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Palatty Allesh Sinu, V. Aiswarya. Leafcutter bee preference of plant saplings in plant nurseries: context for future research and conservation. *Apidologie*, 2023, 54 (6), pp.55. 10.1007/s13592-023-01039-3 . hal-04787732

HAL Id: hal-04787732

<https://hal.science/hal-04787732v1>

Submitted on 18 Nov 2024

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Leafcutter bee preference of plant saplings in plant nurseries: context for future research and conservation

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Received 1 January 2023 – Revised 25 September 2023 – Accepted 3 November 2023

Abstract – Global pollinator decline has prompted pollinator conservation initiatives. Plant nurseries exploited this opportunity by selling bee-friendly ornamental plants. Studies that analysed flower-pollinator networks questioned the suitability of ornamental plants for bee conservation. We evaluated plant nurseries from the perspective of the leaf-foraging habit of leafcutter bees. Leafcutter bees use leaves to construct brood chambers. We found evidence for leafcutter bees using the leaves of 9% of plant species ($n = 238$). Bees foraged ornamental and horticultural plant saplings similarly. Plant species preference was driven by plant clade and plant height. The proportion of plant saplings used by bees in the nurseries was associated with plant abundance and the proportion of ornamental plants. Results provide context for new perceptions toward ornamental plants and plant nurseries for pollinator conservation and restoration and ask questions on the ecology and evolution of leafcutter bee–plant interaction.

pollinator decline / leafcutter bee / Megachilidae / ecological specialization / ornamental plants

1. INTRODUCTION

Pollinator decline is a global concern (Potts et al. 2010, 2016), and several first-world nations have included pollinator conservation in their national research priorities. For example, the agri-environmental schemes adopted by the European Union and North America have made substantial allocation for pollinator management and conservation in agro-landscapes (Image et al. 2022). In the urban environment, pollinator conservation has been mainly linked with urban intensification, pesticide use and pollution (Baldock 2020 and references therein). Restoration and diversification of habitats with flowering plants are the keys to pollinator conservation (Majewska and Altizer 2020; Potts et al. 2005,

2010, 2016). In agricultural and urban landscapes, conservation is being realized through identification and selective propagation of pollinator-friendly plants (Nichols et al. 2019). The ornamental plant supply chains seem to have exploited the opportunity of pollinator decline in some parts of the world and made business with bee-friendly plants (Garbuzov and Ratnieks 2014a). However, researchers have shown that the lion's share of the so-called bee-friendly plants sold by the European supply chains is not helpful for pollinator conservation (Garbuzov and Ratnieks 2014a, b; Garbuzov et al. 2017; Majewska and Altizer 2020). Bee conservation initiatives, though benefiting from the information of nesting opportunities and resources, have given unprecedented attention to manipulate floral foraging sources for achieving success (Harmon-Threatt 2020; Requier and Leonhardt 2020). This is because studies have identified

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Manuscript editor: Mathieu Lihoreau

loss of flower cover as a potential driver of bee decline (Majewska and Altizer 2020; Potts et al. 2010). Plant nurseries are considered as pertinent land-use types in urban areas for the conservation of pollinators (Lentola et al. 2017; Lowenstein et al. 2019; Baldock 2020). In the present research, we critically looked at the plant nurseries of south India not from the angle of flower-pollinator interaction but from the perspective of leaf-leafcutter bee interaction to assess their role in the conservation of leafcutter bees.

Megachilidae, the family of leafcutter bees, mason bees and resin bees (Michener 2007), is cosmopolitan and has about 4100 species worldwide and 105 species in India (Ascher and Pickering 2015). They are crucial pollinators of pulses, oilseeds and important fodder plants, such as alfalfa, around the world (Pitts-Singer and Cane 2011; Haider et al. 2014). As the name implies, leafcutter bees cut fresh young leaves to construct brood cells (Sinu and Bronstein 2018). Although a global trend of the populations of leafcutter bees is lacking, it is reported that scores of these species in North America are missing over a period of time (Young et al. 2016). Their conservation and restoration require both flowers and leaves (Sinu and Bronstein 2018; Cecala and Wilson Rankin 2021a). Our knowledge of leaf plants of leafcutter bees is limited (Kambli et al. 2017; MacIvor 2016; Sinu and Bronstein 2018; Sinu et al. 2022). The pattern and drivers of preference of leaf plants, though important foundations to unravel the mystery of evolution and diversification of Megachilidae and leafcutter bees are yet to be understood (Litman et al. 2011). We recently reported that ornamental roses are important leaf-foraging plants for leafcutter bees (Sinu et al. 2022). Until then, roses were not listed as bee-friendly plant (Garbuzov and Ratnieks 2014a, Garbuzov et al. 2017). This inspired us to survey plant nurseries to identify potential leaf-foraging plants of leafcutter bees.

