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Srivari Illam, No. 61, Karthik Nagar, 10th Street, Saravanampatti, Coimbatore, Tamil Nadu 641035, India
Registered Office: 3A2 Varadarajulu Nagar, FCI Road, Ganapathy, Coimbatore, Tamil Nadu 641006, India
Ph: +91 9385339863 | www.threatenedtaxa.org
Email: sanjay@threatenedtaxa.org

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Cover: A Warty Hammer Orchid *Drakaea livida* gets pollinated by a male thynnine wasp through 'sexual deception' — a colour pencil reproduction of photos by ron_n_beths (flickr.com) and Rod Peakall; Water colour reproduction of Flame Lily *Gloriosa superba* — photo by Passakoran_14; and a bag worm and its architectural genius (source unknown). Art work by Pannagasri G.



Floral traits, pollination syndromes, and nectar resources in tropical plants of Western Ghats

Ankur Patwardhan¹ , Medhavi Tadwalkar² , Amruta Joglekar³ , Mrunalini Sonne⁴ ,
Vivek Pawar⁵ , Pratiksha Mestry⁶ , Shivani Kulkarni⁷ , Akanksha Kashikar⁸ & Tejaswini Pachpor⁹

^{1-7,9} Annasaheb Kulkarni Department of Biodiversity, MES Abasaheb Garware College, Pune, Maharashtra 411004, India.

^{1,2,3} Research and Action in Natural Wealth Administration (RANWA), 16 Swastishree Society, Ganeshnagar, Kothrud, Pune, Maharashtra 411052, India.

⁹ Department of Bioscience and Technology, Dr Vishwanath Karad's MIT WPU, Paud Road Pune, Maharashtra 411038, India.

⁸ Department of Statistics, Savitribai Phule Pune University, Ganeshkhind, Pune, Maharashtra 411007, India.

¹ ankurpatwardhan@gmail.com (corresponding author), ² himedhavi@gmail.com, ³ amrutamjoglekar@gmail.com,

⁴ ssonne929@gmail.com, ⁵ pawarvivek100@gmail.com, ⁶ pratiksha.mestry46@gmail.com, ⁷ shivani.kulkarni46@gmail.com,

⁸ akanksha.kashikar@gmail.com, ⁹ tejaswini.pachpor@gmail.com (corresponding author)

Abstract: Tropical regions are known to have a high percentage of animal-pollinated plants. This study explores the natural history of pollination in an understudied biodiversity hotspot, the tropical forests of India's Western Ghats. It is the first-ever attempt to gain insights into three critical aspects of pollination simultaneously, i.e., pollination syndromes, floral visitors, and standing nectar crop. Data on the attributes of floral visitors of 62 plant species were collected through regular field visits for three years allowing for sampling across seasons. 'Tube' was the most dominant flower type (20) followed by 'Dish to bowl' with 18 species, 'Brush or Head' (13), and 'Gullet' with nine species. The range of nectar quantity per flower varied from 0.05–13.7 μ L. Nearly 40 percent of plant species observed by us have only Lepidopteran visitors. Fifteen plant species were visited by hymenopterans and lepidopterans, whereas five plant species had hymenopteran visitors only. In the light of rapidly declining pollinator diversity, our study highlights the significance of floral visitors in the pollination of some conservation-significant species, as well as points to determinants of floral visitation and success.

Keywords: Biodiversity hotspot, floral visitor diversity, flower colour, flower shape, pollinators, standing nectar crop, northern Western Ghats.

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INTRODUCTION

Flowering plants play a critical role in the ecosystem by not only providing food and rewards to different animal visitors, but also by providing sites for predation, mating, and as oviposition & brooding sites (Larson et al. 2001). Pollination is a crucial ecosystem service provided by diverse floral visitors to both wild and cultivated plants. Plants and pollinators interact in diverse, and complex ways. Pollination syndromes—defined by floral traits such as morphology, phylogeny, and rewards—help predict plant visitors (Barrios et al. 2016). The amount of nectar, its composition, and placement are also determinants of plant-pollinator interactions (Parachnowitsch et al. 2019).

Bees are assumed to be the most important pollinators for crops as well as wild plants. Globally, 56% of plant species rely on bees and wasps for pollination, while butterflies & moths account for 11%, flies 10%, beetles 3%, birds 12%, and 8% are wind-pollinated (Sanchez & Wyckhyus 2019). Without floral visitors, about 1/3rd of the flowering species would be unable to contribute to seed formation, germination, and the survival of the species (Ollerton et al. 2011).

Pollination syndromes are a set of floral characters including colour, presence of nectar guides, flower scent, nectar reward, pollen, and flower shape that play a role in attracting a particular type of pollinator towards the plant (Yan et al. 2016; Dellinger 2020). They are named after the most typical pollinators (Faegri & van der Pijl 1979; Fenster et al. 2004). The blossom classes (flower types) are correlated to a particular pollinating agent. For instance, flowers with long corolla tubes are pollinated by insects having long proboscis, such as butterflies & moths, and are a part of psychophily pollination syndrome. Ollerton et al. (2011) stated that the percentage of animal-pollinated plants is above 90% in case of tropical regions. This has led to increase in the proportion of plants with functionally specialized pollination systems (i.e., pollination by only one functional group of animals such as lepidopterans or hymenopterans) in tropical regions.

The need to shift the focus from studies related to 'bee only pollination process' to pollination carried out by 'non-bee pollinators' have been highlighted by many researchers (Garibaldi et al. 2013; Bartomeus et al. 2014). Cusser et al. (2021), in their recent paper, have shown that non-bee pollinators such as butterflies, and flies contribute much more than reported, and credited for so far. They play a role in providing pollination service to spatially and temporally unique

flowers, which would otherwise remain unpollinated by conventional pollinators such as bees. Considering the significant role played by non-bee pollinators in the process of pollination, there is a need for study of other insects such as butterflies, wasps, flies, and beetles for developing strategies for increasing pollination of wild, and cultivated plant species. In such cases, studying floral visitor networks can be the first step towards understanding the role of diverse pollinators in an ecosystem.

