WILEY **Diversity** and **Distributions**

Foraging preferences of leafcutter bees in three contrasting geographical zones

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Abstract

Aim: Leafcutter bees use plants as pollen and nectar sources, but also cut leaf discs and use them to line their nests. Which plant species they choose as nesting material and why they do so have remained obscure. We asked the following: (1) How are the plant species used by leafcutter bees distributed phylogenetically? (2) Does plant choice differ across geographical regions, and if so, in what ways? (3) Are the leaf plant species natives or exotics? (4) What plant and leaf traits predict selection of plant species by leafcutter bees? And (5) Does the abundance of individuals per species in the habitat influence leafcutter bees' plant preferences?

Location: Tropical South Asia, temperate eastern Canada and US Sonoran Desert

Methods: We mapped taxa known to be used by leafcutter bees both from our own study and published literature onto the most recent angiosperm phylogeny. To determine what plant and leaf traits predict leaf selection, we monitored 6,120 individuals of 214 native and exotic plant species planted in a 3-sq. km. arboretum in Arizona and recorded leaf damage inflicted by bees.

Results: *Megachile* showed a strong preference for species in the rosid clade, particularly the phylogenetic cluster of Fabales, Fagales and Rosales. Thirty-two to forty-five percentage of the leaf plant species were exotic to a given region. Membership in the rosid clade and Fabaceae family predicted plant preference, whereas the plant species' local abundance and geographical origin did not. Leaf water content, morphotype and the presence of latex were important factors influencing plant choice, whereas leaf shape and size did not.

Main conclusion: These patterns point to plant groups whose availability should be monitored to assure persistence of leafcutter bees. Their preference for specific globally distributed plant clades, yet ability to readily adopt certain exotic plant species as nest resources, likely augments their ability to persist.

KEYWORDS
antimicrobial, biogeography, distribution, diversity, evolution, herbivory, leafcutter bee, Megachile, Megachilidae, pollinator, urban ecosystem

1 | INTRODUCTION

Megachilidae is a cosmopolitan bee family made up of 4,097 described species worldwide, making it the third largest family of bees (Ascher & Pickering, 2015). It includes the world's most extensively used managed solitary bees, *Megachile rotundata* (Pitts-Singer & Cane, 2011), and several species of economically important *Osmia* (Haider, Dorn, Sedivy, & Müller, 2014). Megachilid bees are broadly classified

into three major groups based on morphology and the material they use to line brood cells: (1) mason bees (most of which use mud and masticated plant materials), (2) resin bees (most of which use plant resin) and (3) the true leafcutter bees (most of which cut and use live leaf fragments) (Michener, 1964, 2007). Recent molecular studies although support these general phylogenetic groupings of Michener (Litman, Danforth, Eardley, & Praz, 2011; Trunz, Packer, Arrigo, & Praz, 2016), suggested that leafcutter bees arose from the dauber bees of the genus *Chalicodoma* (Trunz et al., 2016). Here, we focus on the true leafcutter bees, the genus *Megachile*. The world's single largest and most cosmopolitan bee genus, *Megachile*, includes about 1,500 species in 52 subgenera (Ascher & Pickering, 2015; Trunz et al., 2016).

Leafcutter bees nest aboveground in pre-existing cavities in rock crevices, pithy stems of trees and canes and man-made structures such as hollow metal tubes (Eickwort, Matthews, & Carpenter, 1981; Litman et al., 2011; Morato & Martins, 2006). Subterranean nesting—an ancestral habit (Eickwort et al., 1981; Litman et al., 2011)—is also reported in few drier climate species of leafcutter bees (Williams, Strand, Elzen, Vinson, & Merritt, 1986).

