Review article

The stingless bees (Hymenoptera: Apidae: Meliponini): a review of the current threats to their survival

Erubiel TOLEDO-HERNÁNDEZ[1], Guadalupe PEÑA-CHORA[2],
Víctor Manuel HERNÁNDEZ-VELÁZQUEZ[3], Caleb C. LORMENDEZ[2],
Jeiry TORIBIO-JIMÉNEZ[1], Yanet ROMERO-RAMÍREZ[1], and
Renato LEÓN-RODRÍGUEZ[4]

[1] Facultad de Ciencias Químico-Biológicas, Universidad Autónoma de Guerrero,
Av. Lázaro Cárdenas s/n. C. P. 39087. Chilpancingo, Guerrero, Mexico
[2] Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Morelos, Av. Universidad núm. 1001,
col. Chamilpa. C. P. 62209. Cuernavaca, Morelos, Mexico
[3] Centro de Investigación en Biotecnología, Universidad Autónoma del Estado de Morelos, Av. Universidad núm. 1001,
col. Chamilpa. C. P. 62209. Cuernavaca, Morelos, Mexico
[4] Instituto de Investigaciones Biomédicas Universidad Nacional Autónoma de México Ciudad Universitaria. C. P. 04510,
Tercer circuito exterior s/n, Coyoacán, Ciudad de México, México

Abstract – Pollination by insects is an essential service for the conservation of plant biodiversity, since it increases the rate of fertilization of flowers and therefore increases the quality and quantity of seeds and fruits. In tropical regions, native plants depend heavily on stingless bees as pollinators since before the introduction of the European honey bee *Apis mellifera*. However, like for many other insect species worldwide, anthropogenic actions represent a true threat to stingless bee populations. In this article, we review the works that evaluated the potential negative impacts of human activities on populations of stingless bees. The studies constitute a strong body of evidence that stingless bee populations are at risk of decline around the world due to threats including habitat loss, agrochemicals, competition for resources, climate change, and the introduction of exotic species, including pathogens.

agrochemicals / deforestation / competition / climate change / pests and diseases

1. INTRODUCTION

Worldwide, bees play a fundamental role in the environment by facilitating the pollination of plant species in both natural ecosystems and agricultural crops, which has a direct impact on the yields of fruits and seeds (Nicholls and Altieri 2013). The approximately 20,000 species of bees belong to the Apidae family of the order Hymenoptera. Bees are one of the main pollinator taxa, responsible for the pollination of about 73% of cultivated plants (Santos et al. 2014), which can result in up to 50% higher production of seeds and fruits (Klein et al. 2007). The Apidae family contains several tribes: Apini, Bombini, Euglossini, Meliponini, Xylocopini, and other, lesser known tribes (Arnold et al. 2018). Advanced eusocial bee taxa are found mainly in two groups: highly eusocial bees (including the european honeybee, *Apis mellifera* Linnaeus Apini and the stingless

Corresponding author: E. TOLEDO-HERNÁNDEZ,
erubielth@hotmail.com
Manuscript editor: Cedric Alaux

bees, Meliponini) and the primitively eusocial bumblebees (Bombini).

The stingless bees are considered the most highly eusocial among bees native to the tropics and subtropics, including the American tropics (Neotropics), sub-Saharan African (Afrotropical), and the Indo-Australian (Australasian) regions. About 500 species of Meliponini have been described worldwide, and 80% of them occur in the western hemisphere from Mexico to Argentina, including the Caribbean and Pacific islands (Ayala et al. 2013). They are found in different ecosystems, including rainforest, cloud forest, and arid lands, and at a variety of altitudes, from sea level to 4000 m above sea level in the Andes. Their continental distribution denotes the importance of their ecological role as pollinators of native wild plants and crops (Ayala et al. 2013; Giannini et al. 2015a).

The stingless bees are distinguished from other bees by morphological features of their wings (weak or lacking submarginal cross-veins and second recurrent vein in the forewing; Michener 2013). All stingless bees live in colonies that consist of tens to hundreds of thousands of workers, and usually a single queen. At any given time, the number of males present in the colony may range from zero to dozen; males and workers are usually similar in size and appearance, while queens are morphologically distinct (Michener 2013). Stingless bees feed on nectar and pollen collected by foraging workers. The honey made from the nectar is placed in separate pots from pollen.

Stingless bees were the main pollinators of plants on the American continent before the introduction honeybees from Europe. In addition to pollination services, stingless bees provide benefits to humans from their honey and geopropolis, which have demonstrated antioxidant, antimicrobial, anti-inflammatory, wound healing, and anticancer activities, among other properties (Seabrooks and Hu 2017; Jalil et al. 2017; Alvarez-Suarez et al. 2018). However, the stingless bees, like many insects groups worldwide, are threatened by habitat devastation, global climate change, and resource competition by the introduction of others bees such as *A. mellifera*

(Becker et al. 2018; Jaffé et al. 2019; Hung et al. 2019). These factors, together with the loss of local ancestral ecological knowledge of meliponiculture, are the main drivers of decreases in the native stingless bee populations (Villanueva et al. 2005; Reyes-González et al. 2020). Studies have also shown that anthropogenic actions such as the inadequate use of pesticides are among the most important factor threatening insect biodiversity in general (Dudley and Alexander 2017). This decline in populations of pollinator species is of concern because it could lead to a parallel decline in plant species (Biesmeijer et al. 2006; Lima et al. 2016). Other threats that are likely just as important and are increasingly clearly linked to pollinator decline include the spillover of pests and diseases from *A. mellifera* to stingless bees (Purkiss and Lach 2019; Tapia-González et al. 2019; Teixeira et al. 2020). Although more studies are needed, it is important to increase awareness to protect these bees. We therefore review each major category of factors threatening stingless bees: chemical pesticides, transgenic crops, deforestation, biotic factors, and climate change. We close the review with some perspectives for better understanding these threats and options to address them.

2. CHEMICAL PESTICIDES

2.1. Insecticides

The application of pesticides to crops kills not only the target pest, but may also have negative effects on beneficial insect which include the pest's predators and parasitoids, as well as pollinators such as beetles, butterflies, and many different species of bees (Apidae) (DiBartolomeis et al. 2019; Sánchez-Bayo and Wyckhuys 2019). Pesticides represent a serious threat to the survival of stingless bees, and there is currently strong scientific evidence demonstrating the toxicological effects of pesticides on Meliponini species (Lima et al. 2016; Tomé et al. 2017). There are still few studies demonstrating stingless bees' level of exposure to pesticides in their habitat;

however, some pioneering work has been done in a meliponary where foragers of *Scaptotrigona* aff. *depilis* were shown to contain neonicotinoid pesticides (Rosa et al. 2015). This led the authors to conclude that *S.* aff. *depilis* is a potential indicator of environmental pesticide contamination. Furthermore, a meta-analysis demonstrated that stingless bees are more sensitive to pesticides than bumblebees, solitary bees, or honey bees (Arena and Sgolastra 2014). Over the last decade, much information has been generated in this respect, by assessing the toxicity of organophosphorus, neonicotinoid, pyrethroid, and other classes of pesticides: lethal effects have often been observed when used according to their respective labels, as well as tissue and organ malformations and changes in social behavior at sublethal doses (Table I). Crops including orange, lemon, apple, and papaya often use toxic bait formulations to manage the economically important fruit fly pest species, but it was recently demonstrated that toxic baits with the active ingredient malathion (Success®, Gelsura®) lead to mortality of worker bees of stingless bee species (Padilha et al. 2019) (Table I).

Most studies of pesticides' lethal effects on stingless bees have focused on adults, but there is experimental evidence of damage to larval health after ingestion of pollen and nectar contaminated with neonicotinoids, organophosphates, and other pesticides. The exposure of larvae of the stingless bee *Scaptotrigona bipunctata* to different doses of chlorpyrifos (Organophosphorus) showed reduced survival probability, likely because they developed into lighter, smaller, and deformed adult workers (Dorneles et al. 2021). Exposure to neonicotinoid products during the larval stage has also been shown to cause brain alterations (Miotelo et al. 2021). A study of *Melipona quadrifasciata anthidioides* exposed to the neonicotinoid imidacloprid from larval stages through adulthood showed a survival rate just above 50%; furthermore, imidacloprid exposure impaired the walking behavior of surviving adults, which was attributed to negative effects on the development of mushroom bodies (MBs) in the brain (Tomé et al. 2012). Similar findings of harmful effects, including the alteration

of caste differentiation, impairment of social behavior, and increased asymmetry in individuals exposed to organophosphorus, carbamate, and pyrethroid pesticides during the larval stage, have been reported in different stingless bee species (Dos Santos et al. 2016a; Rosa et al. 2016; Prado-Silva et al. 2018; Boff et al. 2018).

Currently, several agrochemical products are marketed as safe for non-target insects or as reduced-risk insecticides, but toxicological trials using these pesticides and biopesticides have not always supported these designations. For example, when the toxicity of chlorantraniliprole, a pesticide labeled as a reduced-risk insecticide at recommended label concentrations, was assessed in two species of stingless bees, it impaired flight take-off in worker bees of both species (*Partamona helleri* and *Scaptotrigona xanthotrica*), which could compromise foraging activity and potentially reduce colony survival (Tomé et al. 2015a). This result challenges the claims of non-target safety of such insecticides, particularly for native pollinator species. Further studies, using up-to-date protocols, are needed to better understand the toxicological effects of these chemical pesticides on populations of wild bees (Dorigo et al. 2019; Botina et al. 2020).

