuts on leaves does not vary much among sites.

All quadrants and houses that we surveyed in east, west, north, and south Guwahati city were located at an altitude of about 50 m asl. White Rose was also not a minority in the sample or not clumped to any particular quadrant or house to account for this variation to the local abundance of the plants or to any other local features of the quadrant, including the altitude. Unfortunately, we did not collect information on the pesticide application for this site. Based on our findings that the bees avoid pesticide-treated plants, it is likely that these plants might have been treated by pesticides. One of our (PAS) studies in the arboretum of the University of Arizona in two springs, however, found that the bees hardly discriminated Rose plants by the variety or species.

Conservation of pollinators is an international and intercontinental agenda since the IPBES report¹ flagged the threats the pollinator guild and pollination service are experiencing in the crop systems. Several studies have been concerned about habitat restoration of pollinators and made recommendations for improving the pollinator flowerscape as reports suggest that loss of flowers due to land-use change is a key reason for pollinator decline in the world^{2,3,30}. Improving flower resources becomes a practice in agri-environment schemes and urban landscapes of the developed countries, in particular North America, Europe, and Great Britain. Though late, studies have concerned about the poor quality of nesting grounds of wild pollinators due to tillage and use of agrochemicals in soils^{5,11}.

The leafcutter bees that we are concerned in the present investigation are cavity-nesters. Countries and farmers are relying upon them for crop production, such as Alfalfa and pulses¹⁹. Serious efforts have been made to propagate these bees in crop systems³³. Because they nest in cavities, installing bee hotels became a fashion for managing leafcutter bees in crop systems, public places, and even private premises of the institutions and houses in several parts of the world²⁰. Yet, recent meticulous field and controlled experiments have documented suboptimal propagation of the broods in bee hotels^{14,20}. Studies have related this to an increasing rate of parasitism in bee hotels and poor choice of nesting materials¹⁴. Our findings suggest that Rose leaves may not hamper the development of brood due to leaf chemicals.

Leaves and petals of a range of plant species have been unearthed in the nest tubes of leafcutter bees^{14,21,50}. Plant surveys have reported even a greater number of leaf-foraging plant species in parts of southwest USA¹³ and Asia^{16,51}. However, no recommendations have, so far, been made for the leaf plants for leafcutter bee habitat management and conservation. The recommended plants must meet at least two basic requirements. First, the plant can be manageable in agricultural landscapes and urban centres easily. Second, the nesting materials must allow the brood development.

We found 100% success for broods sheathed by the leaves of Roses. In fact, two of the authors (PAS and AK) have collected nest cells constructed exclusively by the leaves of *Cassia fistula* (Golden-Shower) and *Swietenia macrophylla* (Mahogany tree) in natural nesting places of *Megachile lanata* and *M. disjuncta*, and found 100% brood success for all such cases too (Unpublished). Although studies have found suboptimal brood success for cells retrieved from bee hotels^{14,20}, our findings suggest that the success rate could be higher in natural breeding places. However, unlike those trees, Rose plants are easily manageable in any situation, including the towering apartment complexes, and are already propagated to almost all parts of the world as part of beautification projects⁴⁴⁻⁴⁷. Although Roses attract only very few bees to the flowers, so found no place in any lists of bee-friendly plants (reference⁹ and references therein), are heavily used by leafcutter bees for their reproduction. We, therefore, recommend Roses, for the first time, to the list of bee-friendly plants. Although the leafcutter bees can defoliate the plants considerably, there are no evidences that this unusual “herbivory” hampers the flower output or plant growth. It is an exciting topic for a future investigation. Even though some studies retrieved polyurethane materials in the leafcutter bee nests, which the bee might have foraged under the stress of limited leaf resources, did not show the brood success in such cases^{52,53}. The study underscores that incorporating appropriate nesting material must be an important strategy in solitary bee-, in particular the leafcutter bee-conservation and management.