Most solitary bees, particularly ground-nesting species, use glandular secretions, which have hydrophobic and antimicrobial properties, to line brood cells (Kronenberg & Hefetz, 1984; Mitra, 2013). Leafcutter bees, however, do not do so (Williams et al., 1986). As a consequence, they use plant products, such as leaves and resins to line brood cells so as to protect the provision from microbial infection (Messer, 1985; Müller, Topfl, & Amiet, 1996) and from larval and pupal parasites (Eltz, Küttner, & Lunau, 2015; Kronenberg & Hefetz, 1984). Their preferred nest-lining material is leaves, giving rise to their common name. The bees cut and collect circular to elliptical leaf pieces (Figure S1) and line the brood cells with a roll of layered discs. A single brood cell may contain 50–100 leaf discs; depending on the size of the cavity, an aboveground nest may contain 1–11 brood cells (MacIvor, 2016; Sabino & Antonini, 2017), while the subterranean nests contain a single brood cell (Williams et al., 1986). The leaf discs are also used to partition the brood cells. A brood cell contains leaf discs of variable size and shape (Alqarni, Hannan, Gonzalez, & Engel, 2014; Sabino & Antonini, 2017). In cases where the leaves are very small, the bees bring to their nest entire leaves rather than pieces cut from them (Kambli et al., 2017). Individuals of most leafcutter bee species use leaves of only one plant species to make the inner layer of the roll. The bees may plug the nest using a much larger disc cut either from the same or a different plant species (Alqarni et al., 2014; Sabino & Antonini, 2017).

Which species of leaves leafcutter bees choose should have significant consequences for their nesting success (Morato & Martins, 2006). As the leaves used to line the brood cells are fresh, it is reasonable to conjecture that they are hydrophobic and have traits that limit both fungal growth in provision and invasion by parasites, such as insect parasitoids of bee larvae and pupae. Trap-nesting bees (predominantly the leafcutter bees) have many specialized parasitoids as natural enemies (Klein, Steffan-Dewenter, Buchori, & Tscharntke, 2002).

Surprisingly, information on which species of plants leafcutter bees choose and why is almost entirely lacking (but see, MacIvor, 2016; Kambli et al., 2017). We do not know whether the leafcutter bees have

preference for leaves of certain plant clades, or leaves with certain physical characteristics. This information is vital for understanding their geographical distributions, to predict nest success rates and to manage their habitats in a way that guarantees the persistence and conservation of these ecologically and economically critical pollinators. Knowledge of preferred nesting materials might further help us to predict the conservation implications of selective human removal of certain plant species. The current practice of increasing populations of leafcutter bees is to add nesting substrate, such as trap nests (Pitts-Singer & Cane, 2011). Although this will likely increase nesting opportunities, the success of such nest additions might hinge on the availability of the correct leaves. Here, we explore what leaves the bees choose.

In this study, we used our own primary data on leaf plants of leafcutter bees of south-west United States and global records on the leaf-foraging plants of *Megachile* spp. in conjunction with the most recent angiosperm phylogeny (The APG IV, 2016) to address five questions. First, how are the plant species known to be used by leafcutter bees distributed across the angiosperms? Second, does plant choice differ across geographical regions, and if so, in what ways? Third, are the most heavily used plant species in each region natives or exotics? Fourth, what plant and leaf traits predict selection of plant species by leafcutter bees? Finally, does the abundance of individuals per species in a habitat influence leafcutter bees' species preferences?

2 | METHODS

Most of the data we use here on leaf selection by leafcutter bees were drawn from the published literature (Table S2). To these, we added data from our own studies in India (Kambli et al., 2017) and southeastern Arizona (presented here). Broadly speaking, we compared data from three geographical regions: South Asia, Nearctic Canada and the Nearctic United States. In the Nearctic United States, studies other than our study in the Sonoran Desert of the United States were combined and considered separately in the analyses. We further analysed the data from one Arizona site, the University of Arizona Arboretum, in depth (see below). To determine how leaf plants of the bees were distributed phylogenetically, we mapped taxa known to be used by leafcutter bees onto the most recent angiosperm phylogeny (The APG IV, 2016). We categorized taxa within five clades suggested by The APG IV (2016): Magnoliids (the archaic and basal angiosperm plant clade), Monocots, core Eudicots (neither Rosid nor Asterid Eudicots), Rosids (including super-Rosids) and Asterids (including super-Asterids). With the exception of one exotic, managed bee species (*Megachile rotundata*) shared between the south-western United States and Canada, the bee species studied in different regions were different and were native to those regions (Table S2).

