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Stingless Bee (Apidae: Apinae: Meliponini) Ecology

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Keywords

bee-keeping, honey, pollen, social bees, resin, tropics

Abstract

Stingless bees form perennial colonies of honey-making insects. The >600 species of stingless bees, mainly Neotropical, live throughout tropical latitudes. Foragers influence floral biology, plant reproduction, microbe dispersal, and diverse ecosystem functions. As tropical forest residents since the upper Cretaceous, they have had a long evolutionary history without competition from honey bees. Most stingless bees are smaller than any *Apis* species and recruit nest mates to resources, while their defense strategies exclude stinging behavior but incorporate biting. Stingless bees have diversified ecologically; excel in nesting site selection and mutualisms with plants, arthropods, and microbes; and display opportunism, including co-opting plant defenses. As their biology becomes better known, applications to human endeavors are imposing selective pressures from exploitation and approaches to conservation that entail colony extraction from wildlands. Although some meliponines can adjust to new conditions, their populations shall require tropical diversity for survival and reproduction.

There is a whole new world awaiting the person who determines what individuals actually do and what intrapopulation variation there is in these characteristics. Such a study must, however, take great care to distinguish between the environmental cues used and the selective pressures that led to a phenotype that would respond to those cues.

—D. H. Janzen (68, p. 1)

1. INTRODUCTION

It has long been thought that Cretaceous meliponines were the first honey-bees, and they recruited nest mates to flowers; their queens could not fly after fertilization, and neither the queen nor worker caste had a stinger (see the sidebar titled Noteworthy Stingless Bee Attributes). All of this may be true, but such assertions currently lack an evolutionary chronology. Like the tropical plants that Janzen (68) ecologizes, much remains to be learned about stingless bee (SB) biology, ecology, and evolution (174). My goal in this review is to synthesize the ecology and evolution of SBs. Readers interested in behavior or taxonomy are referred to References 51, 58, 94, 146, and 174, and those interested in pollination biology to References 136, 152, and 168.

Characterization of the more than 600 species of SBs across the tropics is not easy. However, their colonies are in many ways like trees in tropical forests, where ecological interactions daily unfold. Placed within their communities, a queen may live for a year, a worker or male may live for weeks or months, and a colony can last for decades (58, 138, 170). In Cretaceous times, 90 million years ago (mya) (51, 125), one might suppose that SBs sometimes used dinosaur tears, recruiting nestmates to amino acids and nutrients as tiny Asian Meliponini do today (8, 9). The Chicxulub asteroid impact curbed plant photosynthesis and flowering. It removed the dinosaurs, but SB evolution continued apace. Some now forage on vertebrate sweat, motivated by a lack of salt in their diet of honeydew from Hemiptera or by sodium scarcity (42, 44, 75, 137, 140) (**Figure 1b**). There are also some unsavory habits of SBs in resource selection (Section 5.1). An ancient origin of such traits is a distinct possibility.

Comparisons between SBs and honey bees (HBs) in terms of, e.g., microbial ecology (13, 74, 76, 78; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript), nestmate recruitment to resources (28, 58, 91, 117, 120, 123, 133, 149, 171, 172), floral preferences (54, 57, 60, 72, 81, 116, 118, 122, 129, 133, 139, 142), or colony defense (58, 59,

NOTEWORTHY STINGLESS BEE ATTRIBUTES

1. Relatively small, stingless workers (2–15 mm)
2. Pantropical distribution, nesting predominantly in living trees, sometimes in subterranean cavities or exposed on branches or cliffs; rarely in ant or termite nests
3. Small, medium, and large colonies (100–10,000+ individuals)
4. Infrequent, directed swarming with preparation of a new nest site by the female parent colony prior to departure of the swarm—workers and a new (flight-capable) queen, who mates there
5. Queens are physogastric when gravid; cannot fly; and, like workers, lack a stinger
6. Males forage and are self-supporting
7. Stored honey and pollen are often highly acidic
8. Foragers recruit nestmates to resources, mediated by intra- and extranidal communication
9. In-nest mixing of self-secreted wax and saliva with collected resin create cerumen used to build containers for food and broods in diverse architecture

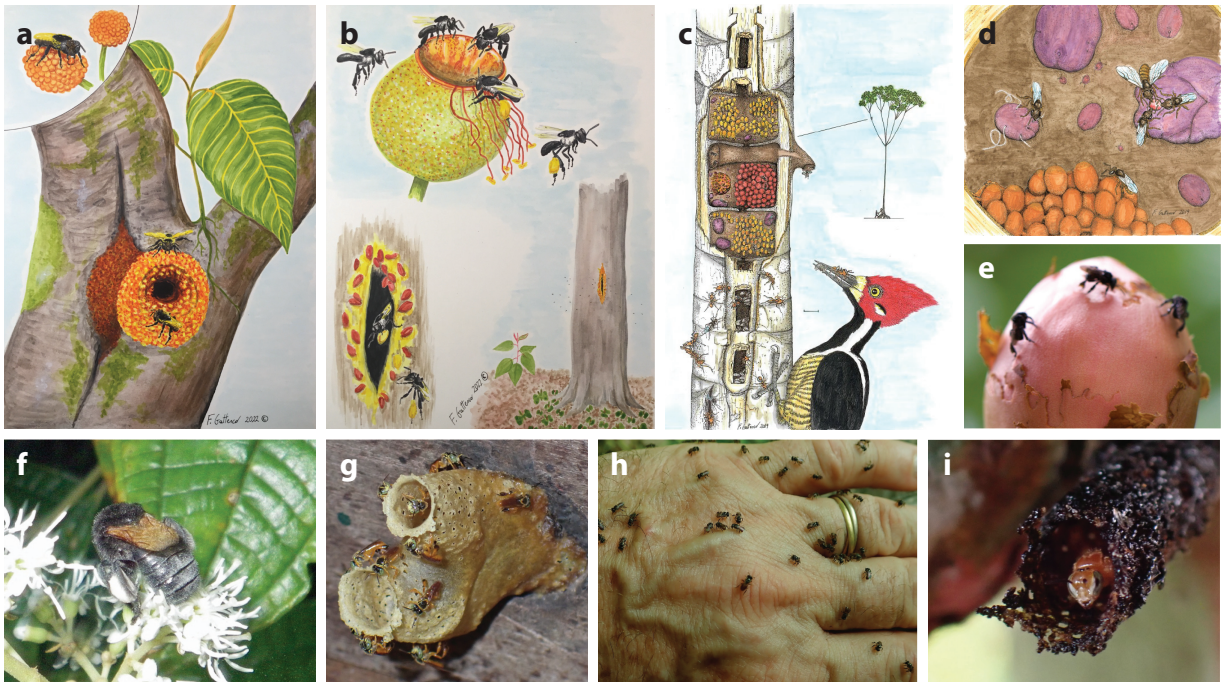


Figure 1

(a) *Melipona fallax* worker foraging building material from fruit of *Coussapoa*, forming the nest entrance with its seeds and waxy material, thus allowing the hemiepiphyte plant to grow on the bee nest tree. (b) *Tetragonula* worker foraging resin from fruit of *Corymbia*, dispersing seeds in flight and depositing resin and seeds around the nest entrance. (c) Hammerhead woodpecker (*Dryocopus*) predating ants and nesting *Plebeia* (*Nanoplebeia*) sp. living with hemipteran *Cryptostigma* females in hollow internodes of living *Cecropia*, showing an internal nest entrance ring made of resin and resin deposit, brood cells, and pollen storage pots. (d) Inside a nest of *Plebeia* (*Nanoplebeia*), showing three workers taking honeydew from large female *Cryptostigma* sp. (Hemiptera: Coccidae), a worker removing wax strands from a smaller female, females and crawlers in the nest, and brood cells. (e) *Trigona fuscipennis* worker chewing buds of *Brownea* to remove nesting material. (f) *Melipona fallax* buzz-foraging *Miconia* and covered with its pollen. (g) Double nest entrance tube of *Tetragonisca angustula* made of flexible cerumen. (h) *Plebeia* (*Nanoplebeia*) spp. foraging sweat on the author's hand. (i) *Plebeia* (*Nanoplebeia*) *franki* worker guarding its nest entrance tube made of firm resin-cerumen. Drawings courtesy of F. Gattesco from photos by the author and inspired by the book by T. A. Heard (63).