Global studies are underway to investigate the roles of pollinators in sustaining both wild and cultivated plant species. In diverse tropical forests, flower-visiting insects remain underexplored for their relationship with plants (Tan et al. 2017). Though there are few studies focusing on identifying floral visitors of agricultural crop species in India (Chaudhary 2006; Sinu & Shivanna 2007), there is dearth of comparative studies involving multiple species of wild forest flora. Certain studies have attempted to explore the plant-floral visitor relationship, but they were largely species specific (Somanathan & Borges 2001; Sharma et al. 2011). Despite extensive research on agricultural pollination in India (Chaudhary 2006; Sinu & Shivanna 2007), studies on pollination syndromes in wild forest flora remain scarce.

According to Johnson & Steiner (2000) and Ollerton & Watts (2000), plants were often categorized according to their perceived syndrome, but mostly in absence of actual data of flower visitation or pollination by animals. Especially in Western Ghats and tropical forests, where the documentation of pollinator data mainly focused on one or few species (Grindeland et al. 2005; Huang et al. 2006; Sharma et al. 2011; Lemaitre et al. 2014). Our study investigates floral traits and visitor diversity across 62 plant species, addressing the following questions:

1. How is floral visitor diversity influenced by flower morphology, color, pollination syndrome, and sexual organ placement?
2. What are the patterns of standing nectar crop (SNC) across species?
3. Is there a relationship between nectar volume, blossom type, and flower color?

MATERIALS AND METHODS

Experimental study sites

Present study was conducted at two locations - evergreen forests of Amboli in northern Western Ghats (NWG) and dry scrub hill forests within the city of Pune (Image 1).

Amboli (15.950° N, 74.000° E), situated at 700 m is located in Sawantwadi Taluka of Sindhudurg District of Maharashtra (Image 1C) in northern Western Ghats. These seasonal forests receive annual rainfall ranging 6,000–7,000 mm, dry period length (DPL) of 7–8 months, and average temperatures of minimum 8°C, and maximum 35°C. Primary vegetation type is evergreen. The forests harbour several endemic and threatened plant species. The area is proposed as ecologically sensitive zone and also forms a part of geographically, and ecologically important Sahyadri–Konkan Ecological Corridor (Bawa et al. 2007).

Pune (18.516° N, 73.850° E) is a plateau city situated near the western margin of the Deccan plateau. It lies on the leeward side of the Western Ghats. It is situated at an altitude of 560 m. The city is surrounded by hills on the east and the south. The climate is typical monsoon, with three distinct seasons, viz., summer, rainy, and winter. The hill forests (Bhamburda–Vetal Hill and Parvati–Pachgaon) are located in the heart of Pune city. The temperature ranges between 10–43 °C with annual rainfall range of 600–700 mm, and DPL of 8–9 months. The fragile hill forests primarily harbour scrub forests

and grasslands, but now witnessed plantation drives of exotic species such as *Glyricidia sepium*, *Dalbergia melanoxylon*, and are 'Habitat Islands' surrounded by ever-increasing urbanization from all sides (Image 1B).

Plant species selection

A total of 62 flowering plant species (48 wild and 14 cultivated) belonging to 30 families were studied for floral visitor documentation. These plant species are found in the study areas 1 and 2. Species - level identification and nomenclature were done using regional flora (Almeida 1990; Singh et al. 2001) and by referring to Plants of the World Online database (<https://powo.science.kew.org>). Endemicity and IUCN Red List status of the species were assigned by referring to standard literature (Pascal 1988; BIOTIK 2008; Singh et al. 2015; <https://www.iucnredlist.org/>). For species-specific floral visitor documentation, individual plants were selected based on peak flowering season, flowering percentage, and ease of access to the flowering branches.

Floral attributes

Each species was classified by flower type such

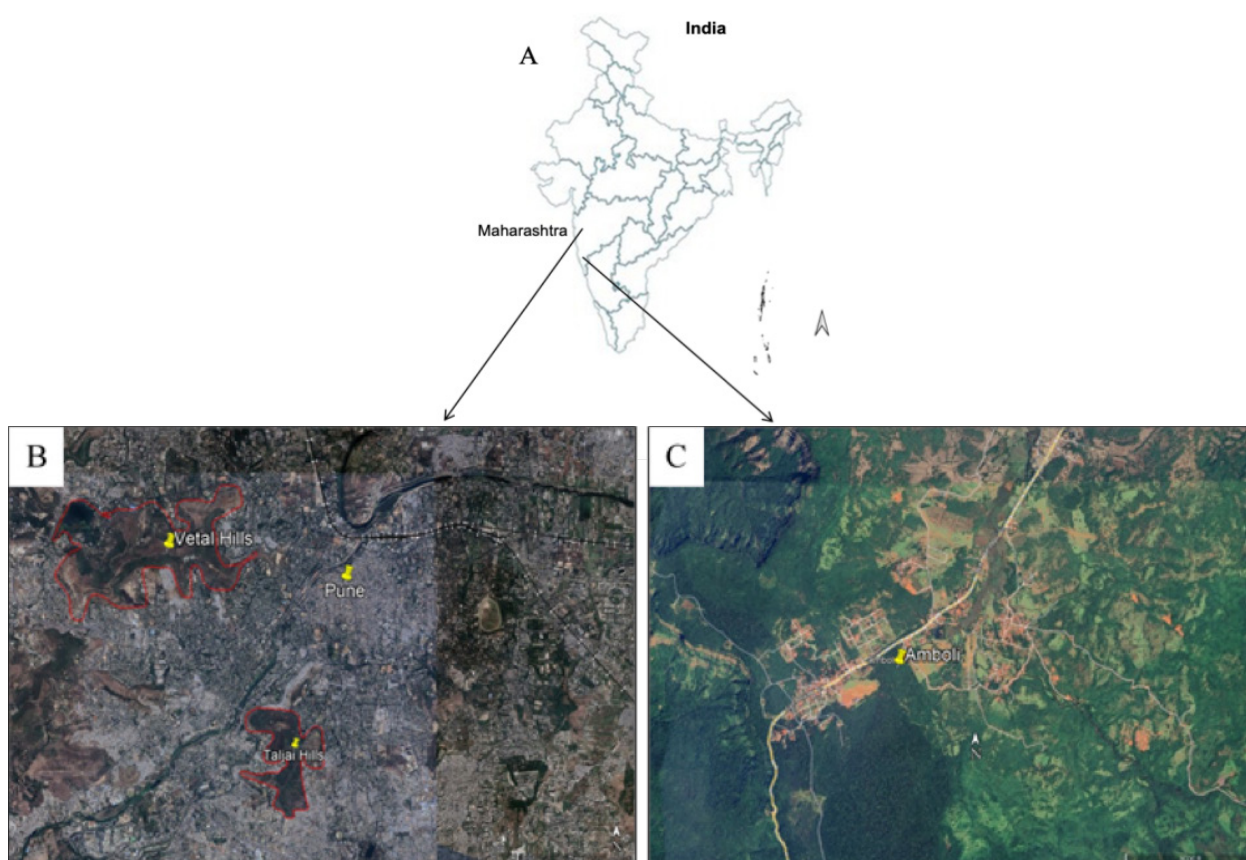


Image 1. Study Area: A—Map of India depicting state of Maharashtra | B—Pune hill forests | C—Evergreen forests of Amboli.