In the present investigation, we surveyed plant nurseries that sell ornamental (plants with flowers and leaves as aesthetic traits) and horticultural plants to identify potential leaf-foraging

ornamental and horticultural plants of leafcutter bees. Apart from identifying such plants, we asked three additional questions. First, is the bees' preference for leaf-foraging plants driven by plant taxa, plant height, plant abundance and leaf dimension? Second, is the proportion of the cut plants and cut species in the nurseries driven by the local abundance of plants, proportion of ornamental plants and plant species richness in nurseries? Third, is the dimension of the leaf cuts proportional to the dimension of the leaves?

2. METHODS

The study was conducted in ten plant nurseries located in two districts, Kasaragod and Palakkad of Kerala, India. The nurseries that claimed not to use pesticides for managing their plant stocks were selected and stood at least 7 km apart. Nurseries that hold both ornamental and horticultural plants were selected (Figure 1). The survey was conducted when the nurseries were opened after the COVID-19 lockdown restrictions during March–May 2022 (the summer months). Summer months have been identified as the best season for leafcutter bee breeding activities in Kerala (Sinu et al. 2022). During the locked-down period, as plant sales were low in nurseries, bees had relatively uninterrupted access to the plant stocks for foraging leaves and flowers for an extended period.

The study covered every single sapling (defined here as juvenile nursery plants) of plant species that the nurseries maintained and closely examined all the leaves for the characteristic urn-shaped notches that the leafcutter bees make on the leaves while foraging leaf discs (Kambli et al. 2017; Sinu and Bronstein 2018; Sinu et al. 2022) (Figure 2). Plants that have at least ten such notches were considered the leaf plants of leafcutter bees. Plants that were pruned as part of plant management were not included in the analyses. Each sapling was identified to its species, higher taxa and use (ornamental or horticultural), and measured on their height and leaf dimensions. Plant clade was considered a potential driver of plant selection as Sinu and Bronstein

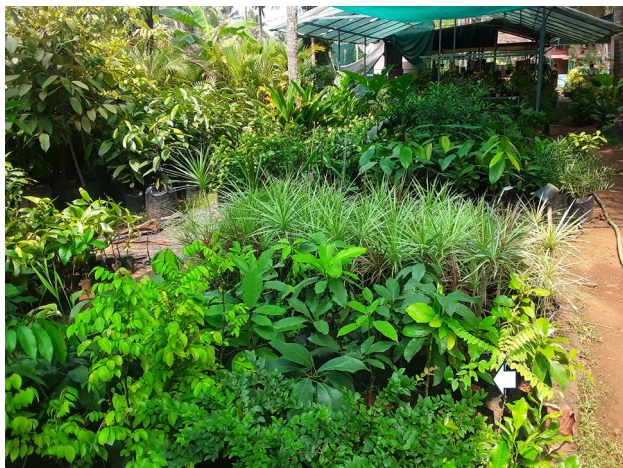


Figure 1. A section of a plant nursery showing plant saplings for sale and a leaf-foraged plant sapling of *Averrhoa carambola* (star-fruit plant; white arrow mark).

(2018) demonstrated that the bees prefer plants of rosid clade. Plant height was measured using a meter scale, and leaf dimensions (maximum length and maximum width) were measured using a centimetre scale following Kambli et al. (2017), Sinu and Bronstein (2018) and Sinu et al. (2022). The cut dimensions were also measured at maximum cut length and maximum cut width, following Sinu and Bronstein (2018). Sapling abundance was also recorded for each plant species. Plant species were grouped primarily into two major clades such as rosids and asterids and those which do not have memberships in these clades were grouped into miscellaneous.