173) reveal similarities and differences, explored below. Competition for resources is important (37, 75, 121, 124, 130, 170). Molecular phylogenetic analysis (13, 86, 123, 125) indicates that SBs coalesced from the same ancestral lineage as *Apis*, but SBs are twice the age of *Apis* and not direct ancestors. In both SBs and HBs, stored food and brood attract natural enemies of all kinds (58, 131, 139) (Tables 1 and 2; see the sidebar titled Examples of Stingless Bee Natural Enemies).

There is evidence that, compared to HBs, SBs became better at biting or sheltering in place. SBs are frequently opportunists and mutualists. In addition, the appearance of HBs as constant competitors—within the last 400 years in the Americas and Australia due to human activity (93, 149) but since 40 mya in the Old World—helped to shape SB evolution. Intensified agriculture and the exploitation of SBs for materials and pollination underscore that humans can also influence SB ecology and evolution.

2. COLONY LIFE AND COMMUNITY ORGANIZATION

SB colonies cannot move. Populations are viscous, and forests contain many SB nests per hectare (26, 50, 58, 66, 70, 139). When a colony does reproduce, it is via a single drone or a singly mated

Table 1 Arthropod natural enemies of stingless bees

Order	Genus and species	Family	Region and prey or host
Hymenoptera	<i>Bembix flava</i>	Bembicidae	Australia; male <i>Tetragonula</i>
Hymenoptera	<i>Bembix tuberculiventris</i>	Bembicidae	Australia; <i>Tetragonula</i> , <i>Austroplebeia</i>
Hymenoptera	<i>Oecophylla smaragdina</i>	Formicidae	Asia; stingless bees
Hymenoptera	<i>Eciton</i> spp.	Formicidae	Neotropics; <i>Melipona</i> , etc.
Hemiptera	<i>Apiomerus</i>	Reduviidae	Neotropics; <i>Melipona</i> , etc.
Hymenoptera	<i>Neivamyrmex</i>	Formicidae	Neotropics; <i>Plebeia</i> , etc.
Hymenoptera	<i>Syntretus trigonaphagus</i>	Braconidae	Australia; <i>Tetragonula</i>
Diptera	<i>Melaloncha</i>	Phoridae	Neotropics; <i>Cephalotrigona</i> , <i>Scaptotrigona</i> , etc.
Diptera	<i>Pseudohypocera kerteszi</i>	Phoridae	Neotropics; many host genera
Diptera	<i>Dobrniphora trigonae</i>	Phoridae	Australia; <i>Tetragonula</i>
Diptera	<i>Ceriana ornata</i>	Syrphidae	Australia; <i>Tetragonula</i> , <i>Austroplebeia</i>
Diptera	<i>Hermetia illucens</i>	Stratiomyidae	Neotropics, invasive; general
Coleoptera	<i>Aethina tumida</i>	Nitidulidae	Africa, invasive; <i>Dactylurina</i> , <i>Meliponula</i> , general
Acari	<i>Pyemotes tritici</i>	Pyemotidae	Neotropics; <i>Friesomelitta</i> , <i>Tetragonisca</i> ^a
Coleoptera	<i>Haptoncus luteolus</i>	Nitidulidae	Asia; stingless bees
Coleoptera	<i>Procoryphaeus wallacei</i>	Histeridae	Asia; stingless bees
Coleoptera	<i>Cleidostethus meliponae</i>	Cucujidae	Africa; stingless bees
Hymenoptera	<i>Lestrimelitta</i> (20+ spp.)	Apidae	Neotropics; <i>Scaptotrigona</i> , <i>Melipona</i> , <i>Plebeia</i> , others
Hymenoptera	<i>Liotrigona</i> (<i>Cleptotrigona</i>) <i>cubiceps</i>	Apidae	Africa; stingless bees

^aManagement issue.

Data taken from References 58, 63, and 133 and the author's personal observations.

queen. When two such individuals succeed, Darwinian fitness is equal to 1; the little field data available indicate that colonies may require two decades to replace themselves (57, 67). Most important, workers always prepare a preswarming nest site (17, 117, 138, 170), a behavior dubbed directed swarming in this review. Although not assured success, the queen and daughter colonies are thereby given food, shelter, and a direct route to security from the mother nest. The new queen mates with one male near that new nest. After its formation, a daughter colony may take resources from the mother colony (170, 174), but documentation of the process is meager. Males of multiple colonies (21) compete for mating opportunities near nests, resulting from queen mortality or colony foundation. The males seem better suited to locating mating sites than females, although females share similar flight capability (65, 103, 154). The presumptive benefit of farther or more male flights is to minimize risks undergone by exposed virgin queens. Males can forage and shelter far from natal nests and also enter other nests (58). In concert, single mating and directed swarming promote local selection and adaptation by SB colonies.

Nuanced dynamics within colonies reduce inbreeding and maintain genetic diversity. A flightless gravid queen has mated only once and cannot disperse, and she or her offspring may be rejected or replaced (170); males are sometimes the offspring of workers (164, 170). Furthermore, males and workers can be the offspring of a mated queen from another nest (164). A newly fertilized queen, prior to becoming gravid and unable to fly, may be accepted by a queenless colony—as has been observed among Neotropical *Melipona* in meliponaries, the SB equivalent to an apiary.

Strict nesting site and dispersal limitations are exemplified in the widespread Neotropical species *Trigona fulviventris*, which has been researched in large study plots of dry forest in Costa Rica and moist forest in Panama (66, 142). Colonies nest underground at the bases of large trees within immense egg-shaped nodules of resin (142). Colonies were found to be overdispersed

Table 2 Supraspecific stingless bee groups (genus or subgenus) and associated microbes, studied using laboratory cultures or RNA amplicon techniques