2.2. Herbicides, fungicides, and fertilizers

Herbicides were developed to eliminate undesirable grasses and other pest plants in crops or in water bodies, and although these compounds are designed to interfere with the metabolic processes of plants, the active compounds may also be toxic to bees. Changes in the expression of isoenzymes were assessed in *T. angustula* and *T. fiebrigi* under oral exposure to the herbicides Sanson[R] 40SC (nicosulfuron) and 200 Gramoxone[R] (paraquat) (Fermino et al. 2011). Nicosulfuron at 75% led to partial inhibition of esterases, and Paraquat led to 10% and 1% complete inhibition of esterases in the two species, respectively, while the superoxide dismutase isoenzyme increased in relative activity in both bee species at 10% of Paraquat herbicide, making these enzymes potentially useful bioindicators

Table I Insecticides reported as toxic to different species and life stages of stingless bees

Pesticide	Pesticide family	Type of exposure	LC_{50} (C), LD_{50} (D), LT_{50} (T), %mortality (M), morphological and physiological alterations, sublethal doses (SD)	Stingless bee species	Life stage	References
Thiamethoxam	Neonicotinoid	Oral	0.0543 ng/bee (C)	*Melipona scutellaris*	Foragers	Miotelo et al. (2021)
Imidacloprid	-	Oral	0.002 mg/mL (SD) color preferences, group activity and respiration rates alterations	*Partamona helleri*	Foragers	Almeida et al. (2021)
Fipronil	Phenylpyrazole	Oral	0.28 ng/μL (C) and morphological alterations in the midgut	*P. helleri*	Workers	Farder-Gomes et al. (2021)
Imidacloprid Deltamethrin	Neonicotinoid Pyrethroid	Topical	0.00146 μg/bee (D) 0.0096 μg/bee (D)	*Nannotrigona aff. testaceicornis*	Foragers	Matos et al. (2021)
Dimethoate	Organophosphates	Diet	172.48 ng/larvae (C)	*Scaptotrigona postica*	Larvae	Rosa-Fontana et al. (2020)
Acetamiprid Malathion Phosmet Acetamiprid Malathionc Phosmet	Neonicotinoid Organophosphates - Neonicotinoid Organophosphates -	Diet Diet	4.20 μg/μL (C), 6.21 μg/μL (D) 18.75 ng/μL (C), 10.9 ng/μL (D) 97.33 ng/μL (C), 19.54 ng/μL (D) 9.84 μg/μL (C), 1.42 μg/μL (D) 8.39 ng/μL (C), 29.29 ng/μL (D) 53.91 ng/μL (C), 41.95 ng/μL (D)	*Plebeia emerina Tetragonisca fiebrigi*	Workers	Padilha et al. (2020)
Malathion	Organophosphates	Toxic baits	12.28 ng/μL (C) 16.62 ng/μL (C)	*P. emerina T. fiebrigi*	Workers	Padilha et al. (2019)
Acetamiprid Imidacloprid Thiacloprid Thiamethoxam Dimethoate	Neonicotinoid - - - Organophosphates	Diet	173.26 ng/μL (C) 1.70 ng/μL (C) 54.09 ng/μL (C) 0.28 ng/μL (C) 7.81 ng/μL (C)	*T. angustula*	Foragers	Jacob et al. (2019a)
Dimethoate	Organophosphates	Oral	27.48 ng/μL (C)	*Melipona scutellaris*	Larvae	Dorigo et al. (2019)
Acetamiprid Imidacloprid Thiacloprid Dimethoate	Neonicotinoid - - Organophosphates	Oral	475.94 ng/μL (C) 89.11 ng/μL (C) 218.21 ng/μL (C) 67.52 ng/ μL (C)	*S. postica*	Workers	Jacob et al. (2019b)
Imidacloprid	Neonicotinoid	Oral	292 ng/mL interfered in the number of prohemocytes, plasmatocytes, and granulocytes	*Melipona quadrifasciata*	Workers	Ravaiano et al. (2018)
Fipronil	Phenylpyrazole	Topical	0.40 ng/bee (D)	*M. scutellaris*	Foragers	de Morais et al. (2018)

Table I (continued)

Pesticide	Pesticide family	Type of exposure	LC_{50} (C), LD_{50} (D), LT_{50} (T), %mortality (M), morphological and physiological alterations, sublethal doses (SD)	Stingless bee species	Life stage	References
Thiamethoxam Fipronil	Neonicotinoid Phenylpyrazole	Oral Topical Oral Topical	5.33 ng/bee (D) 1.86 ng/bee (D) 0.15 ng/bee (D) 0.56 ng/bee (D)	*T. angustula*	Workers	Quiroga-Murcia et al. (2017)
Thiamethoxam Fipronil	Neonicotinoid Phenylpyrazole	Oral Topical Oral Topical	0.37 ng/bee (D) 27.78 ng/bee (D) 1.63 ng/bee (D) 1.12 ng/bee (D)	*Scaptotrigona xanthotricha*		
Deltamethrin Imidacloprid	Pyrethroid Neonicotinoid	Oral Oral	891.1 µg/mL (C) 0.014 ng/bee (D) 573.3 µg/mL (C) 0.091 ng/bee (D)	*Partamona helleri*	Foragers	Tomé et al. (2017)
Chlorpyrifos Phosmet	Organophosphates -	Oral Topical Oral Topical	0.0112 µg/µL (C) 0.0110 µg/bee (D) 0.0245 µg/µL (C) 0.0087 µg/bee (D)	*S. bipunctata*	Workers	Dorneles et al. (2017)
Chlorpyrifos Phosmet	Organophosphates -	Oral Topical Oral Topical	0.0018 µg/µL (C) 0.0033 µg/bee (D) 0.0236 µg/µL (C) 0.0083 µg/bee (D)	*T. fiebrigi*		
Imidacloprid	Neonicotinoid	Topical Oral	25.2 and 24.5 ng/bee (D) 42.5 and 14.3 ng/µL (C)	*S. postica*	Workers	Soares et al. (2015)
Fipronil	Phenylpyrazole	Topical Oral	0.27 ng/bee (SD) 0.24 ng/µL (SD) Changes in the mushroom bodies (brain)	*S. postica*	Workers	Jacob et al. (2015)
Imidacloprid	Neonicotinoid	Oral	23.54 ng/bee (D)	*M. quadrifasciata*	Workers	Tomé et al. (2015b)
Imidacloprid	-	Topical Oral	2.41 and 1.29 ng/bee (D) 2.01 and 0.81 ng/µL (C)	*M. scutellaris*	Foragers	Costa et al. (2015)
Deltamethrin Methamidophos	Pyrethroid Organophosphates	Topical Contact Oral Topical Contact Oral	129.2 µg/bee (D) 5.6 µg/mL (C) 0.082 µg/bee (D) 296.6 µg/bee (D) 96.1 µg/mL (C) 0.066 µg/bee (D)	*M. quadrifasciata* *M. quadrifasciata*	Foragers	Del Sarto et al. (2014)
Fipronil	Phenylpyrazole	Topical Oral	0.54 ng/bee (D) 0.24 ng/µL (C)	*S. postica*	Workers	Jacob et al. (2013)
Fipronil	-	Oral	0.1 µg/kg food (T) DNA fragmentation and glycoconjugates	*S. postica*	Workers	Ferreira et al. (2013)
Fipronil	-	Topical	0.41 ng/bee (D)	*M. scutellaris*	Foragers	Lourenço et al. (2012a)

Table I (continued)

Pesticide	Pesticide family	Type of exposure	LC_{50} (C), LD_{50} (D), LT_{50} (T), %mortality (M), morphological and physiological alterations, sublethal doses (SD)	Stingless bee species	Life stage	References
Fipronil	-	Oral	0.011 ng/µL (C)	*M. scutellaris*	Foragers	Lourenço et al. (2012b)
Permethrin	Pyrethroid	Topical	0.066 µg/bee (D)	*M. beecheii*	Callow workers and Foragers	Valdovinos-Núñez et al. (2009)
-	-	Topical	0.021 µg/bee (D)	*Trigona nigra*		
-	-	Topical	0.010 µg/bee (D)	*Nannotrigona perilampoides*		
Diazinon	Organophosphates		0.19 µg/bee (D)	*M. beecheii*		
-	-		0.18 µg/bee (D)	*T. nigra*		
-	-		0.12 µg/bee (D)	*N. perilampoides*		
Methomyl	Carbamate		0.29 µg/bee (D)	*M. beecheii*		
-	-		0.08 µg/bee (D)	*T. nigra*		
-	-		0.05 µg/bee (D)	*N. perilampoides*		
Imidacloprid	Neonicotinoid	Topical	0.0011 µg/bee (D)	*N. perilampoides*		
Thiamethoxan	-		0.004 µg/bee (D)			
Thiacloprid	-		0.007 µg/bee (D)			
Diafenthiuron	Organophosphates	Topical	3.2 g/L 100% (M)	*Trigona iridipennis*	Workers	Stanley et al. (2009)
Monocrotophos			2 mL/L 100% (M)			
Parathion	Organophosphates	Topical	0.0956 µg/bee (D)	*Trigona spinipes*	Workers	Macieira and Hebling-Beraldo (1989)
Dicrotophos	-		0.1685 µg/bee (D)			
Malathion	-		0.2649 µg/bee (D)			
Acephate	-		0.4234 µg/bee (D)			
Carbaryl	Carbamate		0.7472 µg/bee (D)			
Methomyl	-		0.1402 µg/bee (D)			
Lindane	Organochlorine		0.1331 µg/bee (D)			
Dieldrin	-		0.0289 µg/bee (D)			
Heptachlor	-		0.0168 µg/bee (D)			
Endosulfan	-		0.2097 µg/bee (D)			
Cypermethrin	Pyrethroid		0.0704 µg/bee (D)			
Permethrin	-		0.0724 µg/bee (D)			
Fenvalerate	-		1.0880 µg/bee (D)			

(-) belongs to the same class or family of pesticide

of these herbicides. Such enzymatic alterations might contribute to explain the physiological and behavioral impairments observed upon exposure to herbicides, including the controversial glyphosate as well as mesotrione and atrazine (Table II). Fungicides are another agrochemical product that in recent research have demonstrated toxicological effects against stingless bees, causing alterations in the midgut and morphological signs of cell death as well as reduced survival rate (Table II). However, there are still few studies on the toxicological effects of fungicides and heavy metal-containing leaf fertilizers, so more investigation is needed to assess the impact of these chemicals on wild bees. Fertilizers are important agrochemicals used in extensive agriculture and orchards to improve plant growth and increase yields, but like others agrochemicals, can have adverse impacts on the environment. Works focused on the toxic effects of fertilizers on stingless bee species have shown reduced respiration rate upon oral exposure, compromising their survival (Table II).