In order to ask what plant traits drive bees' preference of plant species for foraging leaves, we constructed a generalised linear model by fitting cut status (yes/no) as the response variable, plant clade (rosid/asterid/miscellaneous), plant height, leaf width, and plant abundance as the predictors, and binominal distribution as the error. Leaf width was positively related to leaf length (Figure S1); therefore, only leaf length was included in the final model to reduce redundancy. From the original dataset, the proportion of cut plant species and abundance of cut plant saplings were derived. They were fitted in two different generalized linear models to examine

whether they were driven by the overall abundance of plants, the proportion of ornamental plants and plant species richness in the nurseries. Binomial distribution was fitted as the error in these models. All the analyses were performed in R Studio (R Studio Team 2020). Parameters and significance were calculated using Wald F or chi-squared tests for GLMs available in the package *car* (Fox and Weisberg 2019). The conditional regression values of the models were found by running the model results in the R package *MuMIn* (Barton 2020). The residuals of the fitted models were examined for homoscedasticity using the R package *DHARMA* (Hartig 2021).

3. RESULTS

In total, 40,554 plants of 238 species—88 horticultural and 150 ornamental species—belonging to 84 families were examined (Table S1). The average number of individual saplings and species in the nurseries were 4060 ± 4140 (mean \pm SD) and 76 ± 34 (mean \pm SD), respectively.

Eight of the ten nurseries surveyed in the present study had leaf-foraged plants. An average of about 5% (range = 0–12.8%) of the plant

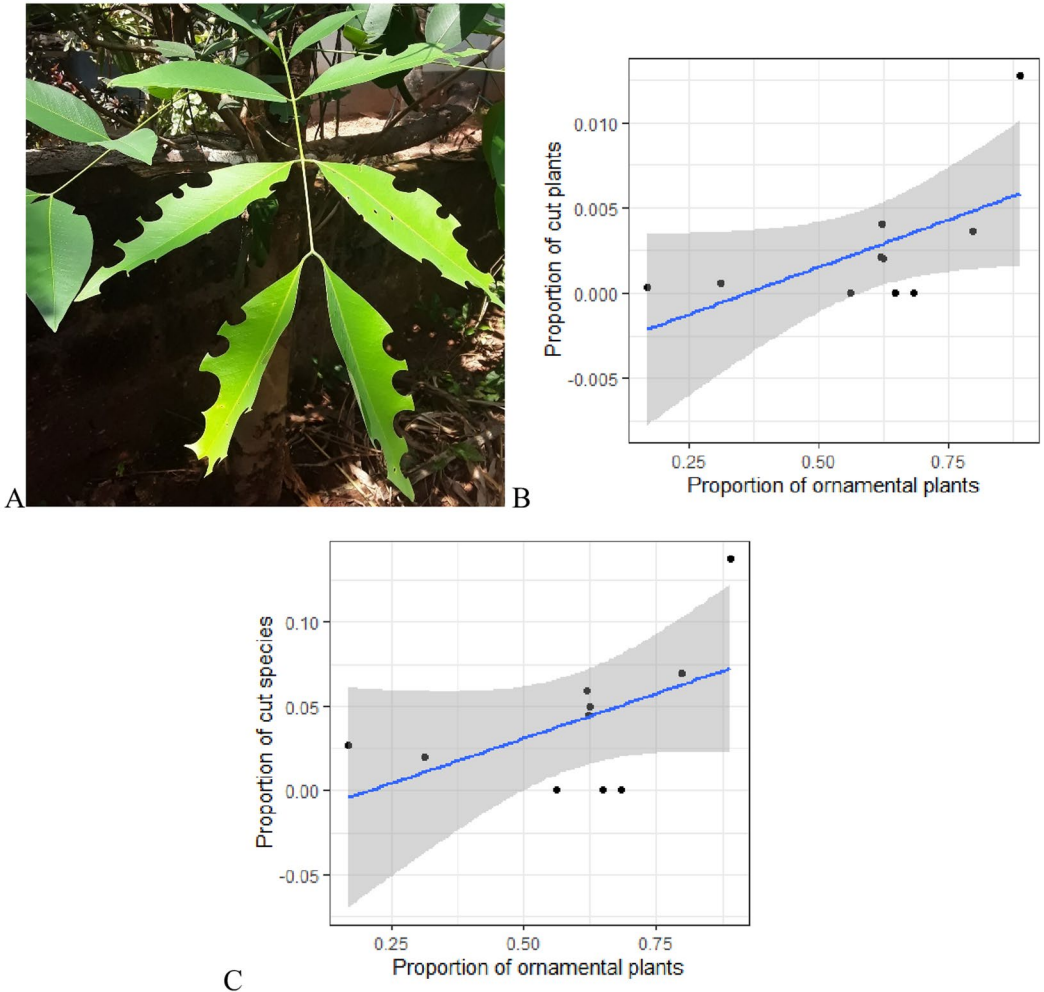


Figure 2. **A** Leaves of *Cassia fistula* having notches of leaf cuts made by leafcutter bees; **B** proportion of cut plant saplings and **C** plant species is directly proportional to proportion of ornamental plants in nurseries.