Only three studies to date (our own in India [Kambli et al., 2017] and Arizona (present study), and MacIvor, 2016) have generated a comprehensive list of plants used by leafcutter bees. However, other researchers, while studying the nesting biology of a given bee species or as part of other investigations connected to leafcutter bee ecology, have reported plant use, and we have included these data in our analyses where

TABLE 1 Summary of the number of plant taxa used by leafcutter bees for foraging leaves in different plant clades in three geographical regions. Full taxonomic information on these species is provided in Table S1 in electronic supplementary material

Clade	Number of orders	Number of families	Number of genera	Number of species
Rosid	12	27	112	206
Asterid	9	22	45	64
Core Eudicot	2	4	6	8
Magnoliid	3	3	6	6
Monocot	2	2	2	2
Total	28	58	171	286

appropriate. The three most comprehensively studied sites are urban habitats containing both native species and introduced ornamentals. Kambli et al. (2017) and MacIvor (2016) provide descriptions of their study sites. The US study took place on the University of Arizona (UA) campus ((3 sq. km. area at 32°14′55.7304′N and 110°59′14.7084″W). This site (referred to hereafter as the UA Arboretum), which is watered and maintained by the University, includes diverse plant species of both native and exotic origin. GIS coordinates, plant names and the geographical origin of every plant maintained in the Arboretum were available (https://apps.cals.arizona.edu/arboretum/map).

The methods used to determine leaf choice in different geographical regions differed markedly. Nesting biology and plant use by leafcutter bees have received the most attention in the Nearctic region (Table S1) (but see Alqarni et al. (2014) and Kambli et al. (2017)). MacIvor (2016) identified plant preferences of three leafcutter bee species (Table S1) based on DNA from leaves collected from trap nests. The study took place in temperate Canada. Kambli et al. (2017) identified leaf choices by directly observing bees cutting leaves and from the characteristic urn-shaped cut marks left on the leaves. The study took place in tropical humid peninsular India. See MacIvor (2016) and Hobbs and Lilly (1954) for methodological details.

At the UA Arboretum, leaf usage was identified by surveying plants that did and did not exhibit characteristic damage, making this the only study to date that has employed a plant community perspective. The site experiences a desert climate, but 57% of the UA Arboretum's plant species and 60% of its total stems are exotics native to Neotropical, Palearctic, Afrotropical, Indomalayan and Australasian regions. We inspected a total of 6,120 individuals of 214 broadleafed species during July 2016 and 2017, immediately after the breeding season of the bees, thoroughly examining leaves at all possible heights (using binoculars if necessary) for leafcutter bee damage. As leafcutter bees are known to have preferences according to plant subspecies, clones and hybrids (Eigenbrode, White, & Tipton, 1999; Nugent & Wagner, 1995), we included all infraspecific categories in the data separately, except for ornamental roses (11 hybrids are present in the UA Arboretum, but these were included in the analysis as a single species, *Rosa* sp.). Although it has been reported that *Megachile* spp. prefer leaves >1 cm² (Horne, 1995), we found Fabaceae with even smaller leaves used at the UA Arboretum site (*Mimosa distachya* (leaf width = 0.68 cm, *Caesalpinia pulcherrima* (leaf width = 0.78 cm)). Therefore, we included plants having leaves ≥0.68 cm width in the survey and the analyses. Plants not listed in campus records were identified with the help of experts

in UA Herbarium. Although we did not study the leafcutter bee species inflicting the damage we recorded, the highly characteristic cuts were likely to be made by the predominant *Megachile lippiae*, *M. gentilis* (pers. observ.) and other southern Arizona species listed in Armbrust (2004), Butler (1965), Eigenbrode et al. (1999) and Krombein, Hurd, Smith, and Burks (1967) (See Table S1).

We recorded a set of plant and leaf traits that were likely to influence bees' selection of resources at the UA Arboretum. Plant clade, family, genus, species, native/exotic status and abundance were recorded. Leaf size (length and width), leaf morphotype (glabrous and non-glabrous (hirsute and scabrose), leaf latex (present or absent) and leaf water content (difference between fresh wet and dry weight of 1-sq. cm oven-dried (60°C; 48 hr) young leaf) were considered as leaf traits.

2.1 | Data analyses

As the Rosid clade appeared to contain a large number of taxa used by leafcutter bees, we used the numbers of Rosid vs. non-Rosid species in all further analyses. We used binomial tests to examine whether the proportions of Rosid species, genera and families used by the bees were significantly higher than non-Rosids. We used plant species, genera, and family composition of plants used within each geographical region to determine the taxonomic level showing the highest similarity (Sorensen similarity index).