as dish to bowl, brush or head, bell or funnel, gullet, flag, tube, and trap, based on the description, and classification of flower type given by Faegri & Van der Pijl (1979) as represented in Image 2. Flower colour was also assigned based on field observations. Dish to bowl type has the reproductive organs more or less at the centre of the blossom and is actinomorphic. Brush or head type defines itself and the external surface as exclusively or partly formed by the sexual organs and is actinomorphic or asymmetric. Bell or funnel type has rim which advertises functions and sexual organs that are distinctly centric, and is actinomorphic. Gullet type has sexual organs that are restricted to the functionally upper side of the blossom, and pollen is deposited on the back of the pollinator, and are zygomorphic. Flag types have sexual organs that are found in the lower part of the blossom, and pollen is deposited on the ventral part of the pollinator, and are actinomorphic or zygomorphic. Tube types are large and narrow, the tubes may be central, subcentric (as a spur) or excentric, excluding all visitors with mouth-parts shorter than effective tube length. In case of trap types pollinators are temporarily held in the blossom, or experience difficulty in leaving the blossom, and are actinomorphic or zygomorphic.

Floral visitor documentation

The data were collected for three years (2018–2021). An uncontrolled observation method was used for data collection. Regular field surveys once in every month for five days were conducted. The areas included Choukul Road, Mahadevgad Road, Hiranyakeshi (Amboli), and various areas of Pune's hill forests (Taljai, ARAI). All the floral visitors observed contacting the reproductive organs of flowers were systematically documented in the morning (0700–1000 h) and evening session (1600–1800 h) with the naked eye, and binoculars (Nikon Action 8 X 40). These time slots were decided based on a literature review Pachpor et al. (2022) and pilot survey conducted in the study area. Digital SLR camera (Nikon D7100, 105 mm macro lens, Sigma 150–500 mm telephoto lens and Canon 1200 D with 18 X 55 mm lens and 55 X 250 mm telephoto lens) was used for the photo-documentation. Insects were also collected using a sweep net method. Floral visitors were identified using standard literature (McGavin 2002; Grimmett et al. 2011; Bhakare & Ogale 2018). For shortlisted species, floral visitors' occurrence was counted based on the number of times the particular visitor foraged on the flower using a 30-minute count method. Floral visitors were assigned to one of the following taxonomic groups: Hymenoptera, Hemiptera, Diptera, Coleoptera, Lepidoptera, Aranae,

and Passeriformes. Butterflies were identified at the species level. Other insect visitors were identified up to the order level.

Nectar collection and standing nectar crop estimation

Nectar was sampled from at least 50 bagged and 50 unbagged individual flowers in the morning hours between 0700–1000 h by probing each flower with a calibrated Drummonds 0.5 µL micro-capillary tube, measuring the lengths of nectar in the tube in order to determine nectar volumes. For the flowering species with large sized nectaries and larger nectar volume, nectar was estimated using Biohit Proline micropipettes of 5–10 µL (FAO 1995). Standing nectar crop was estimated by bagging the inflorescence/flowers with the fine mesh bridal veil the previous evening to ensure that the nectar was not robbed by the floral visitors before sampling.

Statistical analyses

It was observed that the nectar values do not follow normal distribution. The distributions of nectar values are highly skewed. Since median is a better measure of central tendency in skewed data sets, we used non-parametric multi sample bootstrap-based string for differences in the median nectar value for different flower types and different colours. For each flower type and each colour, we have generated 5,000 bootstrap samples, of the same size as in the original data and estimated the mean difference between the medians for each pair of types, and colours. We have also constructed quantile-based confidence interval for the difference of medians. The confidence intervals which do not contain zero, correspond to the pairs which have significantly different values of medians.

RESULTS

Floral attributes

Sixty-two plant species belonging to 30 families were studied for floral morphology and visitors' diversity. Table 1 provides data on flower morphology, flower colour, flower type, odour, primary attractants, sexual organs, and types of floral visitors. Out of 62 plant species (including wild and cultivated varieties), 41 were actinomorphic and 21 exhibited zygomorphic symmetry. In total six flower types were recorded. 'Tube' was the most dominant flower type (20) followed by 'dish to bowl' with 18 species, 'brush or head' (13), and 'gullet' type with nine species, whereas 'flag' and 'bell or funnel'

type was each represented by a solitary species. White colour flowers were seen in case of 25 species. Coloured flowers included orange, lavender, blue, yellow, orange, pink, and red flowers. Sexual organs were exposed in 41 species and concealed in 21 plant species. Twenty seven species possess both flower colour and nectar as primary attractants, whereas in 22 species nectar serves as the sole attractant. Eleven species have characteristic odour associated with them. Seven species had nectar guides, while extra floral nectaries were found only in *Euphorbia*.

Floral visitors

The floral visitors that were encountered during the present study belonged to seven different orders. Floral visitors primarily belonged to Hymenoptera (bees, wasps, and ants), Diptera (flies), and Lepidoptera (butterflies and moths) orders. Few plants were also visited by members of Araneae (spiders), Coleoptera (beetles), Hemiptera (bugs), and Passeriformes (birds). Members of Araneae (spiders) were seen ambushing prey in the flowers. Nearly 40 percent plant species observed by us have only lepidopteran visitors (Table 1). Fifteen plant species were visited by hymenopterans and lepidopterans, and five plant species visited by only hymenopterans. Less than three plants species were visited by Diptera and Hymenoptera; Coleoptera, Diptera, Hymenoptera, and Lepidoptera; Passeriformes; Hymenoptera and Passeriformes; Diptera, Hymenoptera, Lepidoptera, and Passeriformes; Araneae, Diptera, Hymenoptera, and Lepidoptera; Hymenoptera, Lepidoptera, and Passeriformes; Coleoptera, Lepidoptera, and Passeriformes; Coleoptera, Hymenoptera, and Passeriformes; and Coleoptera, Diptera, Hemiptera, and Hymenoptera. Rest all other insect orders were found to be visiting less than 5 percent species (Table 1).