species in the nurseries had notches. Altogether, the leaves of 59 individual saplings (0.14%) and 21 species (8.8%) had notches of leafcutter bees. Of the 21 species, 11 were horticultural and 10 were ornamental species, and 17 belonged to rosoid clade and five were belonged to asterid clade (Table I). Together, these 21 species had 929 saplings in the nurseries; however, only 6.4% ($n=59$ saplings) were used by the bees. Within plant families, bees were more inclined towards Fabaceae. Bees predominantly made elliptical or oblong cuts,

and the length and the width of the cuts were directly proportional (Figure S2).

Plant species preference (yes/no) was driven by clade (Wald chi-square = 23.19, $df=2$, $p < 0.0005$) and sapling height (chi-square = 12.83, $df=1$, $p < 0.0003$). Although the local abundance of plant saplings (chi-square = 2.43, $df=1$, $p=0.11$) and leaf width (chi-square = 0.67, $df=1$, $p=0.41$) contributed to the final model that explained about 95% of the total variance, they were not crucial individual drivers of plant preference. The length of

Table 1 Plant species having cut marks of leafcutter bees

Clade	Plant family	Common name	Species name	Plant type
Asterid	Oleaceae	Chinese privet	<i>Lingustrum sinense</i>	Ornamental plant
	Nyctaginaceae	Bougainvillea	<i>Bougainvillea glabra</i>	Ornamental plant
	Apocynaceae	Crape jasmine	<i>Tabernaemontana divaricata</i>	Ornamental plant
Rosid	Oxalidaceae	Bilimbi	<i>Averrhoa bilimbi</i>	Horticultural plant
	Oxalidaceae	Starfruit	<i>Averrhoa carambola</i>	Horticultural plant
	Fabaceae	Calliandra	<i>Calliandra haematocephala</i>	Ornamental plant
	Fabaceae	Bauhinia	<i>Bauhinia acuminata</i>	Ornamental plant
	Myrtaceae	Guava	<i>Psidium guajava</i>	Horticultural plant
	Rubiaceae	Ixora	<i>Ixora coccinea</i>	Ornamental plant
	Myrtaceae	Eugenia	<i>Syzygium paniculatum</i>	Ornamental plant
	Fabaceae	Butterfly pea plant	<i>Clitoria ternatea</i>	Ornamental plant
	Lythraceae	Pomegranate	<i>Punica granatum</i>	Horticultural plant
	Sapindaceae	Rambutan	<i>Nephelium lappaceum</i>	Horticultural plant
	Phyllanthaceae	Star gooseberry	<i>Phyllanthus acidus</i>	Horticultural plant
	Sapindaceae	Pulasan	<i>Nephelium mutabile</i>	Horticultural plant
	Myrtaceae	Java apple	<i>Syzygium samarangense</i>	Horticultural plant
	Rosaceae	Rose	<i>Rosa damascena</i>	Ornamental plant
	Fabaceae	Golden shower	<i>Cassia fistula</i>	Ornamental plant
Myrtaceae	Water apple	<i>Syzygium aqueum</i>	Horticultural plant	
Myrtaceae	Jaboticaba	<i>Plinia cauliflora</i>	Horticultural plant	
Fabaceae	Indian rosewood	<i>Dalbergia latifolia</i>	Horticultural plant	

the cuts was directly proportional to the length of the leaves (LM: 0.04 ± 0.01 , $t = 4.09$, $p < 0.0005$; $R^2 = 0.05$) (Figure S3). Plant species of the rosid clade were preferred over the other clades (GLM: 1.12 ± 0.05 , $z = 2.35$, $p = 0.01$). The cut plants in the nurseries increased with the height of plant saplings (GLM: 0.01 ± 0.004 , $z = 3.7$, $p = 0.0002$).