Stingless bee	Microbe(s)	Reference(s)
Neotropical		
<i>Asperplebeia</i> ^a	NA	NA
<i>Cephalotrigona</i> ^{a,b}	NA	NA
<i>Duckeola</i> ^{a,b}	NA	NA
<i>Friesella</i> ^{a,b}	NA	NA
<i>Frieseomelitta</i> ^{a,b,c}	<i>Bifidobacterium</i> <i>Lactobacillus</i> <i>Starmarella</i>	33, 92; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript
<i>Geotrigona</i> ^{a,b,c}	NA	NA
<i>Lestrimelitta</i> ^{a,b}	NA	NA
<i>Melipona</i> ^{a,b,c}	Acute paralysis virus Deformed wing virus <i>Bacillus</i> <i>Bifidobacterium</i> <i>Critibidia</i> <i>Lactobacillus</i> <i>Melissococcus</i> <i>Micromonospora</i> <i>Paenibacillus</i> <i>Snodgrassella</i> <i>Streptomyces</i> <i>Aspergillus</i> <i>Candida</i> <i>Curvularia</i> <i>Monascus</i> <i>Monila</i> <i>Nigrospora</i> <i>Penicillium</i> <i>Starmarella</i> <i>Talaromyces</i> <i>Trichoderma</i>	10, 13, 17, 23, 33, 90–92, 96, 109; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript
<i>Melivillea</i> ^{a,b}	NA	NA
<i>Nannotrigona</i> ^{a,b,c}	Acute paralysis virus Deformed wing virus Black queen cell virus <i>Lactobacillus</i>	17, 33; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript
<i>Nogueirapis</i> ^{a,b}	NA	NA
<i>Oxytrigona</i> ^{a,b,c}	<i>Bifidobacterium</i> <i>Lactobacillus</i>	92; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript
<i>Paratrigona</i> ^{a,b,c}	<i>Kodamaea</i> <i>Metschnikowia</i>	33, 165
<i>Paratrigonoides</i> ^{a,b}	NA	NA

(Continued)

Table 2 (Continued)

Stingless bee	Microbe(s)	Reference(s)
<i>Partamona</i> ^{a,b,c}	<i>Bifidobacterium</i> <i>Gilliamella</i> <i>Lactobacillus</i> <i>Snodgrassella</i>	23, 76, 92; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript
<i>Plebeia</i> ^{a,b,c}	<i>Bifidobacterium</i> <i>Lactobacillus</i> <i>Candida</i> <i>Metschnikowia</i>	13, 33, 92, 165; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript
<i>Plectoplebeia</i> ^a	NA	NA
<i>Ptilotrigona</i> ^{a,b,c}	<i>Candida</i>	13, 33, 92
<i>Scaptotrigona</i> ^{a,b,c}	<i>Bacillus</i> <i>Bifidobacterium</i> <i>Lactobacillus</i> <i>Candida</i> <i>Kodamaea</i> <i>Metschnikowia</i> <i>Monascus</i> <i>Zygosaccharomyces</i>	13, 33, 92, 96, 109, 165; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript
<i>Scaura</i> ^b	NA	NA
<i>Schwarzula</i> ^b	NA	NA
<i>Tetragona</i> ^{a,b,c}	Acute paralysis virus Deformed wing virus Black queen cell virus <i>Bifidobacterium</i> <i>Gilliamella</i> <i>Lactobacillus</i> <i>Kodamaea</i>	17, 33, 76, 92, 165; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript
<i>Tetragonisca</i> ^{a,b,c}	Acute paralysis virus Deformed wing virus Black queen cell virus <i>Snodgrassella</i> <i>Streptomyces</i> <i>Aspergillus</i> <i>Candida</i> <i>Curvularia</i> <i>Fusarium</i> <i>Metschnikowia</i> <i>Monila</i> <i>Mucor</i> <i>Nigrospora</i> <i>Starmarella</i> <i>Trichoderma</i>	13, 17, 23, 33, 90–92, 165; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript
<i>Trichotrigona</i> ^{a,b}	<i>Lactobacillus</i>	JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript

(Continued)

Table 2 (Continued)

Stingless bee	Microbe(s)	Reference(s)
<i>Trigona</i> ^{b,c}	<i>Bacillus</i> <i>Bifidobacterium</i> <i>Gilliamella</i> <i>Lactobacillus</i> <i>Snodgrassella</i> <i>Curvularia</i> <i>Rhizopus</i> <i>Starmarella</i>	13, 23, 33, 76, 91, 92, 96, 105, 109; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Weislo, unpublished manuscript
<i>Trigonisca</i> ^b	NA	NA
<i>Aphaneura</i> ^a	NA	NA
<i>Leurotrigona</i> ^{a,b}	NA	NA
<i>Melikerria</i> ^{a,b,c}	NA	NA
<i>Michmelia</i> ^{a,b,c}	NA	NA
<i>Mourella</i> ^{a,b}	NA	NA
<i>Necrotrigona</i> ^{a,c}	NA	NA
<i>Parapartamona</i> ^{a,b}	NA	NA
<i>Schwarziana</i> ^{a,b}	NA	NA
<i>Schwarzula</i> ^b	NA	NA
Afrotropical		
<i>Axestotrigona</i> ^{a,c}	<i>Bifidobacterium</i> <i>Lactobacillus</i>	160
<i>Dactylurina</i> ^{a,c}	<i>Bifidobacterium</i> <i>Lactobacillus</i>	160
<i>Hypotrigona</i> ^{a,c}	<i>Bifidobacterium</i> <i>Lactobacillus</i>	160
<i>Liotrigona</i> ^{a,c}	<i>Bifidobacterium</i> <i>Lactobacillus</i>	160
<i>Meliplebeia</i> ^{a,c}	<i>Bifidobacterium</i> <i>Lactobacillus</i>	160
<i>Meliponula</i> ^{a,c}	<i>Bifidobacterium</i> <i>Lactobacillus</i>	160
<i>Plebeina</i> ^{a,c}	<i>Bifidobacterium</i> <i>Lactobacillus</i>	160
<i>Plebiella</i> ^a	NA	NA
<i>Apotrigona</i> ^a	NA	NA
<i>Cleptotrigona</i> ^a	NA	NA
Paleo-Australian		
<i>Austroplebeia</i> ^{a,c}	<i>Acinetobacter</i> <i>Lactobacillus</i>	33, 96, 159
<i>Geniotrigona</i> ^{a,c}	NA	NA
<i>Heterotrigona</i> ^{a,c}	<i>Lactobacillus</i> <i>Fructobacillus</i>	33
<i>Homotrigona</i> ^{a,c}	NA	NA

(Continued)

Table 2 (Continued)

Stingless bee	Microbe(s)	Reference(s)
<i>Lepidotrigona</i> ^{a,c}	<i>Carnimonas</i> <i>Escherichia-Shigella</i> <i>Pseudomonas</i> <i>Psychrobacter</i> <i>Snodgrassella</i>	96, 154, 159
<i>Lisotrigona</i> ^a	NA	NA
<i>Papuatrigona</i> ^a	NA	NA
<i>Pariotrigona</i> ^a	NA	NA
<i>Tetragonula</i> ^{a,c}	<i>Acinetobacter</i> <i>Carnimonas</i> <i>Escherichia-Shigella</i> <i>Lactobacillus</i> <i>Lysinibacillus</i> <i>Nosema</i> (protozoan) <i>Pseudomonas</i> <i>Psychrobacter</i> <i>Snodgrassella</i> <i>Streptomyces</i> <i>Rhizopus</i>	33, 49, 91, 92, 96, 154, 159
<i>Wallacetrigona</i> ^{a,c}	NA	NA
<i>Borneotrigona</i> ^{a,c}	NA	NA
<i>Lophotrigona</i> ^{a,c}	NA	NA
<i>Platytrigona</i> ^{a,c}	NA	NA
<i>Sabulotrigona</i> ^{a,c}	NA	NA
<i>Sundatrigona</i> ^{a,c}	NA	NA
<i>Tetragonilla</i> ^{a,c}	<i>Rhizopus</i>	47
<i>Tetrigona</i> ^{a,c}	NA	NA

^aGenus or subgenus name following Reference 51.

^bGenus name following Reference 20.

^cSpecies for which at least one study has been conducted.