Materials And Methods

Study area

The study was primarily carried out in peninsular India along the Western Ghats Mountain chains and parts of northeast India including the Darjeeling Himalayas. In peninsular India, the study was carried out in the state of Kerala (8°N-12°N) and Coimbatore and Ooty parts of the state of Tamil Nadu (11°N). In northeast India, the study took place in east, west, north, and south Guwahati city in the state of Assam and Siliguri, Bagdogra, Mirik, and Darjeeling hills of the state of West Bengal (Fig. S1). In each of our major sites (latitudinal points), we had several houses nested in quadrants and local sites. Together, we sampled 2360 roses from 136 local sites (Fig. S1). The use of plants was carried out in accordance with relevant guidelines and regulations.

SAMPLING

Drivers of plant selection

A total of 2,360 Rose plants – 1954 in south India and 406 in northeastern India – were examined for the leafcutter bee-inflicted notches on the leaves (Fig. 1). The notches on the leaves imply leafcutter bee activity^{13,16}. Plants that have very few leaves (<10 leaves), brought less than three months before our surveys to the gardens/ premises, or having a history of pruning were not included in the survey. All the surveys were made during the peak leaf flushing and general flowering season of the respective locations during 2020-2021.

The altitude, latitude, and landscape type (urban or rural) of each of the surveyed Rose plant were recorded. Sites that come within the limits of municipalities and corporations were considered as urban sites, while sites in villages were considered as rural sites. Since the study was replicated at greater spatial scales, latitude was used to represent major site in the analyses. At each latitude band, we had several Rose plants in our surveys. Sites from 8-9°N are considered as 8°N, 9-10°N as 9°N, and so on, when the latitude was used as a driver in the predictive statistical models. The plants were also recorded for the height, pesticide application, leaf length, and leaf width. The height of the plants was used as a measure of the age and the foliage density of the plants. Leaf length and width were considered as the measures of leaf area. It was expected that the bee's response for plant selection might be driven by the size of the leaves.

For the plants that have cut leaves, fifteen first seen cut leaves were collected for measuring the lengths and widths of the leaves and the cuts. Using a centimetre ruler, maximum length, maximum width, maximum cut length, and maximum cut width were measured. For plants that had no cut leaves, middle leaves of first seen fifteen leaf pinnae were collected for measuring the above-mentioned leaf dimensions. The Roses have odd number of leaves in a pinna (normally five), and the middle one is the biggest among all leaves.

For the plants that have cut leaves, first seen fifteen cut leaves were collected without any pre-set conditions and counted for the number of cuts on the leaves. This was used to find out the average number of cuts per leaf, which was designated as the measure of leafcutter bee's dependence for the plant.

Bee preference for Rose varieties

The data of Guwahati city (northeast India) was used to study this, where we recorded the Rose plants by the colour of the flowers. There were four varieties of Roses in the sample – red (N=26), pink (N=11), magenta (N=5), and white (13). Data on plant and leaf variables mentioned in the previous section were collected.

Brood success

To study brood success in Rose-leaf sheathed cells, we used incidental data from a couple of locations in south India (Kanhgad at 12°N; <100 m asl). Female *Megachile lanata* was the bee engaged in nest construction for all the cases. All the broods used for this study were completely constructed with the

leaves of Roses. They were collected from natural nesting places of bees. Six cells in two nests were collected from the laterite compound walls around the garden, eleven nests were collected from metal tubes of a bicycle kept in the garage of one of the authors (PAS). While the nesting site of the former site was about a meter from the rose plant, the latter was found at 6 m from the source. The progress of nest construction was monitored daily. The nest tubes were pulled out of the nesting sites soon after the bees abandoned the nests for three consecutive days. They were reared at room temperature in glass beakers.

Effect of pesticide on bee preference of plants and leaves – experimental approach