The proportion of cut plant species in the nurseries was predicted by the abundance of plant saplings (Wald $F_{1,6} = 22.09$, $p = 0.003$) and the proportion of ornamental plants in the nurseries ($F_{1,6} = 12.43$, $p = 0.01$) (Figure 2); plant species richness was not a crucial driver ($F_{1,6} = 1.24$, $p = 0.31$). The whole model structure explained 69% of the total variation in the proportion of plant species used by the bees. However, the proportion of cut plant saplings in the nurseries was driven by the proportion of ornamental plants ($F_{1,6} = 10.46$, $p = 0.01$). Although

plant abundance ($F_{1,6} = 4.61$, $p = 0.5$) and plant species richness ($F_{1,6} = 0.46$, $p = 0.075$) were the poor drivers of cut plants, they helped to explain about 50% of the total variance.

4. DISCUSSION

Ornamental and horticultural plant nurseries represent a major agri-environment, particularly in urban areas (Lentola et al. 2017). The high floral diversity of native and exotic plant species in a small area makes nurseries important to study from the perspective of pollinator ecology (Lentola et al. 2017). Recent studies have shown that bees may survive more favourably in ornamental and horticultural plant nurseries in urban areas (Lentola et al. 2017; Lowenstein et al. 2019; Baldock et al. 2019; Stoner et al.

2019). However, all these studies have examined nurseries from the perspective of flower visitors. In the present research, we examined plant nurseries from the perspective of leaf-leafcutter bee interaction. Except for the two, all the other nurseries had leaf-foraging plant species, which suggests that bees are utilizing plant resources of plant nurseries.

There is a dearth of knowledge on the leaf-foraging plants and the drivers of bees' choice of plants and leaves. This knowledge gap is gradually being filled with the growing literatures from different parts of the world (Kambli et al. 2017; MacIvor 2016; Sinu and Bronstein 2018; Sinu et al. 2022). It is suggested that plants of Fabaceae are preferred over other plant families, and plants of rosid clade are preferred over other plant clades (Kambli et al. 2017; MacIvor 2016; Sinu and Bronstein 2018). The plant nursery data of over 40,000 saplings belonging to over 230 species of plants in the present study are also in agreement with these general predictions (Sinu and Bronstein 2018).

Bees used saplings of ornamental and horticultural plants similarly. However, the proportion of the foraged plants in the nurseries was positively associated with the proportion of the ornamental plants in the nurseries. Recent studies have demonstrated the positive aspects of ornamental plants in conserving pollinators in towns and cities (Baldock 2020 and references therein). However, they are resulted from the flower-pollinator network studies. Our findings suggest that the leafcutter bees benefit from the leaves of the ornamental plants. Leafcutter bees approach leaves as small as 1.5 cm for foraging leaf fragments (Kambli et al. 2017; Sinu and Bronstein 2018). However, our findings agree with Kambli et al. (2017) and Sinu and Bronstein (2018) that the dimension of the cuts can be proportional to the size of the leaves.

Though the plant species richness remained an insignificant driver of the proportion of the plant species used by the bees, the local plant sapling abundance remained as a pertinent factor. Leafcutter bees have a preference for the plants of certain lineages (Sinu and Bronstein 2018). For instance, plants of Fabaceae and

ornamental roses are preferred over other plants in plant communities (MacIvor 2016; Kambli et al. 2017; Sinu and Bronstein 2018; Sinu et al. 2022). Therefore, their abundance is crucial than the richness of non-preferred plant species for foraging leaves.

Bees belonging to Megachilidae are considered specialists of flowers of certain plant lineages (Sedivy et al. 2013). For instance, papilionaceous flowers (irregular and butterfly-like corolla) of Fabaceae fit well with the ventral gastral scopa (pollen-carrying hairs) of Megachilid bees. Our global synthesis of studies that have reported leaf sources of brood chambers of leafcutter bees suggests that the bees have a similar preference for plants of Fabaceae for foraging leaves too (Sinu and Bronstein 2018). This interesting association may help us further understand the evolution and adaptive radiation of Megachilidae around the world. Apart from the leaf morphological and leaf physical variables, leaf and plant chemistry and the evolutionary lineage of both plants and leafcutter bees may also be pivotal for the evolution of leaf plant-leafcutter bee interaction, which remains a pertinent future study.