To determine factors predicting plant selection by the bees, we grouped the variables measured in this study in two and used them separately in two generalized linear models (GLMs). In one model, plant clade or family and plant abundance were used as fixed factors. In the second model, leaf traits (leaf unit weight, leaf morphotype, leaf latex and leaf size) were used as the fixed factors. We used the presence–absence of cuts in leaves of plant species as the response variable in all the models. We specified binomial error as the distribution of the data with logit link function in both the GLMs. All the analyses were performed in R 3.2.3 (R core team, 2014).

3 | RESULTS

3.1 | Leaf-foraging plants of leafcutter bees

Across geographical regions, 286 plant species from 172 genera, 57 families and 28 orders were used by leafcutter bees (Tables 1; S2). These were spread disproportionately into five clades (Figure 1a,b). Rosid species were the most commonly used leaf sources, both

worldwide (Rosid [72%] vs. non-Rosids [28%]: Binomial test: $\chi^2 = 102.01$, $p = .0000$), and within each of the three geographical regions (Canada: $\chi^2 = 25.97$, $p < .00005$; South Asia: $\chi^2 = 32.03$, $p < .00005$; SW USA: $\chi^2 = 50.28$, $p < .00005$; UA Arboretum: $\chi^2 = 35.06$, $p < .00005$) (Figure 2). Among plants used by the bees in each of the four sites, proportions of Rosid leaf-foraging plants were similar (Binomial test: $\chi^2 = 1.18$, $df = 3$, $p = .757$; Figure 2).

As expected, the compositional similarity of leaf-foraging plant species was very low among the three geographical zones (2.8% ± 1.44%; Table 2). However, similarity was relatively high at the levels of plant genus (14.73% ± 4.24%) and family (43% ± 6.17%).

In Canada and South Asia, although native plants were most commonly cut, leafcutter bees also used exotic species fairly often. In Canada, 38.9% of the leaf-foraging plants were exotics; in South Asia, 31.67% of the plants were exotics. However, these studies did not report the proportions of plants at their focal study sites that were exotic. In Arizona, where we did know the proportions of native (43%) and exotic plants (57%) available at the UA Arboretum, the bees used native (53%) and exotic plants (47%) in nearly equal proportions.