Abbreviation: NA, not applicable.

(uniformly distributed) in dry forest, but in moist forest, they occurred in a straight line following a LiDAR-detected dry stream bed. One observed colony killed another, as sometimes occurs between kleptoparasitic *Lestrimelitta* that compete for victim SB colonies (59, 139, 142). Because 230,000 trees and 40 of the same size and species that hosted the eight *T. fulviventris* were

EXAMPLES OF STINGLESS BEE NATURAL ENEMIES

Many predators [such as birds (see also **Figure 1c**) and dragonflies, e.g., Anax] take stingless bees in flight. There are persistent predators at nest entrances, including salticid spiders and lizards such as *Tropidurus hispidus* in the Neotropics and *Hemidactylus mabouia* worldwide. Studies of bee defenses against these predators have seldom been made; bee-keepers protect their hives by placing an inverted funnel collar around hive entrances. Various toads, especially the cane toad, *Rhinella*, stand and consume bees at nest or hive entrances. While many invertebrates are minor predators, the social insects and vertebrates eat far more bees or nest contents. Bears, anteaters, apes, armadillos, civets, procyonids, pangolins, aardvarks, humans, and mustelids are among the macropredators.

scattered in the 75 ha Panama study plot, there was no tree species preference, but instead a consistent topographical choice. No investigation has been made of subsoil conditions for nesting SBs, but pre-existing cavities were essential for the populations in this study. SB nesting preferences, resource requirements (50, 66, 70; see Section 5), and colony competition must be better known to understand the factors that shape colony number or size per unit area, survival and reproduction, and many other subjects.

3. DISTRIBUTION AND ABUNDANCE

The origin of SBs and the entire corbiculate (hindleg pollen-basket) clade of bumble bees, orchid bees, SBs, and HBs was Neotropical (86); SB diversity evolved in the Neotropics over at least 80 million years (125). Deep ocean already separated Africa from South America throughout this time, and multiple dispersal modes must have been used by SBs (58, 125). However, fewer species live in Old World forests. There are approximately 10–20 species in all of Australia or in any single African or Asian tropical locale (58, 91, 138, 146).

SB richness is far greater in the Neotropics than in other regions (174). In contrast, all HBs are Asian save one—the African lineage *Apis mellifera* (94, 146). Although these observations led to the hypothesis that SB diversity is related to resource competition with HBs (133), thereby making SB or HB geographic dominance inversely related, additional hypotheses apply.

Honey storage potentially evolved among tropical bees to reduce competition (68) and to make it possible to hoard food (or nesting materials) to be used during scarcity. SB colonies store both pollen and honey that can last the colony a few months (136; see Sections 4 and 5). These stores can also allow marine dispersal of colonies via rafting. Terrestrial nesting (139) likely prevented arrival of minute *Pariotrigona* or *Lisotrigona* in Australia from Southeast Asia (8, 9), for example, because nests underground or among rocks cannot float. In contrast, tiny bees that had multiple nests in floating trees or vegetation mats may well have dispersed populations while avoiding inbreeding. Small size has been repeatedly documented in fossilized taxa (51, 58). SB diasporas were thus often made up of tiny Meliponini a few millimeters in length. Tiny meliponines inhabit almost all tropical forests, whereas large species are quite restricted (see below).

3.1. Comprehending Stingless Bee Global Patterns

The usual latitudinal gradient encountered with insects is higher diversity and richness in the tropics. In contrast, bee communities and richness often show the reverse trend, largely understood to be the result of perennial bees colonies—the SBs and HBs. Competitive interactions hypothetically led to the reverse latitudinal gradient in bee species. Some middle latitudes have more bee species per habitat than any equatorial forest, but only in the Old World do they contain the perennial colonies of *Apis*. The omnipresence of bee colonies in the tropics may severely limit bee diversity due to niche pre-emption (134, 135). A continental gradient in eusocial bee diversity (93) also appears to be linked to competition for food and nesting resources.

Bee colonies, whether those of HBs or SBs, apparently limit general bee species richness, all other things being equal. Yet there are additional explanations for this phenomenon (107). One is biogeographical, considering isolation by barriers; a second is botanically driven; and a third includes the time since colonization or divergence, as well as extinction rates. The appearance of HBs in any part of the world would lower SB diversity and success. However, habitat disturbance often corresponds with HB distribution by humans, and therefore the roles of different selective factors, including interspecific competition, are often difficult to assess. There are at least 80 formal supraspecific names applied to SBs (51), as suggested by recent inquiries. Attendant biogeographic studies should soon follow and be used to test hypotheses.

3.2. Explaining the Richest Highly Eusocial Bee Communities

The skewness of SB species distribution, with 80% of the world's species being Neotropical (5, 140), makes biogeography central to understanding SBs. Importantly, no HB is native to the New World. The recent discovery that a western Amazon field station has almost as many SB species as found in the entire Old World (140) underscores the diversity divide. Australia has two SB genera, whereas there are nine in Asia, eight in Africa, and 26 in the Neotropics (51, 58) (**Table 2**). Isolation, mountain ranges, and large arid areas have helped to create relatively depauperate SB faunas while likely leading to the prevalence of other solitary or seasonal bees (93, 133). Considering SB fauna by country area, Costa Rica is richest with nearly 70 species in 55,000 km², while India and Australia have the lowest richness (146). Approximately 400 species occupy South America (110, 140), while another 100 occur from Mexico to Panama (18, 20, 167, 168). These subcontinents share few species. The Old World contains approximately 120 SB species, 30 of them African. In the most diverse SB community studied, that of the Yasuní Biosphere Reserve, Ecuador, 40% of the recorded 100 SB species are still unnamed, and 25% are small or tiny (140, 141).

Drought, deserts, winter, or prolonged dry seasons often thwart development of rich biotic communities. In contrast, high floral diversity and lack of an extensive dry season best explain the high insect biotic diversity in Amazonian and other tropical forests (12, 45, 140). SBs follow this trend but are unique, as seen in their likely response to HB competition. In Yasuní, the lack of a dry season and an unrivaled 3,000 native tree species, 600 vines and lianas, and 1,000 herbs afford SBs many resource options. Evidence from 30 forest fragments in Costa Rica (15) and in tropical Australia also suggest that plant diversity increases SB species richness (46, 71, 163); moreover, forest degradation in equatorial Africa decreases SB species richness (73). In Yasuní, the fact that the forest grows on low rolling hills allows light environments to vary. As known by Kayapó tribal SB experts in central Amazonia, along with thousands of human generations in the tropics, regenerating forest patches and varied light environments correlate with SB diversity (18, 72, 116, 140), particularly when surrounded by an older forest.

3.3. Explaining Bee Size Distributions

There is no robust analysis of bee diversity, and a distributional listing (93, 107) fails to evaluate competition from perennial colonies. The richness and abundance of flower species broadly correlate with tropical SB diversity (12), but this trend excludes extinction data. Size seems to affect the evolution of highly eusocial bees, since the largest SB and HB workers have similar masses (58, 134, 149, 157). Furthermore, small *Apis* species have similar masses to medium-sized SBs, but most SBs are smaller than small HBs. This must reduce competition. Large SB species—most Neotropical *Melipona*, some *Trigona*, *Duckeola*, *Ptilotrigona*, *Cephalotrigona*, and some African *Meliponula*—evolved in environments with no HBs or with only one *Apis* species present. Asian SBs are dominated by *Tetragonula* of varied size, but only four Asian SBs reach even medium size (6–8 mm), similar to a small Asian *Apis* or small *Melipona*. SB and HB foraging niches and frequency of flower visitation most likely are determined by forager size, regardless of phytochemistry, but many research avenues are needed to assess generalization or specialization in foraging niche (see Section 5).