Out of 62 total plant species, we further shortlisted eight species from evergreen forests for detailed investigation of floral visitor study. This selection was based on either their endemic status (for e.g., *Holigarna grahamii*, *Moullava spicata*, and *Ligustrum robustum* ssp. *perrottetii*), or significance for conservation (*Syzygium caryophyllatum* is endangered) or potential for medicinal value (*Mappia nimmoniana*, *Symplocos racemosa*, *Salacia chinensis*, and *Lagerstroemia microcarpa*). In depth investigation of actual floral visits by different visitors revealed their foraging patterns (Figure 1). Of the total visits recorded, Diptera (flies) and Hymenoptera (bees) were the primary floral visitors, accounting for 39% and 28% of the visits, respectively, followed by Lepidoptera (18%). Members of

Hymenoptera, Diptera, and Lepidoptera were amongst the most common foragers in all the species studied. Maximum observations of lepidopteran visitors were recorded on *Holigarna grahamii*. In species like *Mappia nimmoniana* nearly 50% observations were of dipteran flies. Three species of *Apis* were found to be foraging on *Syzygium caryophyllatum*. Ants were main floral visitors of *Salacia chinensis*. Few spiders (Order Araneae) were seen ambushing in the flowers and preyed upon the floral visitors, while insects like thrips were observed residing in the flowers of *Holigarna grahamii*. Birds like Crimson-backed Sunbird *Leptocoma minima* and Pale-billed Flowerpecker *Dicaeum erythrorhynchos*, were observed foraging on flowers of *H. grahamii* and *M. spicata*. Although we did not specifically compare the diversity of floral visitors between the two sites (wild vs. urban), we did record certain observations. For example, *Leptocoma minima* was found visiting plant species such as *Leea indica* in the wild, whereas, the same plant species in the urban area was found attracting Purple Sunbird *Cinnyris asiaticus*. Figure 1 illustrates the dominance of Hymenoptera and Diptera in floral visits, with Lepidoptera showing species-specific preferences.

Standing nectar crop

Nectar serves as a primary reward for most pollinators. Pollinators' visit to a particular flower is guided by various factors. Various olfactory & visual cues and nectar rewards play a role in predicting which pollinator visits, and successfully pollinates the plant (Barrios et al. 2016). Standing nectar crop (SNC) is the total amount of nectar available for pollinators at a given time. We collected data on the standing nectar crop for 52 plant species. Nectar volume ranged from 0.05–13.7 μ l.

Association of nectar volume with flower type and flower colour

Mean difference between median values of nectar volume was calculated for each pair of flower types. We have considered five flower types. Hence, there are 10 possible pairs. The mean difference between median nectar volumes ranged from 0.19–8.8 μ l. Maximum mean difference between median nectar values (>8) was observed between 'flag' type and other flower types (rush or head, gullet, dish to bowl and tube). Thus, flag type flowers contain significantly more nectar than the other types.

Similarly, mean difference between median values of nectar volume was calculated for each pair of colours. We have considered 17 colours. Hence, there are 136

Table 1. Pollination syndromes, floral attributes, and floral visitors of plant species in the study area.

	Plant species	Family	Flower symmetry	Colour	Type	Odour	Primary attractants	Sexual organs	Nectar volume (μl) (Mean ± SD)	Floral visitors (present study)	Floral visitors (previous study)
1	<i>Crossandra undulifolia</i> Salisb. ^{**s}	Acanthaceae	Zygomorphic	Orange	Tube	Not significant	Colour and nectar	Concealed	0.27 ± 0.23	Hymenoptera and Lepidoptera	—
2	<i>Cynraspermum asperinum</i> Nees ^s	Acanthaceae	Zygomorphic	Blue	Gullet	Not significant	Colour and nectar	Exposed	0.68 ± 0.18	Lepidoptera	—
3	<i>Eranthemum roseum</i> (Vahl) R.Br. ^s	Acanthaceae	Zygomorphic	Blue	Tube	Not significant	Colour and nectar	Concealed	1.87 ± 0.55	Lepidoptera	—
4	<i>Hygraphila serpyllum</i> (Nees) T.Anderson ^s	Acanthaceae	Zygomorphic	Blue	Gullet	Not significant	Colour and nectar; guides present	Exposed	0.44	Lepidoptera	—
5	<i>Justicia santapauli</i> Bennet ^s	Acanthaceae	Zygomorphic	White	Gullet	Not significant	Nectar; nectar guides present	Exposed	10.06 ± 0.16	Hymenoptera and Lepidoptera	—
6	<i>Holigarna grahamii</i> (Wight) Kurz [*]	Anacardiaceae	Actinomorphic	Cream	Dish to Bowl	Not significant	Nectar	Exposed	-	Coleoptera, Lepidoptera and Passeriformes	—
7	<i>Carissa spinarum</i> L. ^s	Apocynaceae	Actinomorphic	White	Tube	Mild sweet	Odour and nectar	Concealed	4.27	Lepidoptera	Lepidoptera (Raju et al. 2004)
8	<i>Catharanthus roseus</i> (L.) G.Don ^{**s}	Apocynaceae	Actinomorphic	Pink	Tube	Not significant	Colour and nectar	Concealed	0.69 ± 0.32	Lepidoptera	Lepidoptera (Raju et al. 2004)
9	<i>Gynema sylvestre</i> (Retz.) R.Br. ex Schultes ^s	Apocynaceae	Actinomorphic	Yellowish white	Dish to Bowl	Not significant	Nectar	Exposed	0.57 ± 0.17	Lepidoptera	—
10	<i>Schefflera</i> spp. ^s	Araliaceae	Actinomorphic	Pinkish White	Dish to Bowl	Not significant	Colour and nectar	Exposed	0.04 ± 0.2	Hymenoptera	—
11	<i>Adelocaryum coelestinum</i> (Lindl.) Brandis ^s	Boraginaceae	Actinomorphic	Bluish white	Dish to Bowl	Mild sweet	Colour, odour and nectar; nectar guides present	Exposed	0.522 ± 0.28	Lepidoptera	—
12	<i>Boswellia serrata</i> Roxb. [*]	Burseraceae	Actinomorphic	White	Dish to Bowl	Not significant	Nectar	Exposed	-	Hymenoptera and Lepidoptera	Hymenoptera (Sunnichan et al. 2005)
13	<i>Capparis maonii</i> Wight ^s	Capparaceae	Actinomorphic	White	Brush or Head	Not significant	Nectar	Exposed	3.34 ± 0.27	Hymenoptera	—
14	<i>Salacia chinensis</i> L. [*]	Celastraceae	Actinomorphic	Green	Dish to Bowl	Pungent	Nectar	Exposed	-	Diptera and Hymenoptera	—
15	<i>Garcinia talbotii</i> Raiz. ex Sant. ^s	Clusiaceae	Actinomorphic	White	Dish to Bowl	Strong unpleasant	Odour and nectar	Exposed	0.8 ± 0.41	Hymenoptera and Passeriformes	—
16	<i>Euphorbia terracina</i> L. ^s	Euphorbiaceae	Zygomorphic	Green	Dish to Bowl	Not significant	Nectar, extra floral nectar present	Exposed	0.095 ± 0.11	Hymenoptera and Lepidoptera	—
17	<i>Albizia chinensis</i> (Osbeck) Merr. [*]	Fabaceae	Actinomorphic	Pink	Brush or Head	Not significant	Colour and nectar	Exposed	-	Hymenoptera	—