3.2 | Effect of plant and leaf traits on leaf preference

At the UA Arboretum, we identified 136 taxa (including subspecies and hybrids) with leafcutter bee damage and 78 taxa with no evident damage. Forty-two species of Fabaceae (500 plant individuals) at this site were present, and among these, 41 species (98%) were in fact used. The model that used information on leafcutter damage showed that membership in the Rosid clade was significantly associated with use by leafcutter bees (GLM: $z = 3.661$, $p = .0002$). When we used plant family as a fixed factor in the model, membership in the Fabaceae also had a significant effect (GLM: $z = 3.022$, $p = .002$). The abundance of individuals in the UA Arboretum did not predict bees' preference for a given plant species (GLM: $z = -1.455$, $p = .14$). Nor did the geographical region of origin of plant species predict bees' preferences (GLM: $F_{5,204} = 6.76$, $p = .23$). When we used the clade and abundance of individuals as the predictive variables in a mixed model, clade alone predicted leaf preference of the bees (GLM: $z = 2.641$, $p = .008$). There were no statistically significant interactions among variables. None of the latex-producing species in either the Rosid (7.69%) or Asterid
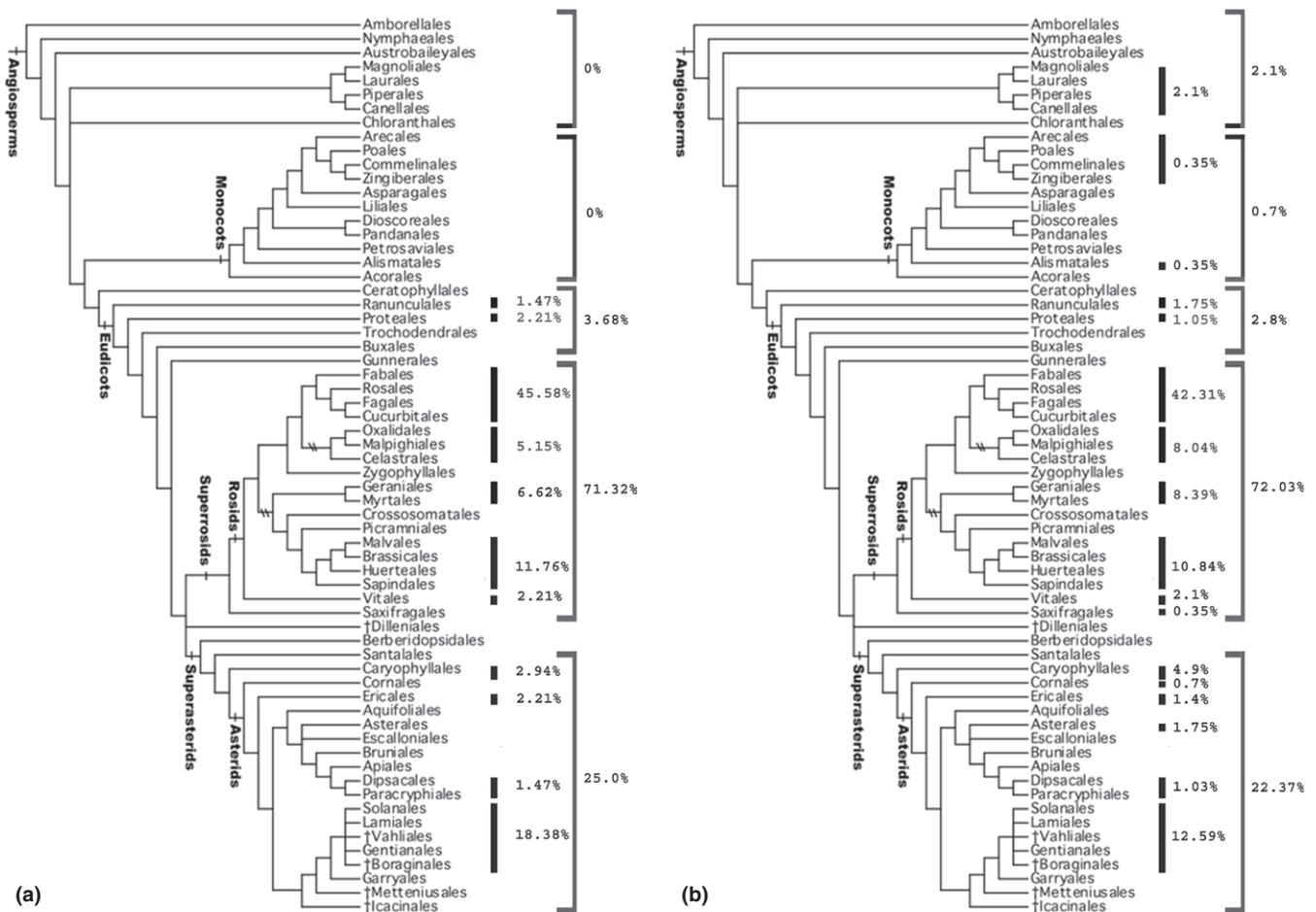

FIGURE 1 The current phylogeny of the angiosperms shows the distribution and proportion of leaf-foraging plant species of leafcutter bees within closely related plant orders (inner bars) and five major clades of flowering plants (outer parentheses) across the three geographical regions (left) and in UA Arboretum (right) suggests that Rosid plants in general and the cluster of Fabids in particular are preferred over other species. (The angiosperm phylogeny tree from: An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: The APG IV (2016): Copyright © 2016 The Linnean Society of London)
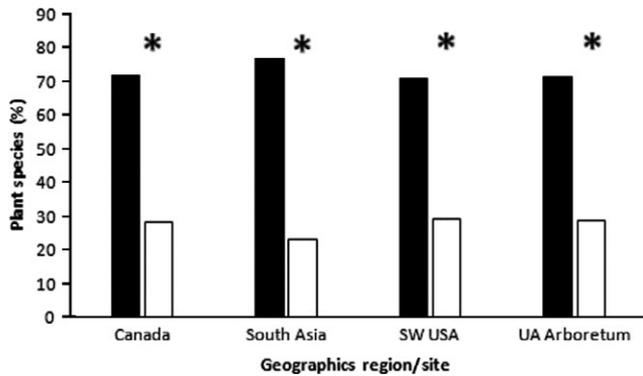
FIGURE 2 Proportions of Rosid (closed bars) and non-Rosid leaf-foraging plant species (open bars) of *Megachile* spp differ significantly within each geographical region (p < 0.00005), but not among the geographical regions (p > 0.75)