4. DEFENSE STRATEGIES AND SOLUTIONS

4.1. Guards and Nest Construction

SBs can no longer sting, but they have other modes of defense (58, 139). Workers are chemically labeled, which permits nest mate recognition and further classification by other bees (102). Why

SBs lost one of their primary lines of defense is unknown, but the tiny meliponines like contemporary *Plebeia*, *Trigonisca*, *Hypotrigona*, *Liotrigona*, *Lisotrigona*, and *Pariotrigona* (Table 2) were likely too small to manage effective stinging. Their defense strategies have thus diversified.

SBs of all sizes carefully select preformed cavities. The colonies shelter in solid constructs including underground, in hardwood trees or lianas, or in an exposed nest on rock or wood. Nest walls are reinforced with hard resin, bee fecal pollen exines (143), mud-clay, or pebble barriers. Sticky resin provides glue for the colony constructs; vertebrate feces or resin deposits in the nest are rigorously applied to invaders by *Melipona* and *Trigona*, which carry resin or mixed materials on their hindlegs; however, these behaviors are seldom studied (58, 139, 150, 173).

Workers of species that always make exposed or vulnerable nests predictably bite intruders, but so do roughly half of all species regardless of nest type (see the sidebar titled Examples of Stingless Bee Natural Enemies); biting is rarely combined with spitting formic acid (Neotropical *Oxytrigona*), but much more commonly involves applying resin and release of alarm pheromones and acrid odors (58, 133, 148, 173). Soldier workers are slightly larger than others. They may repel raiding obligate kleptobiotic colonies, such as those of *Lestrimelitta* (over 20 spp.; see 18) in the Neotropics, *Liotrigona* (*Cleptotrigona*) *cubeiceps* in Africa, and possibly *Trichotrigona* in the Amazon; they remain best studied in a Neotropical species (58, 59). Nest raiding within species seems rare. Obligate kleptoparasites must reproduce by usurping a host nest, but Neotropical *Tetragonsia angustula* may turn a raid by a robber into nest usurpation by the victim (139). Information on intraspecific nest robbing or aggression that leads to colony death is fragmentary at best, and obtaining more information would shed light on soldier subcaste evolution and kleptobiosis.

4.2. Nest Component Complexity

Colonies procure living symbionts while harvesting food, resins, latex, gum, or mud, which also may carry secondary plant metabolites or other chemicals that are repellent or antimicrobial (115, 150; see Section 5). Resin flavonoids function as antimicrobials within the nest, while terpenoids repel ants at nest entrances (58, 173), but these functions are only the beginning.

Meliponines certainly have co-opted phytochemical adaptations against ants and vertebrates. Seeds that are protected from vertebrate herbivores sometimes result in plants that have fruit with resins or waxes used by SBs. This presumably led to pollination mutualisms (see below). Resins are applied at the SB nest entrance and renewed after disturbances by large animals (see the sidebar titled Examples of Stingless Bee Natural Enemies) or attack by salticid spiders, lizards, ants, and others (Table 1); entrance borders are often sticky (58, 139, 173) (Figure 1).

As SBs use resin and gum to fashion nests, they also mix salivary gland secretions with self-made wax and foraged resin to make cerumen (58, 89). SB cerumen is produced in nests (see the sidebar titled Noteworthy Stingless Bee Attributes; Figure 1) as worker mandibles combine secreted wax and collected resins, stored in large single or in multiple deposits. Cerumen differs in composition and texture from *Apis* wax and propolis (58, 115, 139, 150). SBs and HBs entomb invaders with resin; HBs target wax moths (*Galleria*) (149). In contrast, SBs mostly entomb large beetles, and sticky resin, often with irritant chemicals, is carried by defending workers to deposit on vertebrates. Is resin in cerumen an effective deterrent of wax moths, which never invade SB nests?

SB cerumen functions as the major nest material and generally provides a malleable, recyclable substance. It is recycled from brood cells after the pupal cocoon is formed and is likely recycled throughout SB nests (33, 58, 111, 139, 150, 175). Circulation among nest elements has not been studied. Marked individual bees (marked with RFID tags; see 103, 173) and labeled cerumen, wax, or resin would ideally sort through the labyrinth of intranest material cycling of clay-like cerumen and collected substances.

Cerumen may be a precise mix of wax and resin and is sometimes sticky (like resins) due to the contribution of hemipteran wax (139). Within the large Neotropical genus *Plebeia* (18), only *Plebeia droryana* removes the wax of *Ceroplastes* scale insects feeding on *Myrcia* (Myrtaceae) and is not a mutualist but an opportunist (112); SBs also often forage sap (44, 133). In contrast, *Cecropia* bees (*Nanoplebeia*) opportunistically create melittophytes by co-opting ant plants and coevolved mutualism with *Cryptostigma* (Coccidae) as obligate nest inhabitants (77, 141). Those mutualists within nests provide wax and honeydew, and bees who form this mutualism store no honey (141) (**Figure 1**). Unrelated Amazonian *Schwarzula* also use honeydew and wax from symbiotic *Cryptostigma* but make copious honey and harvest wax using specialized morphology (20, 141).

4.3. Protection Mutualisms

Protection modes likely evolved sequentially and diversified as opportunism or mutualism evolved from established nest architecture, construction behavior, and materials chemistry. The nest must be chemically disinfected by the bees and their collected materials (33, 79) and protected from other natural enemies (see the sidebar titled Examples of Stingless Bee Natural Enemies). Although SB brood develop in closed cells used only once, they also have associates (59, 114). The adult SBs defecate in their nest. Their colony trash, except that deposited in latrines leading from nest cavities, is ejected by worker bees (58, 139). Mutualisms may evolve when brood are accompanied by microbes or mites and detritus or excreta attract nematodes, collembolans, or beetles that surround the brood areas (30, 58). Whether all such invertebrates contact bee immatures is unknown but appears unlikely. Mutualism in nesting associations, either concerning nesting site plants (where SBs attack defoliators of spiny species, like Rutaceae and Arecaceae) or among arthropods, is far less common (139, 175).

4.3.1. Arthropod associates. Arthropod associates are too many and varied to adequately characterize, but certain groups are better researched. Opportunism is unlikely in mite and blind beetle associates. Mites in healthy colonies feed on detritus and other mites, fungi, and nematodes (30). Three meliponine genera in Brazil nest with 3 orders, 14 genera, and 18 species of Acari that overlap little. Common taxa include *Hypoaspis alfabetica*, *Melissotydeus bipunctata*, *Proctotyaedus quadrifasciatae*, *Lorryia meliponarum*, and *Tyrophagus putrescentiae*. Laelapidae may specialize on SBs, and Tydeidae may specialize on SB colony fungi. It seems likely that mites make a living on colony trash but are not indispensable. However, mite population dynamics in bee nests are unknown, and immigration to bee nests of such mutualists has barely been studied. Phoretic beetles (Leiodidae) travel on *Melipona* and *Cephalotrigona* workers (139). These beetles have evolved notched mandibles for transport upon bee hairs fringing the corbiculae and can achieve inter-colony transfer at mud collecting sites. *Scotocryptus*, blind and flightless leioid beetles, live only with meliponine colonies and consume detritus, slime molds, and pollen (139).