Plant preference was positively associated with the height of saplings in the nurseries. Although it is not clear why, the fact that the bees prefer trees and shrubs over herbs for foraging leaves (Sinu and Bronstein 2018) may be applicable here. It is also likely that the relatively taller plants with abundant foliage may be more attractive for the bees than the short saplings arranged in clumps in the nurseries (Figure 1). We recommend surveying mature plants of these nursery saplings in gardens and orchards before making a final list of leaf-foraging plants for leafcutter bee management and conservation. The 21 plant species that the bees used from the present sample, though present in multiple nurseries, were not foraged similarly in all nurseries. Leafcutter bees may use crevices or cavities above ground for constructing brood chambers (Sinu et al. 2022). None of the nurseries we surveyed had trap-nests or bee-hotels for nesting opportunities for leafcutter bees. Also, it is worth mentioning that the bees return to a preferred leaf and a plant for foraging leaves until

the leaves exhaust (Figure 2). Therefore, the proportion of preferred plants in a given site can be predicted both by the nesting opportunities and the abundance of breeding bees during the period of foliage sprouting in plants.

The two major challenges that urban pollinators face are the use of pesticides and pollution (Baldock 2020 and reference therein). Plant nurseries, though can be pertinent land-uses for bee conservation in urban areas, are highly exposed to several agro-chemicals, which the owners use to present the saplings as attractive as possible to the buyers (Lentola et al. 2017). Several studies referred by Baldock (2020) have highlighted how pollinators are affected by agro-chemical uses in urban areas around the world. However, those studies have examined the pesticide residues in flowers. The threat from the agro-chemical use in nurseries and urban parks may be double for the leafcutter bees because they might be exposed to the contaminated leaves and flowers, and how the leafcutter bees manage the agro-chemicals on the leaves can be a potential future study.

5. CONSERVATION IMPLICATION

Pollinator conservation is a major area of research around the world. Improving flower resources in landscapes is the key to enhancing the population and diversity of pollinators. In the pretext of stimulating this, plant nurseries and plant supply chains have lists of bee-friendly plants (Garbuzov and Ratnieks 2014a). While the efficiency of those plants has been tested through empirical studies on flower-pollinator networks (Garbuzov and Ratnieks 2014b; Garbuzov et al. 2017), how they benefit leaf-foraging bees is tested less (Kambli et al. 2017; MacIvor 2016; Sinu and Bronstein 2018; Sinu et al. 2022). Pollinator conservation needs non-flower resources from plants (Requier and Leonhardt 2020) and nesting opportunities (MacIvor and Packer 2015). Plant nurseries are pertinent sites for pollinator conservation in urban areas. The use of leaf material by leafcutter bees indicates that plant nurseries could

be an important resource in urban bee conservation. Pollinators may find the plant stocks of nurseries as an ephemeral resource for two reasons. First, the use of agro-chemicals in plant nurseries can be a potential threat for the pollinators that find the nurseries an opportunity (Cecala and Wilson Rankin 2021b). Second, the constant rotation of plant stocks due to sales. Although the nursery managers and workers are aware of the damage caused by leafcutter bees, they are not aware that the bees—the friends of plants—are responsible for this, which they learnt from our interaction. While business is prime for the nurseries, we do not believe that our outreach might change their attitude towards herbivores, which include the leafcutter bees. However, we are optimistic that the customers of nurseries might bear the cost of this unusual “herbivory” for the sake of conservation of pollinators. The present study might prompt researchers and conservation practitioners worldwide to perceive plant nurseries as an opportunity for leafcutter bee conservation and address relevant questions on the ecology and evolution of leafcutter bees.

SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at <https://doi.org/10.1007/s13592-023-01039-3>.

ACKNOWLEDGEMENTS

PAS thanks SERB for a research grant (CRG/7170/AS) which partially met the travel costs of the project. We thank R. Ramasubbu for determining plant species. We also thank the two anonymous referees and Rajendran K.V. for their critical comments into the manuscript.

AUTHOR CONTRIBUTION

PAS conceived the study; PAS and VA conducted field work; VA curated data; PAS did analyses and wrote the manuscript that all authors have approved.

FUNDING

The work was supported by Science Engineering Research Board through a core research grant (7170) awarded to PAS.

AVAILABILITY OF DATA AND MATERIAL

The data will be shared to the readers upon a genuine request.

CODE AVAILABILITY

We used R program for all statistical analyses. Codes of the statistical models used in the present research can be obtained from the section “Statistical analyses”.

DECLARATIONS

Ethics approval This is not applicable for the present research.

Consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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