TABLE 2 Sorensen similarity index values of the species/genera/families (in sequential order) of leaf-foraging plants of leafcutter bees between pairs of geographical zones based on plant compositional data suggest that the compositional similarity is higher at higher taxa and lower at species

Geographical region	Canada	South Asia	SW USA
Canada	*		
South Asia	0/5.7/30.7	*	
SW USA	3.6/15.4/48.3	4.8/20.1/50	*

(15.94%) clade was selected by the bees. Therefore, 21 such plant species and 586 individuals were removed from further analyses. Among other leaf traits, leaf weight (GLM: $z = -3.251$, $p = .001$) and non-glabrous leaf type (GLM: $z = -2.741$, $p = .006$) had negative effects on plant selection. Leaf size had no effect on leaf preference of bees. There were no statistically significant interactions among the leaf variables.

4 | DISCUSSION

Although leafcutter bees are abundant, distributed worldwide and important pollinators of several crop plants, they have received little attention from the perspective of nesting biology, even though this information may be critical for predicting the distribution of *Megachile*, managing their habitats and assuring the persistence of healthy populations. The present study is unique in documenting the full range of plants that leafcutter bees do and do not use in a region.

Our observations suggest that plant preferences are expressed by leafcutter bees at higher taxonomic levels, such as genus, family, order or root clade. Generic and familial similarity of plants chosen by bees was high across the three regions (Table 2). As the three regions differ greatly in area and ecological history and are geographically distant from each other, it is not surprising to find very low plant species similarity across sites. To the extent to which plant species usage did overlap between the United States and South Asian sites (5.4%) (Table 2), this was attributable either to the presence of shared

exotic species (e.g., *Bouganvillea spinosa*, *Caesalpinia pulcherrima* and *Vitis vinifera*) or to the use in the US of species introduced from South Asia (e.g., *Cassia fistula*, *Dalbergia sissoo*, *Albizzia lebeck*, *Justicia adhathoda* and *Desmodium gangeticum*). For example, *Cassia fistula* is a highly preferred plant species of native *Megachile* spp. in India (Kambli et al., 2017). Even though a single *C. fistula* individual was present in the UA Arboretum, almost every leaf on every branch was heavily cut by native south-western US *Megachile*. This result also suggests that the abundance of a plant species is not a good predictor of preference by the bees.

Megachile have suggested that they are selective with regard to plant species (Hobbs & Lilly, 1954; Horne, 1995; MacIvor, 2016). However, the pattern of preference has not been clear. In this study, the leaf-foraging plants of leafcutter bees ranged from species in the most ancient angiosperm clade (Magnoliales) to the most advanced plants in the clade Asterid, but with a clear dominance of plant species in the clade Rosid. Our synthesis of the literature reveals a clear pattern of preference for Fabaceae in particular, and for Rosid species more generally. Seventy to seventy-seven percentage of the preferred plants in each of the three geographical regions we studied were the members of the Rosid clade (Figure 2). The Fabid clade (including the orders Fabales, Fagales and Rosales) included about 42% of the plants recorded as used by leafcutter bees, and the family Fabaceae alone supported 27% (74 spp.) of them across regions. In the UA Arboretum, we found that membership in the Rosid clade and Fabaceae family was the most important predictive factors of plant preference. Although globally, the Asterid clade is considerably more species rich (130,245 species) than the Rosids (84,325 species) in any terrestrial habitats (Christenhusz & Bung, 2016), Asterid species were rarely used by the bees in any of the four sites in the three geographical regions we investigated.

Megachilidae are important visitors and often the exclusive pollinators of flowers of Fabaceaen plants worldwide, including many economically important crop plants (Haider et al., 2014; Pitts-Singer & Cane, 2011). However, they very rarely exploited Asteracean plants for pollen foraging (Haider et al., 2014). Although our study was on leaf foraging, the findings of Haider, Dorn, Sedivy, and Müller (2013) are relevant to our findings. Sedivy, Dorn, Widmer, and Müller (2013) and Williams (2003) demonstrated that larvae of several species of *Osmia* (sister genus of Megachile) were incapable to complete their development on provision made up exclusively of Asteraceae plant species. In the wake of these findings, it might be worth comparing development of leafcutter bee larvae in brood cells lined by leaves of preferred Fabaceae and non-preferred Asteraceae plant species.