Table II Herbicides, fungicides, and fertilizers reported to be toxic to different species of stingless bees

Agrochemical	Origin (herbicide, fungicide, fertilizer)	Type of exposure	LC50 (C), LD50 (D), LT50 (T), field doses (FD), morphological and physiological alterations, sublethal doses (SD)	Stingless bee species	Life stage	References
Chlorothalonil + Thiophanate-metyl	Fungicide	Oral	1.5 mg/mL: 0.49 mg/mL (SD) color preferences and respiration rates alterations	*Partamona helleri*	Foragers	Almeida et al. (2021)
Mesotrione and Atrazine mix (Calaris®)	Herbicide	Oral	31% mix (C) damage to the midgut, behavior and feeding alterations	*P. helleri*	Foragers	Araújo et al. (2021)
Difenoconazole	Fungicide	Oral Topical	5.0 μg/μL (C) 67.0 μg/bee (D)	*Melipona scutellaris*	Workers	Prado et al. (2020)
Pyraclostrobin	-	Oral	0.125 ng/μL, 0.025 ng/μL, and 0.005 ng/μL (SD) midgut lesion, signs of cell death and reduced survival rate	*M. scutellaris*	Workers	Domingues et al. (2020)
Copper sulfate (Penta 24)	Fertilizer	Oral	362.6 μg/mL (C)	*P. helleri*	Foragers	Botina et al. (2019)
Glyphosate + 2,4-D Picloram Glyphosate Glyphosate + 2,4-D 2,4-D	Herbicide - - - -	Topical Oral	760 g/ha, 1000 g/ha (FD) 305.6 h (T) 56 h (T) (FD); 113.6 h (T) (2FD) 292.8 h (T) (FD); 269.6 h (T) (2FD) 115.2 h (T) (FD); 45.6 h (T) (2FD) 147.2 (T) (FD)	*M. scutellaris*	Workers	Nocelli et al. (2019)
Glyphosate	-	Oral	3μL glyphosate in 150 μL total volume, 100% (M)	*M. quadrifasciata*	Larvae	Seide et al. (2018)
Thiophanate-metyl + Chlorothalonil	Fungicide	Oral	990.2 μg/mL (C)	*P. helleri*	Foragers	Tomé et al. (2017)
Copper sulfate (Penta 24) Micronutrient mix (Arrank L)	Fertilizer	Oral Topical Oral	24 h (T), 100 L/ha (L) Higher respiration rate Compromised the respiration rate 400 L/ha (L)	*Friesella schrottkyi*	Workers	Rodrigues et al. (2016)

2.3. Biopesticides

There is currently a global drive to decrease the environmental impact of synthetic chemicals, which has led to the increased use of products based on microorganisms or metabolites over the past few decades. This trend is particularly strong in organic agriculture, because such products are assumed to be more selective against the target pest or disease, innocuous to human health, and

not leave long-term residual compounds in the environment (van Lenteren et al. 2018). However, research has shown some adverse effects of biopesticides on stingless bee health (Table III). Work related to the effects of botanical pesticides was performed by Xavier et al. (2010) on adult *Tetragonisca angustula* and *Nannotrigona testaceicornis*. Their findings showed that the most toxic botanical insecticide to *T. angustula* was citronella oil and the least toxic was andiroba oil. Eucalyptus oil and neem oil presented intermediate toxicity to *T. angustula*, and garlic extract and rotenone were non-toxic to *T. angustula*. None of these botanical insecticides were toxic to *N. testaceicornis*. Another botanical bioinsecticide on the market is based on the bioactive molecule azadirachtin, a metabolite derived from the Indian neem tree (*Azadirachta indica*) which has shown high efficacy against arthropod pest species (Barbosa et al. 2015). In 2015, initial studies of azadirachtin toxicity to important native pollinators including *Partamona helleri* and *Scaptotrigona xanthotrica* showed harmful effect when used as recommended on the label. Individual flight take-off of worker bees was impaired (Tomé et al. 2015a), and *P. helleri* adult workers and queens showed behavioral alterations and deformations (Bernardes et al. 2017, 2018).

In the last decade, some biological pesticides formulated from bacterial metabolites are recognized as biopesticides or reduced-risk pesticides. One the most popular insecticides used today is Spinosad, a bioinsecticide made from spinosyn metabolites produced by the actinobacteria *Saccharopolyspora spinosa*. It is an agonist of the nicotinic acethylcholine receptors and interferes with aminobutiric acid (GABA) receptors in the nervous system (Tomé et al. 2015b). Previous studies of Spinosad product GF-120, a toxic commercial bait used in the management of fruit flies, evaluated the toxic effects on the stingless bee *Plebeia moureana* (Sánchez et al. 2012). This preliminary research showed that using the recommended label concentration mixed with food did not discourage engaged foragers, and foraging behavior was not significantly impaired over time by the continuous collection of contaminated food. However, although spinosad was initially considered a safe bioinsecticide, later studies have shown otherwise in others species. In 2014, a study showed that *Trigona fulviventris* and *Scaptotrigona mexicana* clearly avoid food sources baited with GF-120 and. *S. mexicana* colony sizes decline (Gómez-Escobar et al. 2014, 2018). Years later, other works have shown elevated toxicity of spinosad against these stingless bee species, causing morphological and behavioral alterations, among other harmful effects (Table III).

Another biomolecule with potential insecticidal properties called Abamectin is a metabolite of *Streptomyces avermitilis*, belonging to the Avermectin class. This biochemical compound is extremely toxic to humans (0.002 mg/kg) and other vertebrates as well as invertebrates (Prado et al. 2020). A study of abamectin verified its bioaccumulation in tissues of adult forager bees of *Melipona scutellaris* after oral and topical exposure, and mortality was higher from oral than topical exposure (Table III) These studies challenge the common perception of non-target safety of these bioinsecticides, particularly for stingless bee species (Table III).

3. TRANSGENIC CROPS

The demand for food has increased with the expanding global population, increasing the need to produce crops more efficiently, and with improved quality traits such as disease resistance, prolonged shelf-life, and drought resistance. This has given rise to genetically modified plants, a technology that purports to help solve this growing issue (Kamle et al. 2017). However, like many technological tools, it has limitations. For example, the expression of Bt toxins against pests requires applications of herbicides such as glyphosate (Hardee et al. 2001). One of the most common traits in transgenic maize and cotton is the expression of the Cry1F and Cry2Aa proteins from the bacterium *Bacillus thuringiensis*, which are toxic against Lepidopteran, Hemipteran, and Dipteran insect pests (Seide et al.

Table III Bioinsecticides reported to be toxic to different species of stingless bees

Bioinsecticide	Organism of origin of the bioinsecticide	Type of exposure	LC50 (C), LD50 (D), LT50 (T), %mortality (M), field doses (FD), morphological and physiological alterations, sublethal doses (SD)	Stingless bee species	Life stage	References
Spinetoram Essential oils	*Saccharopolyspora spinosa* *Lippia sidoides* Thymol *p*-cymene (*E*)-caryophyllene	Topical	0.0112 µg/Bee (D) 33.7 µg/Bee (D) 33.6 µg/Bee (D) 198 µg/Bee (D) 306 µg/Bee (D)	*Nannotrigona aff. testaceicornis*	Foragers	Matos et al. (2021)
Abamectin	*Streptomyces avermitilis*	Oral Topical	0.006 µg/µL (C) 0.028 µg/bee (D)	*Melipona scutellaris*	Foragers	Prado et al. (2020)
Spinosad	*Saccharopolyspora spinosa*	Oral	2.89 µg/mL (C)	*Partamona helleri*	Foragers	Botina et al. (2019)
Spinosad	-	Oral	8.16 µg/mL (C)	*P. helleri*	Workers	Araújo et al. (2019a)
Spinosad	-	Oral	3.264 µg/bee (FD) reduced the survival, 32.64 ng/bee (SD) morphological and physiological alterations	*P. helleri*	Larvae	Araújo et al. (2019b)
Spinosad Spinosad	- -	Oral Topical Oral Topical	4.96 ng/µL (C) 1.90 ng/bee (D) 5.65 ng/µL (C) 29.79 ng/bee (D)	*Plebeia emerina* *Tetragonisca fiebrigi*	Workers Workers	Padilha et al. (2020)
Spinosad	-	Oral	6.92 ng/µL (C) 4.37 ng/µL (C)	*P. emerina* *T. fiebrigi*	Workers	Padilha et al. (2019)
Essential oil	*Corymbia citriodora*	Topical	39.98 µg/mg of insect 100% mortality	*T. angustula*	Workers	Ribeiro et al. (2018)
Spinosad	*Saccharopolyspora spinosa*	Topical Oral Topical Oral	20.4 mg/L (FD) 1 h (T) (FD) 22.79 ng/bee, 2 h (T) 4 h (T) (FD) 15.82 ng/bee, 2 h (T)	*P. helleri* *Scaptotrigona xanthotrica*	Workers	Tomé et al. (2015a)
Spinosad	-	Oral	12.07 ng/bee (D)	*Melipona quadrifasciata*	Workers	Tomé et al. (2015b)
Spinosad Azadirachtin	- *Azadirachta indica*	Oral	114 ng/bee greater numbers of deformed individuals 210 ng/bee deformed pupae and adults	*M. quadrifasciata*	Larvae	Barbosa et al. (2015)
Abamectin	*Streptomyces avermitilis*	Oral Topical Contact	0.015 µg/bee (D) 134.6 µg/bee (D) 3.8 µg/mL (C)	*M. quadrifasciata*	Foragers	Del Sarto et al. (2014)

2018). Currently, there are few works evaluating the risks posed by transgenic crops harboring these insecticidal proteins on stingless bee species. Lima et al. (2013) assessed the effects of ingestion of the Cry1Ac protein on larvae of *Trigona spinipes*. They found a slight increase in larval mortality, and exposure did not cause impaired development of worker larvae. They mention that according to their results, Cry1Ac toxin is unlikely to be harmful to stingless bee larvae under field conditions. However, a later study conducted by feeding larvae of *M. quadrifasciata* with Cry1F and Cry2Aa contaminated food demonstrated delayed development of the bee larvae (Seide et al. 2018). Still, further investigations are needed since there are not enough studies to conclude on the toxicity of Cry toxins in stingless bees.