Nesting associations sometimes give more benefit to one participant than the other. Two *Melipona* with dissimilar defensive behavior, *Melipona fallax* and *Melipona panamica*, sometimes coinhabit a single nest (133, 145). Another infrequent but widespread SB adaptation is nesting within nests of defensive and well-protected ants or termites or near wasp nests (58, 133, 136, 141). Most conesting bees defend little, but conesting *Trigona* or *Partamona* are violently aggressive. A few SBs (some *Plebeia*, *Partamona*, *Tetragonula*) nest in aggregations and collectively attack intruders (139). A chemical or food basis has yet to be worked out: Is this opportunism or mutualism? When they are unaggressive and provide no food or materials, associated SBs do not benefit ants or termites. Some ants are significant colony predators (**Table 1**). The ant-deterrent materials added to bee nests could have permitted the evolution of protective mutualism by thwarting host retaliation. Over the course of evolution, SBs may gain protection, as the balance in benefits

is modified to feed or protect ants or termites, but we still do not know if this is the case. In the *Melipona*, foragers of *M. panamica* give nectar to defending *Melipona fallax* workers as they enter a nest (133).

4.3.2. Microbe associates in colony ecology. Theoretically, host bee ecology should be related to bacterial strain (species) and potentially give evidence for host-switching, coevolution, or independent introduction of microbes (74, 165; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript). The acidity of SB honey and pollen helps control fermentation that occurs because moisture content is high. It also, at pH4, favors acidophilic bacteria (2, 33, 88, 154, 158).

What do acidophilic bacteria and other microbiota do? SBs use microbial symbionts to detoxify plant resources, process sugars, and displace harmful bacteria (33, 55, 171, 175). Yeasts, molds, fungi, and bacteria are common within adult bees in portions of the alimentary tract or in labial and hypopharyngeal glands (48), in the nest (resin, building material), in the processed pollen provisions eaten by larvae and newly emerged adults, and in stored honey or stored nectar (unripe honey). Trehalulose in SB honey might derive from behaviors and biochemistry that convert disaccharides (54, 114); the sugar also occurs in hemipteran honeydew, resulting from symbiotic bacteria (16), and likely constitutes a source of trehalulose for SBs.

The developing larva voids its gut microbes, but adults receive new ones. Microbiota come from bees in the same nest (via vertical transmission); from nest materials (also via vertical transmission); or from transmission hubs outside the nest, primarily at flowers (horizontal transmission) (52, 88, 89). During feeding or foraging, spores (5 μm in size) are removed by the proventriculus in the gut portion that receives honey stomach contents (149). Live bacteria pass through the barrier to process food in the stomach; most live in the ileum and hindgut.

Data on microbes (33, 41, 56, 78, 88, 105, 153; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript) imply that they form symbioses with Meliponini, often at the species level; however, in Apinae, whether microbes are harmful, beneficial, or neutral is often unknown (39, 40, 74; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript). Microbe and host SB associations are indicated in **Table 2**. Fungi or a particular mold or yeast may provide nutrition in lieu of honey for the Neotropical *Ptilotrigona* studied by Camargo & Pedro (19). Mutualisms with fungi are widespread in SBs. New species of *Penicillium* were found with *Melipona scutellaris* in Brazil (10). For Neotropical SBs, *Starmerella* may be the most important fungal mutualist (33, 40, 57, 58, 165, 167, 168). A remarkable discovery of a symbiotic mutualism of *Scaptotrigona* with filamentous fungi for nutrition and gene regulation in steroid production (33, 109) lacks confirmed generality among Meliponini.

Preswarming honey stores and newly collected pollen for all SB-directed swarms suggest inoculation with microbes (33, 168), but no detailed study of these phenomena exists. Yet microbes may be lost or exchanged. *Gilliamella apicola* metabolizes toxic sugars (176) and lives with some Neotropical Meliponini but not with other Neotropical, Asian, and African SBs (23, 33, 74, 78, 159, 160). *Lactobacillus malfermentans* inhabits Southeast Asian SB honey (131) (**Table 2**). Neotropical *Melipona* sometimes lack *Snodgrassella* and *Gilliamella* (23, 73, 74, 160; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript), possibly as an artifact of moving colonies (62; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript). They may be replaced by *Starmerella* (57).

In Africa, colonies from Kakamega forest were moved to savanna near Nairobi, where *Liotrigona*, *Plebeina*, *Axestotrigona*, *Hypotrigona*, and *Meliponula* displayed 60% total reads (nucleic acid sequences) in phylum Firmicutes: *Lactobacillus*, *Acetilactobacillus*, and *Bombilactobacillus* (**Table 2**).

The overall similarity was striking and seems too high. Losses due to colony transport were possible; new acquisitions likely came from the environment (62). Studies in Brazil using four SB genera (34) in quite disturbed habitat found 141 operational taxonomic units for bacterial genera, and *Escherichia* (*Melipona quadrifasciata*, *Trigona spinipes*), *Sphingomonas*, *Xanthomonas* (*Tetragonisca angustula*), endophyte *Gluconobacter*, and plant phylosphere surface resident *Pseudomonas* (with *Frieseomelitta* spp.) were dominant. Microbial surveys within nests of *Tetragonisca*, *Frieseomelitta*, *Trigona*, and *Melipona* (common genera in South America) present nest microecoregions that represent phyloplanes—plant surface microbes (34). Pesticides may also circulate in the environment and be taken from plant surfaces into bee nests (60), and all of the above factors have continuous interplay within nests and among SB foragers.

The SB gut biome does not assemble at random and is most similar among bees within phylogenetic units. The four corbiculate apine clades show microbiome similarity that can vary by region, by season, and after hive or colony relocation (23, 62, 74, 91, 158, 159, 160; JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript). Major groups of bacteria are shared among corbiculate bees and others (JG Kueneman, E Bonadies, D Thomas, DW Roubik, and WT Wcislo, unpublished manuscript). Many meliponine genera are unstudied (**Table 2**), and there are few comparative SB data from forests. Three sympatric SB species, *Austoplebeia* and two *Tetragonula* in Northeast Queensland forest, shared *Lactobacillus* that were host-specific, yet closely similar to Halictidae-associated bee bacteria (81).

4.4. Pathogens of Colonies

Studies of virus and phage interactions with SB are ongoing (33). Diseases and pathogens of SBs have been known only since 2015 (3, 17, 33, 35, 40, 43, 52, 60, 61, 91, 118). Transfer of *Nosema* disease from *A. mellifera* to SBs via flowers was recently demonstrated (**Table 2**). The virome of *M. quadrifasciata* in southern Brazil (17) contained Dicistroviridae, Paroviridae, and Circoviridae among mostly unhealthy colonies that were exploited by the viruses.

5. FORAGE AND POLLINATION ECOLOGY

Incoming forage ad infinitum multiplies SB associates—among them flowering plant nectar, pollen, and resin, and also dispersing spores with which Meliponini are associated, even as food (33, 49, 106). SBs visit but do not necessarily pollinate many thousands of tropical flowers (58, 121, 130, 133, 140, 144). Although we cannot say whether the original SB had the kinds of communication and forager recruitment seen today (8, 47, 58, 98, 99, 102, 113, 117, 122, 127, 133, 138), such behavior, which allows masses of SBs to dominate tropical trees and other blooms, permeates tropical ecology worldwide.