Leaf selection was also correlated with some leaf traits. Previous studies have suggested that leaf surface wax (Eigenbrode et al., 1999) and leaf area, but not leaf toughness (Eigenbrode et al., 1999; Horne, 1995), are predictive of use by leafcutter bees (Horne, 1995). However, such conclusions were based on observations on two or few sister species that were assessed on either of those two traits; other leaf physical traits were not considered in the analyses. In our mixed models, we used leaf dimension, leaf morphotype, fresh leaf unit weight of young leaves and leaf latex as the possible predictors

of leaf selection. We found that leaf dimensions are poor predictors of leaf selection by the bees. The bees collected cuttings from leaves of <1 cm (*Mimosa distachya*) to >25 cm (eg; *Cassia fistula*) long and <1 cm (e.g.: *M. distachya*) to >25 cm wide (eg: *Plantanus* spp.). However, as the bee collects leaf fragments of at least three different sizes and shapes (Figure S1) to construct different parts of a brood cell (Sabino & Antonini, 2017), the diversity of leaf morphotypes in a given locality might be critical to make choices. Our results further show that bees do not choose latex-producing species. In the UA Arboretum, this included all members of Moraceae and Euphorbiaceae (Rosid clade), as well as Apocynaceae, Araliaceae and Convolvulaceae (Asterid clade). Latex is likely both to entangle the mandibles of the bees and to increase the unit weight of the leaves. The bees also exhibited a significant preference for glabrous leaves over non-glabrous leaves, including those with scabrose leaves (e.g. *Lantana* spp., *Ehretia* spp.) and some with hirsute leaves. Although *Ficus* spp. (excluding *F. carica*) and *Nerium oleander* have glabrous, tender leaves, those plants were avoided, presumably because of their milky latex.

Although taxonomic preferences explain why in general bees chose closely related plant species, our research strongly suggests that they may be making some adaptive decisions with regard to particular species within preferred clades that would best be avoided. Most Fabacean and Rosacean plants are good sources of flavonoids, phenols and terpenoids (Borchardt, Wyse, & Sheaffer, 2008; Nickell, 1959), and these antimicrobial properties might explain why these plants are preferred (MacIvor, 2016; Morato & Martins, 2006). At the UA Arboretum, almost every Fabaceae is used, with the exception on one: they apparently never cut the leaves of *Piscidia mollis* (*N* = 5 trees) even though they were present in the vicinity of other preferred plant species. This species, commonly named "fish poison tree," contains lethal dose of rotenoids, a chemical family containing compounds such as rotenone, known for its insecticidal and fish sedative properties (Menichini, Delle Monache, & Bettolo, 1982). Bees also selectively avoided some plant families. For instance, the citrus family, Rutaceae, is well represented in terms of species richness (*N* = 5) and abundance (274 trees) in UA Arboretum and flushed glabrous and tender leaves during peak bee activity; however, none of those species was selected by the bees. The insect and bee repellency of the essential oils from *Citrus* and *Citrofortunella* spp. (Deshpande & Naik, 2016; Karr & Coats, 1988; Raina et al., 2007) might be the cause. Future research might investigate whether favoured species share ecological features that are absent from disfavoured species (e.g., in terms of hydrophoby or the presence of antimicrobial defences). Leafcutter bee broods are also under severe pressure from the insect parasitoids of bee larvae and pupae (Klein et al., 2002; Tscharntke, Gathmann, & Steffan-Dewenter, 1998). In India, at least 85% of the brood cells of five species of *Megachile* in trap nests were damaged by a parasitic Eulophid wasp species (Veeresh, Belavadi, & Gupta, 2015). Therefore, future research might also investigate whether the plants selected by the bees for brood cell lining were critical for the parasitism in the bee broods.