4. DEFORESTATION

Habitat loss by conversion to intensive agriculture is a main driver of declining entomofauna (Ceballos et al. 2017). Disturbance and habitat fragmentation caused by human activities had demonstrated negative effects on nest occurrence and species diversity of stingless bee species in Kenya (Kiatoko et al. 2017). It was recently shown that land use change increases the amount of toxic metals and metalloids that are bioaccumulated by *T. angustula* (Barbosa et al. 2021). A study by Brown and Albrecht (2001) demonstrated that the species richness of stingless bees, which ranged from 1 to 5 species, is inversely related to distance to the forest and directly related to percent forest cover. Their study showed that in tropical forest sites, bee community composition in even the smallest forest patches contained a much larger proportion of the local apifauna compared to deforested countryside just a few hundred meters from the forest. In another set of studies, stingless bee abundance decreased with increasing distance to the nearest forest patch, and their species richness was positively correlated with the proportion of forest cover (Brosi et al. 2007, 2008). Negative effects of landscape deforestation and anthropization on

richness and abundance of native bees have been demonstrated in countries including Malaysia, Brazil, Costa Rica and Mexico (Samejima et al. 2004; Venturieri 2009; Brosi 2009; Cairns et al. 2005). For example, Samejima et al. 2004 showed that since stingless bees nest only in large trees, nest density was positively correlated with the density of large trees. In Mexico, communities with the greatest anthropogenic disturbance had lower overall species richness of stingless bees and a higher degree of dominance of the Africanized honeybee (*A. mellifera*) (Cairns et al. 2005). It is now known that the larger body size of honeybees provides them a strong advantage over the far smaller stingless bees, as maximum foraging and recruitment distances are significantly greater for larger foragers (Araújo et al. 2004; Kuhn-Neto et al. 2009). In addition, stingless bee species with larger body size were found in areas with higher degrees of deforestation, while smaller bee species were found in areas with less deforestation, supporting the hypotheses that small stingless bee species might be more negatively affected by deforestation (Mayes et al. 2019). It was also recently demonstrated that thermal stress increases with flight distance in *M. subnitida* nectar foragers, with their body temperatures approaching their critical thermal maxima, which might constrain their activity and survival (Souza-Junior et al. 2020). A study in Costa Rica showed that stingless bee species richness and abundance are strongly related to forest cover; species with the widest dietary niche breadth are less likely to persist in sites with less forest (Brosi 2009).). In this sense, subordinant wild bee species that are displaced by more dominant species may be particularly dependent on the larger or more diversified resource pool of sites with more forest cover, such that the loss of forest cover may affect the meliponine community composition (Brosi, 2009).Similar work was developed in Brazil, and showed that the presence of stingless bee species has strong positive correlation with forest and a strong negative correlation with pastures (Arena et al. 2018). Lichtenberg et al. (2017) suggests that land use change may disassemble bee communities through different mechanisms in temperate and tropical areas, and that community

processes such as competition can be important regulators of community disassembly under land use change. Studies performed on populations of stingless bees in the Brazilian Amazon reinforce the conclusion that anthropogenic activities such as deforestation lead to the decline or absence of *Melipona* species in degraded areas. (Venturieri 2009; Brown and de Oliveira 2014; Pioker-Hara et al. 2014).

5. DISEASES AND PESTS

In the 1980s, the phorid fly *Melaloncha sinistra* was first reported to parasitize workers of *Nannotrigona postica*. Phorid flies were found at the nest entrance, where they laid eggs on foraging bees, and examining samples showed that up to 37% of workers were parasitized (Simões et al. 1980). Male stingless bees often aggregate outside of nests in order to inseminate emerging virgin queens (Brown 1997), and phorid flies take advantage of this behavior to parasitize their host (Table IV). Another insect parasite of the stingless bees is the mantispid *Plega hagenella*. This pest was found extensively infesting two nests of *Melipona subnitida*. Mantispid larvae of *P. hagenella* develop inside closed brood combs, where they fed on bee larvae or pupae; when they emerge as adults, they are removed from the nest unharmed by the bees (Maia-Silva et al. 2013). *Aethina tumida* (Coleoptera), also known as the small hive beetle, is a parasite and scavenger of honey bee colonies (*Apis mellifera*); some scientific notes report the infestation of stingless bee hives by the small hive beetle, such that this beetle may represent a real threat for them (Table IV).

In addition to insect parasites, there are several arachnids that parasitize bees, including several different genera of mites that have been reported infesting stingless bee hives (Table IV). The first report of parasitic mites in stingless bee colonies in Mexico was in a colony of *Melipona colimana*, and the mite was identified as *Pyemotes tritici* (Acari: Pyemotidae); the researchers hypothesized that the mites were likely introduced into the colony by infested passalid beetles or ants (Macías-Macías and Otero-Colina 2004).

The introduction of managed bee species into other habitats has allowed the arrival of pests or diseases that spill over into native species, causing harmful effects on populations and putting endemic organisms at risk (Graystock et al. 2016). The wax moth *Achroia grisella*, a pest of *Apis mellifera*, was found infesting weak colonies of *Melipona bicolor* and *M. quadrifasciata anthidioides* (Cepeda-Aponte et al. 2002). Moth larvae of all developmental stages were observed in the nests, and were extracted from the hives using light to attract them and liquid paraffin placed over the colony to trap them (Cepeda-Aponte et al. 2002). This was the first report of a pest of *A. mellifera* affecting stingless bees.

Viral diseases are another important health problem for bee species. In particular, a few years ago, a first case of viral infection was reported with the identification of the acute bee paralysis virus in *Melipona scutellaris* (Ueira-Vieira et al. 2015); this virus originally affects honeybees. The route or mechanism of infection by different pathogens is through shared foraging areas between stingless bee species and *A. mellifera* (Guimarães-Cestaro et al. 2020). Currently, some surveys have shown other viruses affecting different species of stingless bees (Table IV). To elucidate the impact of viruses on stingless bee population, high-throughput sequencing was used to characterize the virome of *Melipona quadrifasciata* using healthy bees (symptomless) and unhealthy bees (symptoms such as tremors and paralysis). The results showed that unhealthy bees had higher viral load of viruses of the Dicistroviridae family, which includes common pathogenic honeybee viruses, as well as Parvoviridae and Circoviridae, which have never been reported as entomopathogenic (Caesar et al. 2019).

Given the interest in identifying pathogens that could affect populations of stingless bees, Nunes-Silva et al. (2016) carried out at screening for microsporidian and protozoan parasites (Nosematidae, Leishmaniinae and Neogregarinorida) that have been previously reported as pathogenic

Table IV Pests and diseases reported in species of stingless bees

Causal agent	Type of organism	Pest or disease	Stingless bees affected	Isolated from	References
Aethina tumida	Beetle	Pest	*Melipona beecheii*	Hive	Hernández-Torres et al. (2021)
Aethina tumida	Beetle	Pest	*Melipona rufiventris*	Hive	Pereira et al. (2021)
Acute bee paralysis virus (ABPV) Deformed wing virus (DWV) Black queen cell virus (BQCV) Acute bee paralysis virus (ABPV)	Virus	Disease	*Nannotrigona testaceicornis* and *Tetragonisca angustula* *Tetragona elongata*		Guimarães-Cestaro et al. (2020)
Aethina tumida	Beetle	Pest	*Tetragonula carbonaria*	Hive	Nacko et al. (2020)
Deformed wing virus (DWV-A variant) Black queen cell virus (BQCV)	Virus	Disease	*Melipona colimana*	Foragers	Morfin et al. (2020)
Melissococcus plutonius *Nosema ceranae*	Bacterium - - - Microsporidia	Disease	*Melipona marginata* *M. quadrifasciata,* *M. mandacaia,* *M. mondury* *M. marginata*	Brood and adults - - - Brood	Teixeira et al. (2020)
Deformed wing virus (DWV) Black queen cell virus (BQCV)	Virus	Disease	*Melipona colimana* *Nanotrigona per-ilapoides* *Trigona fluviventris* *Scaptotrigona mexicana* *M. colimana* *N. perilapoides* *T. fluviventris* *S. mexicana*	Foragers	Tapia-González et al. (2019)
Nosema ceranae	Microsporidia	Disease	*Tetragonula hockingsi*	Foragers	Purkiss and Lach (2019)
Deformed wing virus (DWV)	Virus	Disease	*Melipona subnitida*	Workers	de Souza et al. (2019)
Deformed wing virus (DWV) Israeli acute paralysis virus (IAPV)	Virus	Disease	*Tetragonisca fiebrigi*	Workers	Alvarez et al. (2018)

Table IV (continued)

Causal agent	Type of organism	Pest or disease	Stingless bees affected	Isolated from	References
Israeli acute paralysis virus (IAPV) Acute bee paralysis virus (ABPV)			*Plebeia emerinoides*		
Israeli acute paralysis virus (IAPV)			*Plebeia droryana* *Trigona spinipes*		
Nosema ceranae	Microsporidia	Disease	*Tetragonisca fiebrigi* *Scaptotrigona jujuyensis*	Adults	Porrini et al. (2017)
		Disease	*Melipona marginata* *M. fasciculata* *M. quadrifasciata anthidioides* *M. rufiventris* *M. mandacaia*		
Deformed wing virus (DWV) Black queen cell virus (BQCV)	Virus	Disease	*Scaptotrigona mexicana*	Workers	Guzman-Novoa et al. (2015)
Aethina tumida	Beetle	Pest	*Melipona beecheii*	Hive	Lóriga-Peña et al. (2014)
Carpoglyphus lactis	Mite	Pest	*Trigona iridipennis*	Hive	Vijayakumar et al. (2013)
Pyemotes sp.	Mite	Pest	*Tetragonula iridipennis*	Hive	Vijayakumar and Jayaraj (2013)
Pyemotes tritici	Mite	Pest	*Tetragonisca angustula* *Frieseomelitta varia*	Hive	Menezes et al. (2009)
Apocephalus apivorus	Phorid fly	Pest	*Trigona dorsalis* *Cephalotrigona capitata*	Males	Brown (1997)

to honeybees. Their findings showed that of the six different species tested, none was positive for Leishmaniinae or Nosematidae parasites, but the protozoan *Apicystis bombi* (Neogregarinorida) was found in two stingless bee species, *Plebeia emerina* and *Tetragonisca fiebrigi*. Although Leishmaniinae and Nosematidae parasites were not found, years later the microsporidium *Nosema ceranae* (Nosematidae) was found parasitizing species of stingless bees (Table IV). Presently, there are only two works related to brood bacterial

infection causing mortality of stingless bee larvae (Table IV). The mosquito entomopathogenic bacterium *Lysinibacillus sphaericus* was found to cause brood losses in the Australian stingless bee *Tetragonula carbonaria*, confirming the disease's causal agent by pathogenicity experiments (Shanks et al. 2017), even though bioassays performed decades ago showed that *L. sphaericus* is not pathogenic to *A. mellifera* (Davidson et al. 1977).