5.1. Natural Products in Meliponine Biology

Resins may amplify defenses already provided by low pH, H₂O₂, and osmolarity in all insect honey (13). They prevent microbial damage of stored food and are heavily foraged by SBs (115, 133). At their source, they deter herbivores, both vertebrate and invertebrate, and antipollinators—nectarivores and pollenivores (mostly bees and ants) (126, 133). In addition, unsavory materials, including urine, feces, and carrion, are sometimes foraged (34, 58, 83, 133). Central American *Trigona necrophaga* was the first obligate necrophage bee discovered (132). Certain meliponines, mostly those that also forage feces (Neotropical *Oxytrigona*, *Trigona*, *Partamona*, and *Melipona*), and primarily obligate necrophages (a few *Trigona*) visit cadavers or moribund animals, including dying wasp larvae and worms, for food, salts, and nutrients (53, 85, 101).

5.1.1. Phytochemical overviews. The diversity of secondary compounds in SB forage involves many plant compounds that have been discussed in recent overviews (79, 82, 96, 115, 129, 150, 154, 162). Surveys of temperate-zone plants and a few tropical genera (*Citrus*, *Persea*, *Solanum*) reveal that flavonoids and alkaloids are common in nectar and pollen, as are terpenoids and acids (105, 108). Such chemical compounds, however, vary within a plant species. There are flavones and terpenes, as well as phenolic compounds, in pure pollen (6, 108, 129). Examinations of antioxidant flavonoid contents in the honey of a common SB in the Neotropics, *Tetragonisca angustula*, suggest that chemicals are potentially exchanged between honey and cerumen in SB nests (2, 111, 168), as has also been found in one African meliponine (114). Exchange between constantly cycled nest material and incoming forage would tend to stabilize the many roles, yet to be proven or adequately studied, of phytochemicals in SB colony and nest ecology.

5.1.2. New paradigms. In *Quassia amara* (Simaroubaceae), the flower-perforating *Trigona fulviventr* makes a ring of floral tissue around its holes in flowers, which may deter ant secondary nectar robbers via the plant tissue-derived repellent quassin (133). Secondary metabolites in pollen (6, 108) may deter ants, which avoid this protein source. Bees have more protein and carbohydrate resources than was previously thought (156). Have SBs experienced strong selection pressures from the actions of ants at plants, and has this led to the use of microbes or enzymes that detoxify nectar or pollen?

Highly eusocial bee harvest of secondary plant metabolites—from buds (171), wounded trees, floral or fruit resins or waxes, and even seeds—appears to be universal. SBs gather mucilage, wax, and resin that protect fruit or seeds from vertebrate herbivores. Such forage from fruit or flowers is documented in *Dalechampia* (Euphorbiaceae), *Clusia* (Clusiaceae), *Coussapoa* (Urticaceae), and *Corymbia* (Myrtaceae) in tropical America and Australia (4; 5; 14; 80; 115; 136, p. 29; 150; 173) (**Figure 1**). Certain *Tetragonula* in Australia and many *Melipona* in Neotropical forests have become seed dispersers (80, 133, 173) (**Figure 1**). In this case, as in many forms of mutualism between SBs and associates, opportunism apparently evolved into a mutualism. Natural selection has produced nest material-based pollination mutualisms with bees, but no one has determined whether the dipterocarp resins of Southeast Asian forests have been selected to support SBs as pollinators.

5.1.3. Analytical approaches. Common among natural product SB investigations are chemical profiling with no assays, or pharmacological tests lacking chemical profiles. This makes claims of medicinal value unconvincing (90, 115, 150). Samples taken from a resin deposit in the nest, a nest entrance, or interior cerumen pots or brood cells differ, but often, source material is not identified or functionally classified. Although species are identified infrequently, studies in the Neotropics and Southeast Asia show that the same bees sometimes have distinctive material chemistry in different places, while different bee species may have similar chemistry in one habitat. Plant resin origins, when identified, are often exotic species or of farmland (79, 82, 83, 96, 115).

Satisfactory bioactivity analysis requires chemical study of taxonomically known bee–plant combinations followed by pharmacological testing using sample fractions and, ultimately, pure compounds (115, 141, 151). In order of frequency of occurrence, antioxidant effects, antifungal and antibacterial effects, free-radical scavenging, anti-inflammatory effects, antiviral effects, anti-cancer cell growth, and inhibition of bone loss compounds have been demonstrated for materials derived from SBs. Many more medically relevant materials are known for SBs than for *Apis*. Pioneering analysis of diterpenes has progressed to mangostins (from cultivated mangosteen *Garcinia*, Clusiaceae) (4), which inhibit human melanoma growth, and xanthine oxidase, which has potential antigout activity, both of which are found in Southeast Asian *Lepidotrigona*, *Tetragonula pagdeni*, and a bee taxonomically near *Tetragonula biroi* (96). Mohammad et al. (96) summarize world data and works in progress.

Gum, latex, and sticky plant polysaccharides contain galactose, arabinose, rhamnose, uronic acids, galacturonic acid, protein, Ca, and Mg as major structural constituents, as well as glucose, xylose, mannose, protein, and fat as minor constituents (95). It is likely that SBs use them as food or building materials, but studies are needed to confirm this.

5.2. Pollen Surveys

SB nests and foragers provide pollen grains, which can be counted and identified under microscopes. Such pollen identification supplements field observations, which are often difficult to conduct in tall forest and canopy settings. Substitution of molecular databases for identified reference pollen slides (163, 168) has been slow due to the sheer size of the tropical flora. Both kinds of databases are incomplete.

5.2.1. Melittopalynology and melissopalynology. Many tropical trees (20–30%) flower infrequently or are unisexual; thus, bee resource use and pollination ecology present complex challenges to ecologists (144, 167, 168). Paradoxically, flowers heavily foraged by SBs and HBs are often nectarless. That is, pollen in the flowers is the only pollinator reward; there is never any nectar. Although pollen from a nectarless species will never indicate a carbohydrate source, honey may contain abundant pollen of nectarless flowers, which is dusted on the bees' bodies and is mixed in foraged nectar within bee nests. Honey is often misclassified as monofloral, in traditional melissopalynology, based on abundant pollen of nectarless species in tropical honey (11, 144). Pollen studies also count grains to quantify utilization or consumption by bee larvae (1, 11, 32) or tally pollen or foraged corbicular pellets (135, 143, 144). If pollen species are similar in size, then comparable methods can be used to quantify them. The difference in size between the pollen of *Miconia* and *Piper* (10 μm) versus the pollen of palms, cucurbits, and euphorbs (50–100 μm), for instance, makes grain counts difficult to interpret unless literally monofloral foraged pollen pellets are measured or weighed. The melittopalynology of bees and their proteinaceous food—pollen—is more straightforward than the melissopalynology—the important honey sources. The latter is more difficult to garner from pollen data.