	Plant species	Family	Flower symmetry	Colour	Type	Odour	Primary attractants	Sexual organs	Nectar volume (μl) (Mean ± SD)	Floral visitors (present study)	Floral visitors (previous study)
18	<i>Crotalaria retusa</i> L. ^{*s}	Fabaceae	Zygomorphic	Yellow	Flag	Not significant	Colour and nectar	Concealed	8.4 ± 0.54	Lepidoptera	Lepidoptera and Hymenoptera (Raju et al. 2022)
19	<i>Moullava spicata</i> (Dalz.) Nicols. ^{*s}	Fabaceae	Zygomorphic	Red and Yellow	Gullet	Not significant	Colour and nectar	Exposed	12.01 ± 0.18	Coleoptera, Hymenoptera and Passeriformes	–
20	<i>Senegalia rugata</i> (Lam.) Britton & Rose [*]	Fabaceae	Actinomorphic	White	Brush or Head	Not significant	Nectar	Exposed	–	Diptera and Hymenoptera	–
21	<i>Mappia nimmoniana</i> (J.Graham) Byng & Stull. ^{*s}	Icacinaceae	Actinomorphic	Yellowish green	Dish to Bowl	Strong foetid rotten	Odour and nectar	Exposed	1.37 ± 0.49	Coleoptera, Diptera, Hymenoptera and Lepidoptera	Diptera, Hymenoptera (Sharma et al. 2011)
22	<i>Callicarpa tomentosa</i> (L) Murr. [*]	Lamiaceae	Actinomorphic	Pink	Brush or Head	Mild sweet	Colour, odour, and nectar	Exposed	–	Diptera and Hymenoptera	–
23	<i>Clerodendrum infortunatum</i> L. ^s	Lamiaceae	Zygomorphic	White	Gullet	Mild sweet	Odour and nectar	Exposed	1.36 ± 0.52	Lepidoptera	Hymenoptera (Laha et al. 2020)
24	<i>Clerodendrum paniculatum</i> L. ^{**s}	Lamiaceae	Zygomorphic	Orange	Tube	Not significant	Colour and nectar	Exposed	0.088 ± 0.067	Lepidoptera	Lepidoptera (Kato et al. 2008)
25	<i>Leucas stelligera</i> Wall. ^{**s}	Lamiaceae	Zygomorphic	White	Gullet	Mild sweet	Odour and nectar	Concealed	0.526 ± 0.4	Hymenoptera and Lepidoptera	Lepidoptera (Kulkarni et al. 2023)
26	<i>Vitex negundo</i> L. ^s	Lamiaceae	Zygomorphic	Blue	Gullet	Not significant	Colour and nectar	Exposed	0.134 ± 0.075	Lepidoptera	–
27	<i>Saraca asoca</i> – Bisexual (Roxb.) ^s	Leguminosae	Actinomorphic	Orange	Tube	Not significant	Colour and nectar	Exposed	0.35	Lepidoptera	–
28	<i>Torenia fournieri</i> Linden ex E. Fourn. ^{**s}	Linderniaceae	Zygomorphic	Pink	Gullet	Not significant	Colour and nectar, nectar guides present	Concealed	0.3 ± 0.37	Lepidoptera	–
29	<i>Torenia fournieri</i> Linden ex E. Fourn. ^{**s}	Linderniaceae	Zygomorphic	Violet	Gullet	Not significant	Colour and nectar, nectar guides present	Concealed	2.14 ± 1.44	Lepidoptera	–
30	<i>Lagerstroemia microcarpa</i> Wight [*]	Lythraceae	Actinomorphic	White	Dish to Bowl	Not significant	Nectar	Exposed	–	Coleoptera, Diptera, Hemiptera and Hymenoptera	Hymenoptera (Kumar & Khanduri 2016)
31	<i>Woodfordia fruticosa</i> (L.) Kurz. ^{*s}	Lythraceae	Zygomorphic	Red	Brush or Head	Not significant	Colour and nectar	Exposed	6.33 ± 0.76	Passeriformes	–
32	<i>Sida acuta</i> Burm.f. ^s	Malvaceae	Actinomorphic	Yellow	Dish to Bowl	Not significant	Colour and nectar	Exposed	0.1	Lepidoptera	Lepidoptera (Raju et al. 2004), Hymenoptera (Laha et al. 2020)