Finally, with respect to fungal diseases affecting populations of the stingless bees, there is no published evidence of natural infection. By evaluating the effect of three commercial formulations of entomopathogenic fungi (*Isaria fumosorosea*, *Beauveria bassiana*, and *Metarhizium anisopliae*) on three species of stingless bees (*Tetragonisca angustula*, *Melipona beecheii*, and *Scaptotrigona mexicana*), Toledo-Hernández et al. (2016) found moderate to high susceptibility (38.9–94.2% mortality) to entomopathogenic fungi; however, field surveys are necessary to support this finding. Even though the aforementioned pathogens have been detected in workers or in the beehive, most of the available data concern only the occurrence of the pathogens and did not examine in detail their effects on bees. Thus, there is currently a near complete lack of data on the detrimental effects on colony development or mortality in populations of stingless bees.

6. COMPETITION FOR RESOURCES

Species of stingless bees are known to compete for food resources such as pollen and nectar flowers, and studies of aggressive behavior of stingless bees have been published since the last century. For example, Johnson and Hubbell (1974) observed the behavior of different species of stingless bees on flowers and artificial baits that varied in their sucrose concentration. The larger *Trigona silvestriana* (10 mm) used aggressive behavior to displace other smaller species of stingless bees *T. corvina*, *T. testacea*, *T. mexicana* (7 mm), and the *T. latitarsus* (4 to 5 mm), especially from the bait with the highest sucrose concentration (2.4 M), as long as no more than 50 to 60 bees were on the bait. Levels of aggression increased in intensity when the species *T. silvestriana* and *T. corvina* visited the baits and flowers at the same time, which sometimes led to lethal conflicts over the resource. When *T. corvina* encountered conspecifics from other colonies on the resource, battles lasting up to 2 days were recorded, with up to 1800 dead bees found. They mention that the observed aggression is not influenced by baits, since similar behavior and

levels of aggression were observed on natural food sources, especially at nectar- and pollen-rich inflorescences. Years later, the same authors reported similar aggressive behavior during competition over bait among species of the genus *Trigona*; the species that showed the strongest interspecific aggression by means of threats, chases, or bumps was *T. fuscipennis*, while *T. fulviventris* had the highest conspecific aggression among workers (Hubbell and Johnson 1978).

While strongly aggressive competition for pollen and nectar resources has been demonstrated among native stingless bees, human activity has introduced other, larger competitors that may leave stingless bees at a disadvantage. Pioneering works related to the food competition between African and neotropical bees were performed by Roubik (1978), who found that after the introduction of Africanized honey bee (*Apis mellifera*) hives near flower patches, native *Melipona* species became less abundant or harvested less resources such as pollen, which may lead into their population decline. Roubik (1980) demonstrated that the combined advantages of large forager size and large colony size provide Africanized honeybee colonies superior competitive ability over the stingless bees at rich and compact resources. Later, in 1983, the same author found that Africanized honey bee colonies had no significant effect on native bee colonies; however, they conclude that the short duration of the study (1 month) and small African populations (100,000 to 150,000 bees in total in the area) were insufficient to evidence the perturbation of native bee communities (Roubik 1983). Later, Ramalho et al. (1990) would report that the stingless bees use the same pollen and nectar resources as Africanized honeybees (*A. mellifera*) in neotropical regions including Brazil, Mexico, Panama, and other countries. Their findings concerning bee food sources showed that 50 plant species provide resources to both stingless bees and honeybees; this leads to competition for foraging sources. Due to their smaller body size and smaller colonies, stingless bees are at a disadvantage, and scarcity of food such as pollen significantly reduces brood production in stingless bee colonies (Maia-Silva et al.

2016). Competition for resources such as pollen and nectar of the Myrtaceae, Melastomataceae, and Asteraceae families of plants were evidenced between *A. mellifera* and stingless bee species in studies by Wilms et al. (1996) and Wilms and Wiechers (1997). In addition, the past century of human activity has introduced other species of bumblebees (*Bombus* sp.), the alfalfa leafcutter bee *Megachile rotundata*, and various other solitary species (Goulson 2003). Research in past decades has called for experimental studies to determine whether the presence of exotic bee species reduces the populations of local wild bees in the long term (Goulson 2003). It should be noted that this competition could be more difficult to detect in floristically rich habitats because the native bees changes their foraging time or floral species, compensating behaviorally for competition (Roubik 2009). Now, there is ever increasing evidence that honey bee density has detrimental effects on wild pollinators, such as decreasing their flower visitation, reproductive success, abundance, and species richness (Garibaldi et al. 2017; Angelella et al. 2021). In conclusion, it is overall clear that there are potential negative impacts of non-native bees, both in terms of disease spillover and in competition with native bees for nutritive resources and nesting sites (Russo 2016; Mallinger et al. 2017; Agüero et al. 2018; Hung et al. 2019).

7. CLIMATE CHANGE

Climate change is an important abiotic factor associated with the decline of worldwide bee populations (Soroye et al. 2020; Giannini et al. 2020). There are some studies of the effects of temperature on the winter diapause of the stingless bee. The diapause phenomenon is based on a temporary interruption of brood cell building by workers and egg-laying by the queen, and some species of the *Plebeia* genus are known to exhibit reproductive diapause (Dos Santos et al. 2015). Experimental works carried out by Dos Santos found that *Plebeia droryana* enter into diapause between 8 and 10 °C in a region with a median winter temperature of 10.1 °C. However,

according to environmental prediction models, the temperature may increase in the coming decades, making climate change an important factor that could disrupt the diapause cycle of *P. droryana* at temperatures between 16 and 22 °C (Dos Santos et al. 2015, 2016b).

These findings have important implications for ecosystem services. Climate change has already been observed or predicted to modify the phenology and behavior of insect pollinators of agricultural importance, including bees, and bees may be displaced from suitable habitat areas, resulting in reduced pollination success in wild plants and economically important crops (Giannini et al. 2012). In 2018, experimental bioassays revealed a strong effect of external temperature on immature stingless bees between 28 and 30 °C, causing an increase in mortality of the *Melipona interrupta* brood (Becker et al. 2018). On the other hand, a recent landscape genomics study (Jaffé et al. 2019) was carried out to determine the influence of habitat degradation and climate change on the genetic diversity of populations of *M. sunitida* distributed across northeastern Brazil, finding that the populations showed a clinal change in genetic structure across the distribution range of sampled area, with four identifiable genetic clusters. In addition, there were genomic signatures of adaptation to temperature, precipitation, and forest cover, as well as latitudinal and altitudinal patterns in the spatial distribution of adaptive genetic variation. According to these findings, the authors concluded that the knowledge obtained could help guide future conservation actions, such as preserving highland and lowland populations separately and conserving or restoring foothill and mountain forests in order to prevent the extinction of this important pollinator (Jaffé et al. 2019). In addition to the works mentioned, there are different studies that relate environmental parameters such as temperature and precipitation to the foraging behavior and honey production of species of the genus *Melipona*, whose flight activity decreases below 21 °C and above 28 °C, and which have lower honey production in warmer years (Souza et al. 2006; Koffler et al. 2015).

8. CONCLUSIONS AND PERSPECTIVES

The studies on stingless bee populations constitute a strong body of evidence that anthropogenic activities are the main drivers that threaten the survival of these wild bee species. Habitat loss and conversion to intensive agriculture, agrochemical pollution, biological factors such as competition for resources and pathogens linked to the introduction of exotic species, and climate change all compromise their survival and constitute an extinction threat to providers of important ecosystem services. Pesticides are the most used in the conventional agricultural, and although the lower doses evaluated in some studies did not cause direct mortality of wild bees, they did have harmful sublethal effects on both adults and larvae, such as physiological, morphological, and behavioral impairments, which may ultimately decrease their fitness. The use of botanical and synthetic pesticides in crop fields alters the flower visitation rates of pollinator bees, which could significantly affect yield (Brittain et al. 2010; Tschoeke et al. 2019). However, there are currently few studies on the levels of pesticides to which stingless bees are exposed to in their habitats; further work in this area will help to better understand the risk caused by pesticides on stingless bee population.

In order to prevent the extinction of native pollinators such as the stingless bees, governments need to develop initiatives to establish biological corridors. Such actions could be crucial to conserving ecosystems that provide services by buffering the joint effects of habitat loss and climate change. According to different studies, protecting conserved areas and restoring disturbed areas could improve habitat connectivity and safeguard ecosystem services, which could facilitate the dispersal and establishment of wild bees during distribution shifts (Giannini et al. 2015b). Promoting urban gardens could be an option to offer food resources for species that inhabit urban areas. This technique has been shown to promote foraging by the Australian stingless bee *Tetragonula carbonaria* even more than natural habitats and plantings, increasing resource availability and potentially enhancing bee fitness (Kaluza et al. 2016). If we are to protect wild bee populations from extinction, it will be essential to develop policies and research related to the protection of the ecological areas of these important pollinators around the world.

AUTHOR CONTRIBUTION

ETH conceived this review article and wrote the manuscript draft; GPC, VMHV, CCL, JTJ, YRR, and RLR participated in the revision, read, and approved the final manuscript.