Leafcutter bees clearly do not avoid exotic plant species within their foraging habitats. This, together with the fact that they can make use of artificial tubular structures in which to nest, might explain why the leafcutter bees are plenty in anthropogenic habitats (Klein et al., 2002; Pitts-Singer & Cane, 2011). Rose and *Bouganvillea* leaves are particularly heavily used by the leafcutter bees in all the geographical regions we compared in this study, and both are plentiful in many human settlements. Indeed, about 47% of the leaf-foraging plants at the UA Arboretum are not native to desert regions of the United States. The majority of the preferred exotics at that site are of Palearctic (30%) or Neotropical (21%) origin. Although the proportion of leaf-foraging plant species from other biogeographical zones is relatively low (Afrotropics, 7.31%; Indo-Malaya, 3.8%; Australasia, 1.9%), the most heavily exploited plant species (plants on which over 60% of the branches bore cut leaves; P.A. Sinu & J. Bronstein, personal observation) include some from these regions. These include *Cassia fistula*, *Dalbergia sissoo*, *Albizzia lebeck* (all from India), *Colophospermum mopane*, *Bolusanthus speciosus*, *Bauhinia bowkeri* (all from the Afrotropics), *Brachychiton populneus* and *Brachychiton rupestris* (Australasia). Consistent with the phylogenetic patterns of preferences we have discussed above, all those species except *B. populneus* and *B. rupestris* (Malvaceae) are Fabaceae. Our interpretations of the bees' preferences for exotic plant species are limited to our findings from the UA Arboretum. Although MacIvor (2016) and Kambli et al. (2017) found that leafcutter bees collected leaves from exotic plants in their sites, they did not provide data on the proportion of species at their study sites that were exotics, or the proportion of exotic species used by the bees. Further community-wide surveys in other regions of the world are clearly needed.

Another major finding of this study was that local abundance of a plant species was not a criterion for selection by leafcutter bees. Many plant species that were heavily exploited across the 2 years of this study are represented by very few individuals in the UA Arboretum. At least thirteen heavily cut plant species in UA Arboretum had only one individual tree. This adds further evidence that leafcutter bees are highly selective. Simultaneously, every individual of some very abundant species (over 50 individuals) were used even though they were widely distributed across the large Arboretum. *D. sissoo*, *Lagerstromia indica*, *Fraxinus velutina* and *Bouganvillea spinosa* are such examples.

5 | CONSERVATION IMPLICATIONS

One of the major challenges of today is to understand and find ways to reduce biodiversity loss and to increase populations and species in ecosystems. The decline of insect pollinators—a major functional group of terrestrial biodiversity—is a global concern (Potts et al., 2010). The reasons are many, but loss of foraging and nesting habitats are key reasons for this decline (Eltz, Brühl, van der Kaars, & Linsenmair, 2002; Potts, Vulliamy, Roberts, & O'Toole, 2005; Potts et al., 2010). Certain leafcutter bees are well-studied, important pollinators in natural and agricultural landscapes (Pitts-Singer & Cane, 2011); however, their requirement for leaves of a limited set of species has been given limited attention. Through the present study, we

contribute to filling that critical gap. Our study suggests that, unlike other bees, populations of leafcutter bees might be affected not only by availability of floral resources, but also by availability of a second group of plants, those whose leaves are used to line their brood cells. Further, we argue that the highly characteristic leaf damage in a given area might be an index for predicting population size of these critical pollinators. Most of the studies on leafcutter bee nesting ecology have focused on anthropogenically altered habitats, such as urban ecosystems and agroecosystems. Urban ecosystems particularly might offer plentiful nesting sites in buildings, parks and streets. In agroecosystems, trap nests might increase nest opportunities, but nesting success might hinge on the presence of brood-friendly leaves. Leafcutter bees make cuttings of three shapes and sizes to line brood cells (Sabino & Antonini, 2017); the outer cover is made up of a large leaf fragment (MacIvor, 2016). Therefore, broadleaves are very critical for the bees to make choices. Leaf preferences vary among *Megachile* spp. (MacIvor, 2016). Recent studies in eastern Canada (MacIvor & Moore, 2013) and Dubai (Gess & Roosenschoon, 2017) have found plastic fragments being used in place of large leaf fragments to close individual brood cells. Although these behaviours might be incidental, these findings indirectly suggest that the bees might be limited by the abundance of broadleaf plants in those localities. To conserve leafcutter bee diversity, it might be critical to maintain a diversity of leaf sources. That leafcutter bees readily cut exotic plants is a matter of conservation significance as well. Planting preferred, fast-growing ornamental species in cities and near agroecosystems might help to increase diversity and numbers of leafcutter bees.

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Author contributions: PAS and JB conceived the idea for this study; PAS analysed the data; PAS and JB wrote the manuscript. Authors report no conflict of interest.

SUPPORTING INFORMATION

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