	Plant species	Family	Flower symmetry	Colour	Type	Odour	Primary attractants	Sexual organs	Nectar volume (μl) (Mean ± SD)	Floral visitors (present study)	Floral visitors (previous study)
33	<i>Memecylon umbellatum</i> Burm.f. ^s	Melastomataceae	Actinomorphic	Blue	Dish to Bowl	Not significant	Colour and nectar	Exposed	-	Hymenoptera	Hymenoptera (Nayak & Davidar 2010)
34	<i>Syzygium caryophyllatum</i> Alston ^s	Myrtaceae	Actinomorphic	White	Brush or Head	Not significant	Nectar	Exposed	0.34 ± 0.20	Coleoptera, Diptera, Hymenoptera and Lepidoptera	-
35	<i>Syzygium cumini</i> (L.) Skeels ^s	Myrtaceae	Actinomorphic	White	Brush or Head	Not significant	Nectar	Exposed	0.26 ± 0.019	Diptera, Hymenoptera, Lepidoptera and Passeriformes	Lepidoptera (Raju et al. 2004)
36	<i>Syzygium hemisphaericum</i> (Wight) Alston ^s	Myrtaceae	Actinomorphic	White	Brush or Head	Not significant	Nectar	Exposed	13.7 ± 20.3	Hymenoptera, Lepidoptera and Passeriformes	-
37	<i>Syzygium zeylanicum</i> (L.) DC. ^s	Myrtaceae	Actinomorphic	White	Brush or Head	Not significant	Nectar	Exposed	-	Hymenoptera and Lepidoptera	-
38	<i>Ligustrum robustum</i> subsp. <i>perrottetii</i> (A.DC.) de Juana ^s	Oleaceae	Actinomorphic	White	Tube	Not significant	Nectar	Exposed	0.28 ± 0.135	Coleoptera, Diptera, Hymenoptera and Lepidoptera	Lepidoptera (Pachpor et al. 2022)
39	<i>Parasopubia delphinifolia</i> (L.) H.-P.Hofm. & Eb.Fisch ^s	Orbanchaceae	Zygomorphic	Pink	Bell or Funnel	Not significant	Colour and nectar, nectar guides present	Concealed	0.06	Lepidoptera	-
40	<i>Periscaria chinensis</i> (L.) H.Gross ^s	Polygonaceae	Actinomorphic	White	Dish to Bowl	Not significant	Nectar	Exposed	0.27 ± 0.17	Lepidoptera	-
41	<i>Catunaregam spinosa</i> (Thunb.) Tirveng ^s	Rubiaceae	Actinomorphic	White and Yellow	Tube	Not significant	Colour and nectar	Exposed	9.34 ± 2.4	Hymenoptera and Lepidoptera	Lepidoptera (Kato et al. 2008)
42	<i>Ixora coccinea</i> L. ^{**s}	Rubiaceae	Actinomorphic	Peach	Tube	Not significant	Colour and nectar	Concealed	0.058 ± 0.019	Lepidoptera	-
43	<i>Ixora coccinea</i> L. ^{**s}	Rubiaceae	Actinomorphic	Pink	Tube	Not significant	Colour and nectar	Concealed	0.11 ± 0.055	Lepidoptera	-
44	<i>Ixora coccinea</i> L. ^{**s}	Rubiaceae	Actinomorphic	Red	Tube	Not significant	Colour and nectar	Concealed	0.06 ± 0.022	Lepidoptera	Lepidoptera (Kulkarni et al. 2023)
45	<i>Pentas lanceolata</i> (Forssk.) ^{**s}	Rubiaceae	Actinomorphic	Lavender	Tube	Not significant	Colour and nectar	Concealed	0.24 ± 0.17	Lepidoptera	-
46	<i>Pentas lanceolata</i> (Forssk.) ^{**s}	Rubiaceae	Actinomorphic	Pink	Tube	Not significant	Colour and nectar	Concealed	0.144 ± 0.16	Lepidoptera	-
47	<i>Psydrax dicoccos</i> (Gaertn.) ^s	Rubiaceae	Actinomorphic	White	Dish to Bowl	Strong sweet	Colour, odour, and nectar	Exposed	1.27 ± 0.322	Lepidoptera and Hymenoptera	Lepidoptera (Kato et al. 2008; Pachpor et al. 2022)
48	<i>Wendlandia thyrsoides</i> (Roth) Steud. ^s	Rubiaceae	Actinomorphic	White	Tube	Mild sweet	Nectar	Concealed	0.09 ± 0.03	Lepidoptera and Hymenoptera	Lepidoptera (Pachpor et al. 2022)

	Plant species	Family	Flower symmetry	Colour	Type	Odour	Primary attractants	Sexual organs	Nectar volume (μl) (Mean±SD)	Floral visitors (present study)	Floral visitors (previous study)
49	<i>Atalantia racemosa</i> Wight* ^s	Rutaceae	Actinomorphic	White	Dish to Bowl	Not significant	Nectar	Exposed	0.36 ± 0.17	Diptera and Hymenoptera	—
50	<i>Allophylus cobbe</i> (L.) Forsyth f.* ^s	Sapindaceae	Zygomorphic	White	Dish to Bowl	Not significant	Nectar	Exposed	0.37 ± 0.18	Lepidoptera	Hymenoptera (Laha et al. 2020)
51	<i>Dimocarpus longan</i> Lour.*	Sapindaceae	Actinomorphic	White	Dish to Bowl	Not significant	Nectar	Exposed	-	Hymenoptera and Lepidoptera	Diptera, Lepidoptera and Hymenoptera (Riswanta et al. 2021)
52	<i>Lepisanthes tetraphylla</i> (Vahl) Radlk.* ^s	Sapindaceae	Zygomorphic	White	Brush or Head	Not significant	Nectar	Exposed	0.42 ± 0.22	Hymenoptera and Lepidoptera	Hymenoptera (Nayak & Davidar 2010)
53	<i>Symplocos cochinchinensis</i> (Lour.) S.Moore* ^s	Symplocaceae	Actinomorphic	White	Brush or Head	Not significant	Nectar	Exposed	0.3 ± 0.2	Hymenoptera	—
54	<i>Symplocos racemosa</i> Roxb.*	Symplocaceae	Actinomorphic	White	Brush or Head	Not significant	Nectar	Exposed	-	Araneae, Diptera, Hymenoptera and Lepidoptera	—
55	<i>Lasiosiphon glaucus</i> (Fresen.) ^s	Thymelaeaceae	Actinomorphic	Yellow	Tube	Mild bitter	Colour, odour, and nectar	Concealed	0.17 ± 0.096	Lepidoptera	—
56	<i>Grewia</i> spp.* ^s	Tiliaceae	Actinomorphic	White	Brush or Head	Not significant	Nectar	Exposed	0.42 ± 0.19	Passeriformes	—
57	<i>Lantana camara</i> L.** ^s	Verbenaceae	Actinomorphic	Yellow	Tube	Mild sweet	Colour, odour, and nectar	Concealed	0.128 ± 0.13	Hymenoptera and Lepidoptera	Lepidoptera (Raju et al. 2004)
58	<i>Lantana camara</i> L.* ^s	Verbenaceae	Actinomorphic	Pink and Yellow	Tube	Mild sweet	Colour, odour, and nectar	Concealed	0.18 ± 0.16	Hymenoptera and Lepidoptera	Lepidoptera (Raju et al. 2004)
59	<i>Stachytarpheta indica</i> (L.) Vahl** ^s	Verbenaceae	Zygomorphic	Blue	Tube	Not significant	Colour and nectar	Concealed	0.3 ± 0.08	Hymenoptera and Lepidoptera	—
60	<i>Stachytarpheta jamaicensis</i> (L.) Vahl** ^s	Verbenaceae	Zygomorphic	Purple	Tube	Not significant	Colour and nectar	Concealed	0.24 ± 0.11	Hymenoptera and Lepidoptera	Lepidoptera (Raju et al. 2004)
61	<i>Stachytarpheta mutabilis</i> (Jacq.) Vahl** ^s	Verbenaceae	Zygomorphic	Red	Tube	Not significant	Colour and nectar	Concealed	2.28 ± 0.39	Hymenoptera and Passeriformes	—
62	<i>Leea indica</i> (Burm. f.) Merr.* ^s	Vitaceae	Actinomorphic	White	Dish to Bowl	Not significant	Nectar	Exposed	0.71 ± 0.73	Diptera, Hymenoptera, Lepidoptera and Passeriformes	—