REFERENCES

Agüero JI, Rollin O, Torretta JP, Aizen MA, Requier F, Garibaldi LA (2018). Honey bee impact on plants and wild bees in natural habitats. Ecosistemas. https://doi.org/10.7818/ECOS.1365

Almeida CH, Haddi K, Toledo PF, Rezende SM, Santana WC, Guedes RNC, Newland PL, Oliveira EE (2021) Sublethal agrochemical exposures can alter honey bees' and Neotropical stingless bees' color preferences, respiration rates, and locomotory responses. Sci Total Environ. https://doi.org/10.1016/j.scitotenv.2021.146432

Alvarez LJ, Reynaldi FJ, Ramello PJ, Garcia MLG, Sguazza GH, Abrahamovich AH, Lucia M (2018) Detection of honey bee viruses in Argentinian stingless bees (Hymenoptera: Apidae). Insect Soc. https://doi.org/10.1007/s00040-017-0587-2

Alvarez-Suarez JM, Giampieri F, Brenciani A et al (2018) *Apis mellifera* vs *Melipona beecheii* Cuban polifloral honeys: A comparison based on their physicochemical parameters, chemical composition and biological properties. LWT - Food Sci Technol. https://doi.org/10.1016/j.lwt.2017.08.079

Angelella GM, McCullough CT, O'Rourke ME (2021) Honey bee hives decrease wild bee abundance, species richness, and fruit count on farms regardless of wildflower strips. Sci Rep. https://doi.org/10.1038/s41598-021-81967-1

Araújo ED, Costa M, Chaud-Netto J, Fowler HG (2004) Body size and flight distance in stingless bees (Hymenoptera: Meliponini): inference of flight range and possible ecological implications. Braz J Biol. https://doi.org/10.1590/S1519-69842004000400003

Araújo RDS, Bernardes RC, Fernandes KM, Lima MAP, Martins GF, Tavares MG (2019b) Spinosad-mediated effects in the post-embryonic development of *Partamona helleri* (Hymenoptera: Apidae: Meliponini). Environ Pollut. https://doi.org/10.1016/j.envpol.2019.06.087

Araújo RDS, Bernardes RC, Martins GF (2021) A mixture containing the herbicides Mesotrione and Atrazine imposes toxicological effects on workers of *Partamona helleri*. Sci Total Environ. https://doi.org/10.1016/j.scitotenv.2020.142980

Araújo RDS, Lopes MP, Barbosa WF, Gonçalves WG, Fernandes KM, Martins GF, Tavares MG (2019a) Spinosad-mediated effects on survival, overall group activity and the midgut of workers of *Partamona helleri* (Hymenoptera: Apidae). Ecotoxicol Environ Saf. https://doi.org/10.1016/j.ecoenv.2019.03.050

Arena M, Sgolastra F (2014) A meta-analysis comparing the sensitivity of bees to pesticides. Ecotoxicology. https://doi.org/10.1007/s10646-014-1190-1

Arena MV, Martines MR, da Silva TN, Destéfani FC, Mascotti JC, Silva-Zacarin EC, Toppa RH (2018) Multiple-scale approach for evaluating the occupation of stingless bees in Atlantic forest patches. Forest Ecol Manag. https://doi.org/10.1016/j.foreco.2018.08.038

Arnold N, Zepeda R, Vásquez DM, Maya MA (2018) Las abejas sin aguijón y su cultivo en Oaxaca, México con catálogo de especies. ECOSUR-CONABIO, San Cristóbal de las Casas.

Ayala R, Gonzalez VH, Engel MS (2013) Mexican stingless bees (Hymenoptera: Apidae): Diversity, distribution, and indigenous knowledge. In: Vit P, Pedro S, Roubik D (eds) Pot-Honey: A Legacy of Stingless Bees. Springer Science & Business Media, New York, pp 135–152. https://doi.org/10.1007/978-1-4614-4960-7_9

Barbosa MM, Fernandes ACC, Alves RSC, Alves DA, Junior FB, Batista BL, Ribeiro MC, Carneiro MFH (2021) Effects of native forest and human-modified land covers on the accumulation of toxic metals and metalloids in the tropical bee *Tetragonisca angustula*. Ecotoxicol Environ Saf. https://doi.org/10.1016/j.ecoenv.2021.112147

Barbosa WF, Tomé HVV, Bernardes RC, Siqueira MA, Smagghe G, Guedes RNC (2015) Biopesticide-induced behavioral and morphological alterations in the stingless bee *Melipona quadrifasciata*. Environ Toxicol Chem. https://doi.org/10.1002/etc.3053

Becker T, Pequeno PACL, Carvalho-Zilse GA (2018) Impact of environmental temperatures on mortality, sex and caste ratios in *Melipona interrupta* Latreille (Hymenoptera, Apidae). Sci Nat. https://doi.org/10.1007/s00114-018-1577-6

Bernardes RC, Barbosa WF, Martins GF, Lima MAP (2018) The reduced-risk insecticide azadirachtin poses a toxicological hazard to stingless bee *Partamona helleri* (Friese, 1900) queens. Chemosphere. https://doi.org/10.1016/j.chemosphere.2018.03.030Get

Bernardes RC, Tomé HVV, Barbosa WF, Guedes RNC, Lima MAP (2017) Azadirachtin-induced antifeeding in Neotropical stingless bees. Apidologie. https://doi.org/10.1007/s13592-016-0473-3

Biesmeijer JC, Roberts SPM, Reemer M et al (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science. https://doi.org/10.1126/science.1127863

Boff S, Friedel A, Mussury RM, Lenis PR, Raizer J (2018) Changes in social behavior are induced by pesticide ingestion in a Neotropical stingless bee. Ecotoxicol Environ Safe. https://doi.org/10.1016/j.ecoenv.2018.08.061

Botina LL, Bernardes RC, Barbosa WF, Lima MA, Guedes RN, Martins GF (2020) Toxicological assessments of agrochemical effects on stingless bees (Apidae, Meliponini). MethodsX. https://doi.org/10.1016/j.mex.2020.100906

Botina LL, Vélez M, Barbosa WF, Mendonça AC, Pylro VS, Tótola MR, Martins GF (2019) Behavior and gut bacteria of *Partamona helleri* under sublethal exposure to a bioinsecticide and a leaf fertilizer.

Chemosphere. https://doi.org/10.1016/j.chemo sphere.2019.06.048

Brittain C, Bommarco R, Vighi M, Barmaz S, Settele J, Potts SG (2010) The impact of an insecticide on insect flower visitation and pollination in an agricultural landscape. Agric For Entomol. https://doi.org/10.1111/j.1461-9563.2010.00485.x

Brosi BJ (2009) The complex responses of social stingless bees (Apidae: Meliponini) to tropical deforestation. Forest Ecol Manag. https://doi.org/10.1016/j.foreco.2009.02.025

Brosi BJ, Daily GC, Ehrlich PR (2007) Bee community shifts with landscape context in a tropical countryside. Ecol Appl. https://doi.org/10.1890/06-0029

Brosi BJ, Daily GC, Shih TM, Oviedo F, Durán G (2008) The effects of forest fragmentation on bee communities in tropical countryside. J Appl Ecol. https://doi.org/10.1111/j.1365-2664.2007.01412.x

Brown BV (1997) Parasitic phorid flies: A previously unrecognized cost to aggregation behavior of male stingless bees. Biotropica. https://doi.org/10.1111/j.1744-7429.1997.tb00439.x

Brown JC, Albrecht C (2001) The effect of tropical deforestation on stingless bees of the genus Melipona (Insecta: Hymenoptera: Apidae: Meliponini) in central Rondonia, Brazil. J Biogeogr. https://doi.org/10.1046/j.1365-2699.2001.00583.x

Brown JC, de Oliveira ML (2014) The impact of agricultural colonization and deforestation on stingless bee (Apidae: Meliponini) composition and richness in Rondônia, Brazil. Apidologie. https://doi.org/10.1007/s13592-013-0236-3

Caesar L, Cibulski SP, Canal CW, Blochtein B, Sattler A, Haag KL. (2019) The virome of an endangered stingless bee suffering from annual mortality in Southern Brazil. J Gen Virol. https://doi.org/10.1099/jgv.0.001273

Cairns CE, Villanueva-Gutiérrez R, Koptur S, Bray DB (2005) Bee populations, forest disturbance, and Africanization in Mexico. Biotropica. https://doi.org/10.1111/j.1744-7429.2005.00087.x

Ceballos G, Ehrlich PR, Dirzo R (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proc Natl Acad Sci. https://doi.org/10.1073/pnas.1704949114

Cepeda-Aponte OI, Imperatriz-Fonseca VL, Velthuis HHW (2002) Lesser wax moth Achroia grisella: First report for stingless bees and new capture method. J Apic Res. https://doi.org/10.1080/00218839.2002.11101077

Costa LM, Grella TC, Barbosa RA, Malaspina O, Nocelli RCF (2015) Determination of acute lethal doses (LD50 and LC50) of imidacloprid for the native bee Melipona scutellaris Latreille, 1811 (Hymenoptera: Apidae). Sociobiology. https://doi.org/10.13102/sociobiology.v62i4.792

Davidson EW, Morton HL, Moffett JO, Singer S (1977) Effect of Bacillus sphaericus strain SSII-1 on honey bees, Apis mellifera. J Invertebr Pathol. https://doi.org/10.1016/S0022-2011(77)80041-4

de Morais CR, Travençolo BAN, Carvalho SM, Beletti ME, Vieira Santos VS, Campos CF, de Campos Júnior EO, Pereira BB, Carvalho Naves MP, de Rezende AAA, Spanó MA, Vieira CU, Bonetti AM. (2018) Ecotoxicological effects of the insecticide fipronil in Brazilian native stingless bees Melipona scutellaris (Apidae: Meliponini). Chemosphere. https://doi.org/10.1016/j.chemosphere.2018.04.153

de Souza FS, Kevill JL, Correia-Oliveira ME, de Carvalho CAL, Martin SJ (2019) Occurrence of deformed wing virus variants in the stingless bee Melipona subnitida and honey bee Apis mellifera populations in Brazil. J Gen Virol. https://doi.org/10.1099/jgv.0.001206

Del Sarto MCL, Oliveira EE, Guedes RNC, Campos LAO (2014) Differential insecticide susceptibility of the Neotropical stingless bee Melipona quadrifasciata and the honey bee Apis mellifera. Apidologie. https://doi.org/10.1007/s13592-014-0281-6

DiBartolomeis M, Kegley S, Mineau P, Radford R, Klein K (2019) An assessment of acute insecticide toxicity loading (AITL) of chemical pesticides used on agricultural land in the United States. PLoS ONE. https://doi.org/10.1371/journal.pone.0220029

Domingues CEC, Inoue LV, da Silva-Zacarin EC, Malaspina O (2020) Fungicide pyraclostrobin affects midgut morphophysiology and reduces survival of Brazilian native stingless bee Melipona scutellaris. Ecotox Environ Safe. https://doi.org/10.1016/j.ecoenv.2020.111395

Dorigo AS, Rosa-Fontana A, Soares-Lima HM, Galaschi-Teixeira JS, Nocelli RC, Malaspina O (2019) In vitro larval rearing protocol for the stingless bee species Melipona scutellaris for toxicological studies. PLoS ONE. https://doi.org/10.1371/journal.pone.0213109