Diet breadth in studies conducted over longer periods of time (32, 84, 85, 128, 143, 145, 166, 167, 168) reveals diversity together with specialization. *Scaptotrigona fulvicutis*, the largest bee in its genus, utilizes 98 plant species in central Amazonia (85). This is comparable to the number of pollen species from *Melipona panamica* at 9°N in Panama (145). To obtain comprehensive pollen resource data, two studies examine accumulated bee pollen feces. *Cephalotrigona* deposits feces in a block at the nest floor, called loloc in Yucatecan Mayan, and studies of a 20-year-old *Trigona corvina* colony dissected a scutellum nest shell of pollen feces (143, 145). *Cephalotrigona* colonies were relatively specialized on palms (*Iriartea*), *Pterocarpus* and *Machaerium* (legumes), an unidentified Asteraceae, and *Arrabidaea* and *Brosimum* (Bignoniaceae and Moraceae). The *Trigona* heavily used *Cecropia*, *Pseudobombax*, *Machaerium*, *Spondias*, and particularly *Chamaesyce* (Euphorbiaceae) and palms (*Elaeis*, *Attalea*). In-depth studies of *Melipona beecheii* nest pollen across central Yucatan, Mexico revealed a large amount of pollen from the so-called living fenceposts *Gliricidia* and *Bursera* (167, 168). Remarkably, another study in Northeast Brazil within similar forest and farm landscapes found comparable pollen representation of the same top-five plant families (those most frequently recorded among taxa) for *Melipona scutellaris* (122, 168) as those seen in Yucatan for *M. beecheii*. Additional work with honey in Brazilian Amazon floodplain forest discovered that *Melipona interrupta* and *Melipona seminigra* honey had *Miconia* (Melastomataceae) and *Tapirira* (Anacardiaceae) in greatest abundance. The first is nectarless; the second is unisexual and contains powerful antimicrobials (128, 147, 161).

The sources of native tropical honey, as well as bee fitness and food, remain somewhat elusive but appear to depend on both successional and mature plant assemblages. Brazilian pollen studies, which were largely performed to inform honey source management (36), list an impressive 50 SB species from 16 genera; these studies highlight Australian *Eucalyptus*, which indicates Anthropocene habitat, and also find many nectarless plants. Studies heavily favor the large *Melipona* and highly adaptable (nesting in buildings, cities, countryside, and wildlands) *Scaptotrigona* and *Tetragonisca angustula*, which are widely kept (1, 7, 11, 29, 32, 38, 58, 64, 84, 85, 104, 105, 122, 128, 144, 145, 167, 168). A few studies have been conducted in natural forests. If comprehensive information were available for plant species, and ground truth was established with observation at flowers, then relative floral resource importance for SBs could be clarified in reasonably well-documented floral landscapes and wildlands.

SBs forage extrafloral nectar that attracts ants, which discourage herbivory (11, 36, 97). Such nectar contains honeydew elements such as fungal hyphae, frequently found in the honey of SB species, excluding *Melipona* (in 18 of 28 samples), and sometimes in the honey of *Apis* (11, 13). A large SB survey found that 12 botanical families provided the dominant pollen types (>45%) (11); however, as in many tropical pollen surveys, genera or families but not species were identifiable. When a botanical survey establishes how many species are in a genus and their flowering phenology, studies of bee pollen harvest can yield better ecological insights. Knowledge from a small sample does not allow one to rank plant importance to bees, and acetolyzed (cleaned and cleared) pollen is needed for identification at most generic and species levels (143, 144, 168).

5.2.2. Bee-cycling of carbon and energy. Bee pollen, nectar, and resin can be quantified by registering forager traffic. Mechanical counts are preferable, but the data at hand came from direct observation. Combining detailed pollen-load and body weight studies (120); forest surveys of bee colony activity in Panama and the Amazon at 9°N and 10°S, respectively (28, 142); and nest surveys in Borneo at 5°N (50) indicate that 20–200 kg of pollen and resin are taken annually by SBs residing in a hectare of forest. Viewed as a carbon sink, SBs of 1–10 colonies $\times$ ha⁻¹ observed in tropical forests (26, 50, 66, 70, 136) recycle large amounts of carbon and energy. In the reference studies, approximately 50–70% of nonpollen or resin forage was nectar, which varied during wet versus dry seasons.

6. BEE-KEEPING ECOLOGY

Stingless bee-keeping (2, 24, 25, 27, 38, 58, 65, 69, 100, 116, 119, 166), indoor and field crop pollination, illegal trade, and disease spread are now studied closely (3, 17, 22, 31, 29, 35, 40, 43, 52, 60, 87, 152). Harvested by humans from wild bee nests, different kinds of cerumen are historically prized for the fletching of arrows, metal lost-wax foundry, and boat patching (113, 150, 155). Floral resin from *Dalechampia* and *Clusia* foraged by SBs hardens slowly (5; 14; 133, p. 29) and makes cerumen more pliable. Taffy-like or tar-like SB resins and other SB-produced substances are widely applicable. Harvest of SB products, particularly resins and honey, is switching from extraction in wildlands to cultivation and husbandry, and thus may foster sustainability.

The relative ease of SB colony management has galvanized research, but SBs seem less robust to manipulation than HBs. In the coming years, meliponines may be found to resemble *A. mellifera* in studies of disease spillover, toxins, parasite and microbe transfer at floral hubs, interbreeding, competition with native species, pillaging, or negative pollination impact (e.g., 52, 126). New management and technology may address some problems in advance, and lessons from honey bee biology provide a potential scenario (89, 118). Commercial success has led to administrative and legal guidelines to obtaining or selling SBs. Nonetheless, among six Brazilian biomes, transfers frequently occur over hundreds or thousands of kilometers, covering 10.8–27.6° in latitude

(43). The possibility that exotic SB colonies may colonize or substantially alter biota is a concern (22). Some SBs may form new mutualisms or adapt to climate (62), but ecological predictions are somewhat tentative (67). Natural enemy hubs at flowers are mostly unresearched.

Industrial production of SB colonies creates unanticipated results. *Scaptotrigona* in commercial hives threaten traditional *Apis* bee-keeping by pillaging and have caused reprisals (172). In Brazil, artificially produced queens for new *Scaptotrigona* colonies demand management. They are not, like HBs in the United States, shunted between regions. Whether they will become disposable pollination units, like commercial *Bombus* spp. in mid-latitudes, is difficult to predict. Many colonies are extracted from trees and kept by inexperienced bee-keepers, then die and are replaced. Husbandry, education, and innovations are needed.

7. CONCLUSIONS

The longer a bee lineage lives within tropical diversity, the more likely it is that it accumulates significant interactions. A review of SBs in 1983 (175) mentions 20 biological traits, many revisited in this review. Research since 1983 has overturned some views held then, including that a stinger remnant in *Melipona* indicates antiquity. *Melipona* arose in the Miocene (123). I previously suggested that vulture bees give a carrion slurry to receiver bees (132, 133). However, we now know that these bees directly deposit forage in cerumen pots, where microbes convert it into glucose and amino acids (18, 53, 55, 87, 101). Seeds gathered by *Melipona* from fruit were once thought to be from *Vismia* but are instead from *Coussapoa* in a matrix of wax, not resin (133); behavior-inducing chemicals are from labial glands, not mandibular glands (58, 148); and there is no fossil *Nogueirapis* (51). It has been confirmed that *Lestrimelitta*, *Cleptotrigona*, and obligate necrophage *Trigona* never visit flowers (58). In all cases, an HB analogy fails to guide investigation. Study of comparative ecology, sometimes by contrasting SBs with *Apis*, now profits more by considering SBs alone.

FUTURE ISSUES

1. Do obligate necrophage foragers also provision brood with glandular secretions?
2. Why do Amazonian *Ptilotrigona* store no honey?
3. Does any kind of stingless bee-keeping help sustain natural communities or populations?
4. Why are there kleptobiotic Meliponini in tropical America and Africa but not Asia, and why do obligate necrophages occur only in the Neotropics?
5. Why has the microbiome of meliponines shifted so often, and which microbes are truly essential?

DISCLOSURE STATEMENT

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