This part of the study was conducted in the city of Hyderabad (17° 21' 47.052" N and 78° 30' 30.1644" E; 512 m asl). We purchased stem cuttings of Rose plants from a local nursery in the city. The mother plant used for the cuttings had the leaves damaged by the bees. We arranged twenty cuttings, clipped all the foliage, and planted them individually in twenty pots with garden soil and organic manure (40% sand, 40% red soil, and 20% vermicompost). The pots were spaced out by half a meter and kept in the balcony of the house of one of the authors (SS) at an elevation of 4.4 m above the ground. They were monitored for leafcutter bee and other defoliator activities and irrigated twice daily. When we saw leafcutter bee activities on the plants (33rd day onwards from the day of planting), we grouped the plants into two halves: control (water sprayed; N=10) and contact pesticide-treated (Monocrotophos at 0.01% concentration; N=10). The leaves of control plants were again divided into two: control leaves (approximately half of the foliage sprayed by water) and pesticide-treated leaves (pesticide sprayed). This allowed us to reduce the plausible variability due to plant individuals when testing for the effect of pesticide application on plant selection by the bees. For experimental purposes, plants that were not used by the bees prior to our experiments were set as our control plants. All the cut leaves on the plants used by the bees were clipped before the experimental observations, because, the bees are tended to return to cut leaves for more cuts (13). To reduce pesticide contamination to control plants, the pots were brought to a quarantine place for pesticide application, and to avoid pesticide contamination to the control leaves, they were bagged in polyurethane covers when the remaining leaves of the control plants were hand-sprayed with the pesticide. All the pesticide treatments were made during morning hours (at around 8 AM). The bags were removed half an hour after pesticide application and the pots were brought to their original position. A total of 121 control leaves and 90 treated leaves were observed on the control plants. On pesticide-treated plants, 177 leaves were observed.

Statistical analyses

We used a) cut status (binomial: cut or uncut designated by 1 and 0, respectively) and b) the average number of cuts on leaves as the response variables in two sets of models to discern the drivers of plant selection and the level of dependence the bees have on Roses. We included an interaction term among variables, but dropped them when their inclusion was found not improving model fit. All the cut plants had ten or more of their fresh leaves used by the bees for foraging leaf fragments.

We used landscape type (rural vs. urban), altitude bands (<100 m, 100-300m, 300-600m, 600-800 m, 800-1100 m, >1100 m asl), locations represented by latitudes (8°N, 9°N, 10°N, 11°N, 12°N, 26°N, and 27°N), and pesticide usage (used/ unused) as fixed effect variables, and leaf length and plant height as covariates in a generalized linear model to study the drivers of plant selection by the bees. In the Model, binomial distribution was fitted as the error. When the number of cuts on leaves was the response variable, the subset of cut plants was used for testing the model fit. Pesticide usage and plant height were not included in the Model as they were either not relevant or redundant in the model. In this Generalized Linear Model, Poisson distribution was fitted as the error. Before the decision of using leaf length as a driver in the predictive model, the relationship between leaf length and leaf width was examined, and found that they were colinear (0.54 ± 0.007 , $t=69.8$, $P<0.005$; $R^2_{\text{adjusted}}=0.69$; Fig. S2).

To study the effect of Rose variety on the response of leafcutter bee's preference for the plants, the cut responses were included as the response variable and Rose variety as the fixed effect in a Generalized Linear Model. The significance of the overall Models was examined using Anova available in the R-package "car". The R^2 values of the models were calculated using the R-package "MuMIn". Unless not mentioned mean \pm SD was represented in the entire text. All the analyses were performed in R⁵⁴.

Declarations

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Author contributions:

PAS conceived the idea and planned the study. MJ, GS, MH, GV, AK, AD, KA, and PR did field surveys in south and northeast India. PAS, AK, and VA performed nesting biology and brood success studies. SS did toxicology studies. PAS analysed data and wrote the first draft of the manuscript. All other contributed to data curating and approved the manuscript.

Competing interests:

The authors declare that they have no competing interests.

Data and Materials availability:

All data needed to evaluate the conclusions in the paper are present in the paper and the supplementary materials. The raw data can be provided by PAS pending scientific review and a completed material transfer agreement. Requests for the data should be submitted to: sinu@cukerala.ac.in