*—Wild | **—Cultivated | ^s—nectar sample collected.
Plant species are arranged family-wise in alphabetical order.

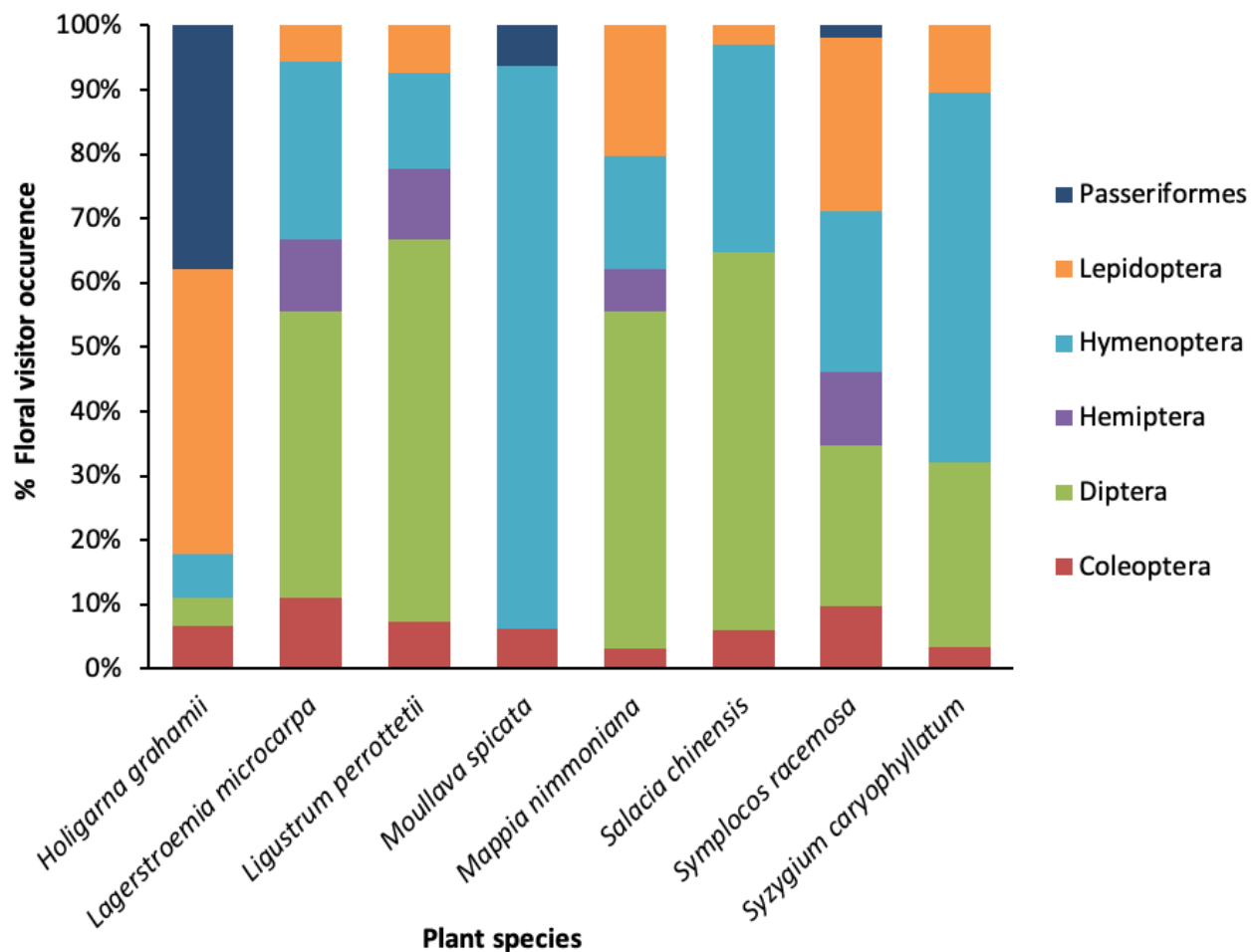


Figure 1. Floral visitor diversity in selected endemic and conservation-significant plant species.

possible pairs. Maximum mean difference between median nectar values (>9) was observed between 'white & yellow' flowers and coloured flowers (peach, orange, green, red & yellow, pink, yellowish-white, pink & yellow, lavender, purple, pinkish-white, blue, white).

DISCUSSION

Documentation of floral visitor diversity is important for understanding the role of specific pollinators in the survival of particular plant species (Rader et al. 2016). In tropical forests, the relationships between plants, and insect visitors remain largely unexplored (Tan et al. 2017). Though attempts have been made to document floral visitors of economically important agricultural crop species, there is dearth of studies pertaining to wild plants. Most studies on pollinator diversity in wild plants have focused on single species (Raju & Medabalimi 2016; Balducci et al. 2019; Cusser et al. 2021). Juan

Fernandez Islands in Chile were explored in detail for studies related to floral traits, breeding systems, floral visitors, and pollination systems, by Bernardello et al. (2001). Widespread presence of 'dish-shaped' flowers, followed by 'tubular' flowers, and dominance of green coloured flowers, followed by white & yellow coloured flowers, was reported by them. However, in the present study, we observed that 'tube' was the most dominant flower type followed by 'dish to bowl'. White colour flowers were seen in case of 42% species followed by yellow, and pink coloured flowers.