Dorneles AL, de Souza Rosa A, Blochtein B (2017) Toxicity of organophosphorus pesticides to the stingless bees Scaptotrigona bipunctata and Tetragonisca fiebrigi. Apidologie. https://doi.org/10.1007/s13592-017-0502-x

Dorneles AL, Rosa-Fontana A, Dos Santos CF, Blochtein B (2021) Larvae of stingless bee Scaptotrigona bipunctata exposed to organophosphorus pesticide develop into lighter, smaller and deformed adult workers. Environ Pollut. https://doi.org/10.1016/j.envpol.2020.116414

Dos Santos CF, Acosta AL, Dorneles AL, Dos Santos PD, Blochtein B (2016a) Queens become workers: pesticides alter caste differentiation in bees. Sci Rep. https://doi.org/10.1038/srep31605

Dos Santos CF, Acosta AL, Nunes-Silva P, Saraiva AM, Blochtein B (2015) Climate warming may threaten

reproductive diapause of a highly eusocial bee. Environ Entomol. https://doi.org/10.1093/ee/nvv064

Dos Santos CF, Nunes-Silva P, Blochtein B (2016b) Temperature rise and its influence on the cessation of diapause in *Plebeia droryana*, a eusocial bee (Hymenoptera: Apidae). Ann Entomol Soc Am. https://doi.org/10.1093/aesa/sav096

Dudley N, Alexander S (2017) Agriculture and biodiversity: a review. Biodiversity. https://doi.org/10.1080/14888386.2017.1351892

Farder-Gomes CF, Fernandes KM, Bernardes RC, Bastos DS, Martins GF, Serrão JE (2021) Acute exposure to fipronil induces oxidative stress, apoptosis and impairs epithelial homeostasis in the midgut of the stingless bee *Partamona helleri* Friese (Hymenoptera: Apidae). Sci Total Environ. https://doi.org/10.1016/j.scitotenv.2021.145679

Fermino F, Penteado FJR, Arnaut De Toledo V.D.A., Ruvolo-Takasusuki MCC (2011) Isoenzymes and cytochemical analysis in *Tetragonisca angustula* and *Tetragonisca fiebrigi* after herbicide contamination. Sociobiology. **58**:353-366

Ferreira RAC, Silva Zacarin ECMS, Malaspina O, Bueno OC, Tomotake MEM, Pereira AM (2013) Cellular responses in the Malpighian tubules of *Scaptotrigona postica* (Latreille, 1807) exposed to low doses of fipronil and boric acid. Micron. https://doi.org/10.1016/j.micron.2012.12.008

Garibaldi LA, Requier F, Rollin O, Andersson GK (2017) Towards an integrated species and habitat management of crop pollination. Curr Opin Insect Sci. https://doi.org/10.1016/j.cois.2017.05.016

Giannini TC, Acosta AL, Garófalo CA, Saraiva AM, Alves-dos-Santos I, Imperatriz-Fonseca VL (2012) Pollination services at risk: Bee habitats will decrease owing to climate change in Brazil. Ecol Model. https://doi.org/10.1016/j.ecolmodel.2012.06.035

Giannini TC, Boff S, Cordeiro GD, Cartolano EA, Veiga AK, Imperatriz-Fonseca VL, Saraiva AM (2015a) Crop pollinators in Brazil: a review of reported interactions. Apidologie. https://doi.org/10.1007/s13592-014-0316-z

Giannini TC, Costa WF, Borges RC, Miranda L, da Costa CPW, Saraiva AM, Imperatriz Fonseca VL (2020) Climate change in the Eastern Amazon: crop-pollinator and occurrence-restricted bees are potentially more affected. Reg Environ Change. https://doi.org/10.1007/s10113-020-01611-y

Giannini TC, Tambosi LR, Acosta AL, Jaffé R, Saraiva AM, Imperatriz-Fonseca VL, Metzger JP (2015b) Safeguarding ecosystem services: A methodological framework to buffer the joint effect of habitat configuration and climate change. PLoS ONE. https://doi.org/10.1371/journal.pone.0129225

Gómez-Escobar E, Liedo P, Montoya P, Méndez-Villarreal A, Guzmán M, Vandame R, Sánchez D (2018) Effect of GF-120 (spinosad) aerial sprays on colonies of the stingless bee *Scaptotrigona mexicana* (Hymenoptera: Apidae) and the honey bee (Hymenoptera: Apidae). J Econ Entomol. https://doi.org/10.1093/jee/toy152

Gómez-Escobar E, Liedo P, Montoya P, Vandame R, Sánchez D (2014) Behavioral response of two species of stingless bees and the honey bee (Hymenoptera: Apidae) to GF-120. J Econ Entomol. https://doi.org/10.1603/EC13490

Goulson D (2003) Effects of introduced bees on native ecosystems. Annu Rev Ecol Evol Syst. https://doi.org/10.1146/annurev.ecolsys.34.011802.132355

Graystock P, Blane EJ, McFrederick QS, Goulson D, Hughes WO (2016) Do managed bees drive parasite spread and emergence in wild bees?. Int J Parasitol Parasites Wildl. https://doi.org/10.1016/j.ijppaw.2015.10.001

Guimarães-Cestaro L, Martins MF, Martínez LC, Alves ML, Guidugli-Lazzarini KR, Nocelli RC, Malaspina O, Serrão JE, Teixeira ÉW (2020) Occurrence of virus, microsporidia, and pesticide residues in three species of stingless bees (Apidae: Meliponini) in the field. Sci Nat. https://doi.org/10.1007/s00114-020-1670-5

Guzman-Novoa E, Hamiduzzaman MM, Anguiano-Baez R, Correa-Benítez A, Castañeda-Cervantes E, Arnold NI (2015) First detection of honey bee viruses in stingless bees in North America. J Apic Res. https://doi.org/10.1080/00218839.2015.1100154

Hardee DD, Van Duyn JW, Layton MB, Bagwell RD (2001) Bt cotton and management of tobacco budworm and bollworm complex. U.S. Department of Agriculture (USDA)- Agriculture Research Service (ARS), Stoneville.

Hernández-Torres H, Georgievich-Kirejtshuk A, Núñez-Vázquez C, García-Martínez O (2021) On *Aethina tumida* Murray (Coleoptera: Nitidulidae: Nitidulinae) in hives of *Apis mellifera* Linnaeus (Hymenoptera: Apidae) in Campeche, México. J Apic Res. https://doi.org/10.1080/00218839.2021.1889223

Hubbell SP, Johnson LK (1978) Comparative foraging behavior of six stingless bee species exploiting a standardized resource. Ecology. https://doi.org/10.2307/1938227

Hung KL, Kingston JM, Lee A, Holway DA, Kohn JR (2019) Non-native honey bees disproportionately dominate the most abundant floral resources in a biodiversity hotspot. Proc Royal Soc B. https://doi.org/10.1098/rspb.2018.2901

Jacob CRO, Malaquias JB, Zanardi OZ, Silva CAS, Jacob JFO, Yamamoto PT (2019b) Oral acute toxicity and impact of neonicotinoids on *Apis mellifera* L. and *Scaptotrigona postica* Latreille (Hymenoptera: Apidae). Ecotoxicology. https://doi.org/10.1007/s10646-019-02070-w

Jacob CRO, Soares HM, Carvalho SM, Nocelli RCF, Malaspina O (2013) Acute toxicity of fipronil to the stingless bee *Scaptotrigona postica* latreille.

Bull Environ Contam Toxicol. https://doi.org/10.1007/s00128-012-0892-4

Jacob CRO, Soares HM, Nocelli RC, Malaspina O (2015) Impact of fipronil on the mushroom bodies of the stingless bee *Scaptotrigona postica*. Pest Manag Sci. https://doi.org/10.1002/ps.3776

Jacob CRO, Zanardi OZ, Malaquias JB, Silva CAS, Yamamoto PT (2019a) The impact of four widely used neonicotinoid insecticides on *Tetragonisca angustula* (Latreille) (Hymenoptera: Apidae). Chemosphere. https://doi.org/10.1016/j.chemosphere.2019.02.105

Jaffé R, Veiga JC, Pope NS et al (2019) Landscape genomics to the rescue of a tropical bee threatened by habitat loss and climate change. Evol Appl. https://doi.org/10.1111/eva.12794

Jalil AMA, Kasmuri AR, Hadi H (2017) Stingless Bee Honey, the Natural Wound Healer: A Review. Skin Pharmacol Physiol. https://doi.org/10.1159/000458416

Johnson LK, Hubbell SP (1974) Aggression and competition among stingless bees: Field studies. Ecology. https://doi.org/10.2307/1934624

Kaluza BF, Wallace H, Heard TA, Klein AM, Leonhardt SD (2016) Urban gardens promote bee foraging over natural habitats and plantations. Ecol Evol. https://doi.org/10.1002/ece3.1941

Kamle M, Kumar P, Patra JK, Bajpai VK (2017) Current perspectives on genetically modified crops and detection methods. 3 Biotech. https://doi.org/10.1007/s13205-017-0809-3

Kiatoko N, Raina SK, Van Langevelde F (2017) Impact of habitat degradation on species diversity and nest abundance of five African stingless bee species in a tropical rainforest of Kenya. Int J Trop Insect Sci. https://doi.org/10.1017/S174275841700011X

Klein AM, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke, T (2007) Importance of pollinators in changing landscapes for world crops. Proc Royal Soc B. https://doi.org/10.1098/rspb.2006.3721

Koffler S, Menezes C, Menezes PR, Kleinert AMP, Imperatriz-Fonseca VL, Pope N, Jaffé R (2015) Temporal variation in honey production by the stingless bee *Melipona subnitida* (Hymenoptera: Apidae): Long-term management reveals its potential as a commercial species in northeastern Brazil. J Econ Entomol. https://doi.org/10.1093/jee/tov055

Kuhn-Neto B, Contrera FAL, Castro MS, Nieh JC (2009) Long distance foraging and recruitment by a stingless bee, *Melipona mandacaia*. Apidologie. https://doi.org/10.1051/apido/2009007

Lichtenberg EM, Mendenhall CD, Brosi B (2017) Foraging traits modulate stingless bee community disassembly under forest loss. J Anim Ecol. https://doi.org/10.1111/1365-2656.12747