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Figures

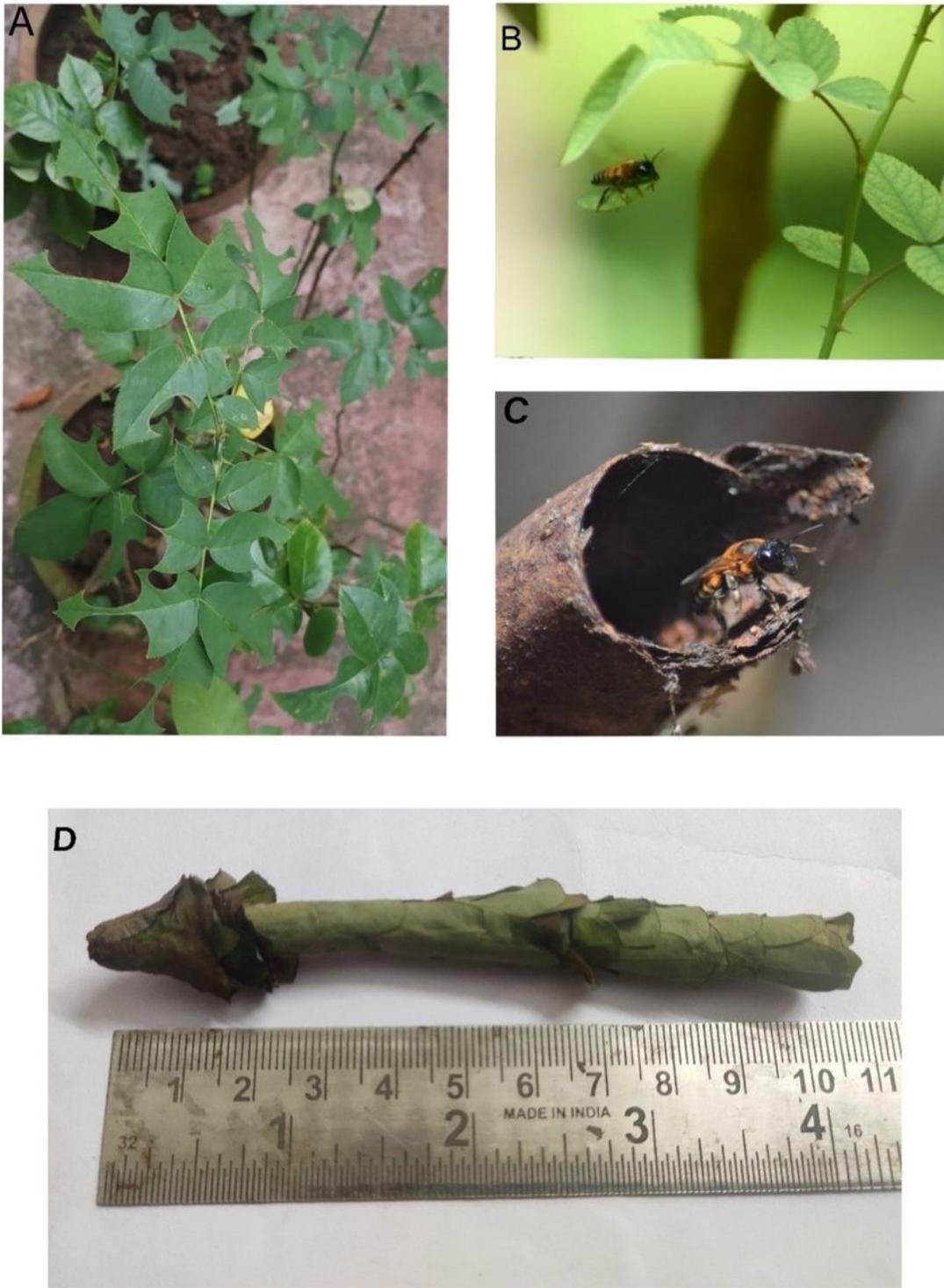
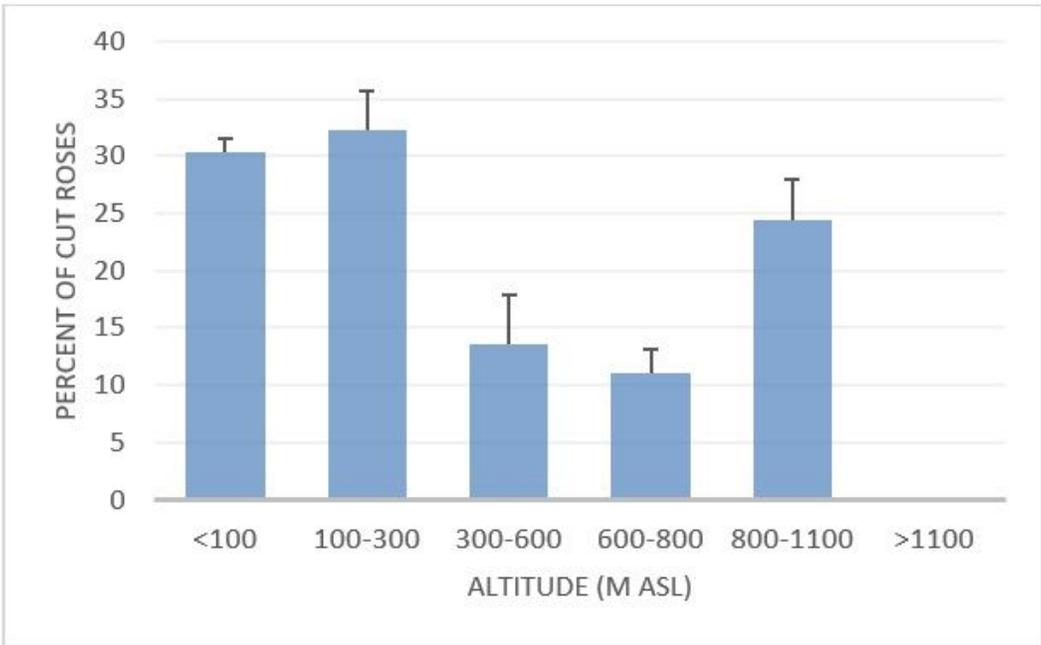