Few researchers have attempted to show how floral colour influences pollinator partitioning in plant communities (Reverté et al. 2016). Sourakov et al. (2012) has shown the preferences for flower colour influencing the type of butterfly visitors. Selwyn & Parthasarathy (2006) recorded white as the most common flower colour (similar to the present study) with predominance of night-blooming flowers. Present study showed dominance of day blooming species.



Image 2. Representative flower types in the study area: A—Dish to bowl type flowers of *Leea indica* | B—Tube flowers of *Lantana camara* | C—Brush or head type flowers of *Syzygium caryophyllatum* | D—Gullet type flowers of *Hygrophila serpyllum* | E—Bell or funnel shaped flowers of *Parasopubia delphinifolia* | F—Flag type flowers of *Crotalaria retusa*. © Ankur Patwardhan.

According to Leppik (1969) and Faegri & van der Pijl (1979) the blossom classes (flower types) are correlated to a particular pollinating agent. Many species in the tropics may have morphologically simple flowers, allowing the access of different categories of visitors, such as bees, butterflies, moths, flies, and wasps (Bawa 1990). The 'dish' and 'brush' type of flower morphology thus provide a simple entry to the floral resources for a diverse range of floral visitors. In the present study, out of seven orders of floral visitors, 'dish to bowl' and 'brush or head' flower type supported six orders each.

In the mid-elevation evergreen forests of Western Ghats, majority of the plant species were categorized as specialized for single pollinator taxa – bee, beetle or moth (Devy & Davidar 2003). The study also revealed the importance of bees as pollinating agents, as majority of the plants were visited by bees across varied floral traits. The plant species in the current study could not be assigned to a specific pollinating agent as many plant species were visited by a wide variety of pollinators ranging from bees to birds. Our findings are in accordance with studies conducted by Bawa et al. (1985) in the tropical lowland forest at La Selva, which showed that most of the plant species in the study area were found to have pollinators with wide foraging ranges. The bipartite network shows that lepidopterans visit and pollinate the highest number of plant species.

Available nectar at the time of foraging and the nectar composition are other key factors that determine the floral visits by pollinators. As per the observations by Kaeser et al. (2008), standing nectar crop is affected by both rate of nectar production (that will depend on nectar production mechanism and will vary from flower to flower) as well as nectar consumption by pollinators. We recorded a wide range of nectar volumes 0.05–13.7 µl during the present study.

CONCLUSION

Our study documents the pollinators of tropical plant species in India and indicates that, although pollination syndromes are important in defining the diversity of floral visitors, other factors such as nectar composition, and flower type may play a more significant role in the process. Further exploration of this aspect is essential to understand the relationship between nectar volume, nectar production rate, and the number of visits by pollinators. More efforts to study the extent to which flower colour and other visual cues influence visitors' flower choice are needed for improved understanding

of the costs, and rewards of the pollination process to the plants, and the pollinators. These trade-offs will be valuable in understanding the evolution of pollinator-plant relationships.

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Author details: ANKUR PATWARDHAN—is an associate professor and entrepreneur. He holds a doctorate in Environmental Sciences. His main interests include assessment of ecosystem services, understanding impact of climate change on phenology in plants, plant-insect interaction, seed biology and urban ecology. He undertakes 'Ecological Surveys' and drafts 'Biodiversity Management Plans' (essential for Environmental Sustainability Disclosures) for industrial establishments and developmental projects. MEDHAVI TADWALKAR—holds a doctorate degree in environmental science. She has worked as an assistant professor in the field of biodiversity, ecology. She is a co-founder and director of Ecovrat Enviro Solutions, a startup committed to aid businesses achieve their sustainability goals and combat climate change. She aims to bring the research aptitude to on-ground implementation of biodiversity enhancement, sustainable livelihood practices, and nature-based solutions. AMRUTA JOGLEKAR—holds a doctorate degree in environmental science. She has research experience in field of forest ecology and natural resources database management. She is a co-founder and director of Ecovrat Enviro Solutions, a startup committed to aid businesses achieve their sustainability goals and combat climate change. Her startup work helps businesses, local community groups and organizations to attain SDGs and environmental compliance under sustainability frameworks. MRUNALINI SONNE—is a PhD research scholar at the Annasaheb Kulkarni Department of Biodiversity at M.E.S. Abasaheb Garware College, Pune, India. Her doctoral research focuses on developing biocontrol agents for freshwater purification and environmental sustainability. VIVEK PAWAR—is an assistant teacher. He holds a master's degree in biodiversity from the Annasaheb Kulkarni Department of Biodiversity, M.E.S. Abasaheb Garware College, Pune. As well as he holds another master's degree in zoology from Department of Zoology, Shivaji University Kolhapur. PRATIKSHA MESTRY—holds a master's degree in biodiversity from the Annasaheb Kulkarni Department of Biodiversity, M.E.S. Abasaheb Garware College, Pune. As a project coordinator at RANWA, she has explored plant-insect interactions, woody species diversity, and reproductive phenology cycles in tree species in evergreen forests of northern Western Ghats. Currently, she works on the conservation of threatened plant species. She is a recipient of Prakriti Research Fellowship for conservation two endangered plant species. SHIVANI KULKARNI—is a field researcher at the Applied Environmental Research Foundation (AERF), where she is currently involved in a project focused on promoting green economy for biodiversity conservation. She holds a master's degree in biodiversity. Shivani's research interests lie at the intersection of biodiversity conservation and sustainable development, with a particular focus on the SDGs through nature-based solutions. AKANKSHA KASHIKAR—an associate professor in the Department of Statistics, Savitribai Phule Pune University, specializes in stochastic processes including count data time series, and applied statistics. She is involved in interdisciplinary projects related to biodiversity and astrophysics. She recently authored the book, "Probability Theory: An Introduction Using R", published by CRC press. TEJASWINI PACHPOR—is assistant professor at Dr Vishwanath Karad's MIT WPU. She has a doctorate in microbiology and her research interests include environmental biotechnology, bioprocess technology.

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