Figure 1

Leafcutter bee-Rose leaf interactions. A) Herbivory damage by leafcutter bees on a Rose plant; B) a female *Megachile lanata* foraging a leaf fragment of Rose leaf; C) a female *Megachile lanata* at its natural nesting site; D) a nest tube of *Megachile lanata*

A



B

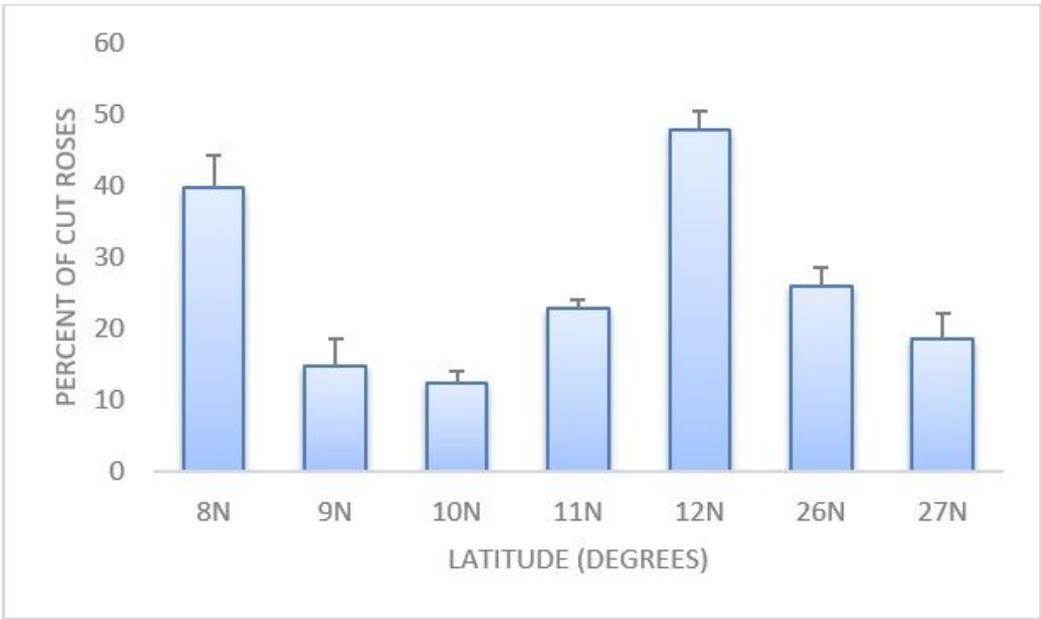


Figure 2

Percent of Roses used by leafcutter bees. A) The bees hardly used any Roses in very high altitude sites, B) The use of Roses fluctuated across latitudinal points. mean±SE are provided.

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