Lima MAP, Martins GF, Oliveira EE, Guedes RNC (2016) Agrochemical-induced stress in stingless bees: peculiarities, underlying basis, and challenges. J Comp Physiol A Neuroethol Sens Neural Behav Physiol. https://doi.org/10.1007/s00359-016-1110-3

Lima MAP, Pires CSS, Guedes RNC, Campos LAO (2013) Lack of lethal and sublethal effects of Cry1Ac Bt-toxin on larvae of the stingless bee *Trigona spinipes*. Apidologie. https://doi.org/10.1007/s13592-012-0151-z

Lóriga-Peña W, Fonte-Carballo L, Demedio-Lorenzo J (2014). Report of *Aethina tumida* Murray (Coleoptera, Nitidulidae) in colonies of the stingless bee *Melipona beecheii* Bennett of Matanzas and Mayabeque. Rev Salud Anim. **36**(3):201-204

Lourenço CT, Carvalho SM, Malaspina O, Nocelli RC (2012a) Determination of fipronil LD50 for the Brazilian bee *Melipona scutellaris*. Julius-Kühn-Archiv. https://doi.org/10.5073/jka.2012.437.046

Lourenço CT, Carvalho SM, Malaspina O, Nocelli RCF (2012b) Oral toxicity of fipronil insecticide against the stingless bee *Melipona scutellaris* (Latreille, 1811). Bull Environ Contam Toxicol. https://doi.org/10.1007/s00128-012-0773-x

Macías-Macías JO, Otero-Colina G (2004) Infestation of *Pyemotes tritici* (Acari: Pyemotidae) on *Melipona colimana* (Hymenoptera: Apidae: Meliponinae): A case study. Agrociencia. **38**(5):525-528

Macieira OJD, Hebling-Beraldo MJA (1989) Laboratory toxicity of insecticides to workers of *Trigona spinipes* (F., 1793) (Hymenoptera, apidae). J Apic Res. https://doi.org/10.1080/00218839.1989.11100813

Maia-Silva C, Hrncir M, Imperatriz-Fonseca VL, Schorkopf DL (2016) Stingless bees (*Melipona subnitida*) adjust brood production rather than foraging activity in response to changes in pollen stores. J Comp Physiol A Neuroethol Sens Neural Behav Physiol. https://doi.org/10.1007/s00359-016-1095-y

Maia-Silva C, Hrncir M, Koedam D, MacHado RJP, Imperatriz-Fonseca VL (2013) Out with the garbage: The parasitic strategy of the mantisfly *Plega hagenella* mass-infesting colonies of the eusocial bee *Melipona subnitida* in northeastern Brazil. Naturwissenschaften. https://doi.org/10.1007/s00114-012-0994-1

Mallinger RE, Gaines-Day HR, Gratton C (2017) Do managed bees have negative effects on wild bees?: A systematic review of the literature. PLoS ONE. https://doi.org/10.1371/journal.pone.0189268

Matos WB, Santos AC, Lima AP, Santana ED, Silva JE, Blank AF, Araújo AP, Bacci L (2021) Potential source of ecofriendly insecticides: Essential oil induces avoidance and cause lower impairment on the activity of a stingless bee than organosynthetic insecticides, in laboratory. Ecotox Environ Safe. https://doi.org/10.1016/j.ecoenv.2020.111764

Mayes DM, Bhatta CP, Shi D, Brown JC, Smith DR (2019) Body size influences stingless bee (Hymenoptera: Apidae) communities across a range of deforestation

levels in Rondônia, Brazil. J Insect Sci. https://doi.org/10.1093/jisesa/iez032

Menezes C, Coletto-Silva A, Gazeta GS, Kerr WE (2009) Infestation by *Pyemotes tritici* (Acari, Pyemotidae) causes death of stingless bee colonies (Hymenoptera: Meliponina). Genet Mol Res. https://doi.org/10.4238/vol8-2kerr021

Michener CD (2013) The Meliponini. In: Vit P, Pedro S, Roubik D (eds) Pot-Honey: A Legacy of Stingless Bees. Springer Science & Business Media, New York, pp 3–17. https://doi.org/10.1007/978-1-4614-4960-7_1

Miotelo L, Dos Reis AL, Malaquias JB, Malaspina O, Roat TC (2021) *Apis mellifera* and *Melipona scutellaris* exhibit differential sensitivity to thiamethoxam. Environ Pollut. https://doi.org/10.1016/j.envpol.2020.115770

Morfin N, Gashout HA, Macías-Macías JO, De la Mora A, Tapia-Rivera JC, Tapia-González JM, Contreras-Escareño F, Guzman-Novoa E (2020) Detection, replication and quantification of deformed wing virus-A, deformed wing virus-B, and black queen cell virus in the endemic stingless bee, *Melipona colimana*, from Jalisco, Mexico. Int J Trop Insect Sci. https://doi.org/10.1007/s42690-020-00320-7

Nacko S, Hall M, Duncan M, Cook J, Riegler M, Spooner-Hart R (2020). Scientific note on small hive beetle infestation of stingless bee (*Tetragonula carbonaria*) colony following a heat wave. Apidologie. https://doi.org/10.1007/s13592-020-00799-6

Nicholls CI, Altieri MA (2013) Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. Agron Sustain Dev. https://doi.org/10.1007/s13593-012-0092-y

Nocelli RCF, Soares SMM, Monquero PA (2019) Effects of herbicides on the survival of the brazilian native bee *Melipona scutellaris* latreille, 1811 (Hymenoptera: Apidae). Planta Daninha. https://doi.org/10.1590/s0100-83582019370100156

Nunes-Silva P, Piot N, Meeus I, Blochtein B, Smagghe G (2016) Absence of Leishmaniinae and Nosematidae in stingless bees. Sci Rep. https://doi.org/10.1038/srep32547

Padilha AC, Piovesan B, Morais MC, Arioli CJ, Zotti MJ, Grützmacher AD, Botton M (2019) Toxicity, attraction, and repellency of toxic baits to stingless bees *Plebeia emerina* (Friese) and *Tetragonisca fiebrigi* (Schwarz) (Hymenoptera: Apidae: Meliponini). Ecotoxicol Environ Safe. https://doi.org/10.1016/j.ecoenv.2019.109490

Padilha AC, Piovesan B, Morais MC, Pazini JdB, Zotti MJ, Botton M, Grützmacher AD (2020) Toxicity of insecticides on Neotropical stingless bees *Plebeia emerina* (Friese) and *Tetragonisca fiebrigi* (Schwarz) (Hymenoptera: Apidae: Meliponini). Ecotoxicology. https://doi.org/10.1007/s10646-019-02150-x

Pereira SN, Alves LHS, da Costa RFR, Prezoto F, Teixeira EW (2021) Occurrence of the small hive beetle (*Aethina tumida*) in *Melipona rufiventris* colonies in Brazil. Sociobiology. https://doi.org/10.13102/sociobiology.v68i1.6021

Pioker-Hara FC, Drummond MS, Kleinert AMP (2014) The influence of the loss of Brazilian savanna vegetation on the occurrence of stingless bees nests (Hymenoptera: Apidae: Meliponini). Sociobiology. https://doi.org/10.13102/sociobiology.v61i4.393-400

Porrini MP, Porrini LP, Garrido PM et al (2017) *Nosema ceranae* in south american native stingless bees and social wasp. Microb Ecol. https://doi.org/10.1007/s00248-017-0975-1

Prado FSR, dos Santos DM, de Almeida Oliveira TM, Burgarelli JAM, Castele JB, Vieira EM (2020) Determination and uptake of abamectin and difenoconazole in the stingless bee *Melipona scutellaris* Latreille (1811) via oral and topic acute exposure. Environ Pollut. https://doi.org/10.1016/j.envpol.2020.114313

Prado-Silva A, Nunes LA, dos Santos JM, de Mello APRA, Waldschmidt AM (2018) Morphogenetic alterations in *Melipona quadrifasciata anthidioides* (Hymenoptera: Apidae) associated with pesticides. Arch Environ Contam Toxicol. https://doi.org/10.1007/s00244-018-0509-y

Purkiss T, Lach L (2019) Pathogen spillover from *Apis mellifera* to a stingless bee. Proc Royal Soc B. https://doi.org/10.1098/rspb.2019.1071

Quiroga-Murcia DE, Zotti MJ, de Polanía IZ, Pech-Pech EE (2017) Toxicity evaluation of two insecticides on *Tetragonisca angustula* and *Scaptotrigona xanthotricha* (Hymenoptera: Apidae). Agron Colomb. https://doi.org/10.15446/agron.colomb.v35n3.65447

Ramalho M, Kleinert-Giovannini A, Imperatriz-Fonseca V (1990) Important bee plants for stingless bees (*Melipona* and *Trigonini*) and Africanized honeybees (*Apis mellifera*) in neotropical habitats: a review. Apidologie. https://doi.org/10.1051/apido:19900508

Ravaiano SV, Barbosa WF, Tomé HVV, Campos LAO, Martins GF (2018) Acute and oral exposure to imidacloprid does not affect the number of circulating hemocytes in the stingless bee *Melipona quadrifasciata* post immune challenge. Pestic Biochem Physiol. https://doi.org/10.1016/j.pestbp.2018.08.002

Reyes-González A, Camou-Guerrero A, del-Val E, Ramírez MI, Porter-Bolland L (2020) Biocultural diversity loss: the decline of native stingless bees (Apidae: Meliponini) and local ecological knowledge in Michoacán, Western México. Human Ecology. https://doi.org/10.1007/s10745-020-00167-z

Ribeiro AV, de Sá FE, Santos AA, Filomeno CA, dos Santos IB, Barbosa LCA, Picanço MC (2018) Selection of an essential oil from Corymbia and Eucalyptus plants against *Ascia monuste* and its

selectivity to two non-target organisms. Crop Prot. https://doi.org/10.1016/j.cropro.2017.08.014

Rodrigues CG, Krüger AP, Barbosa WF, Guedes RNC (2016) Leaf fertilizers affect survival and behavior of the neotropical stingless bee *Friesella schrottkyi* (Meliponini: Apidae: Hymenoptera). J Econ Entomol. https://doi.org/10.1093/jee/tow044

Rosa ADS, I'Anson Price R, Ferreira Caliman MJ, Pereira Queiroz E, Blochtein B, Sílvia Soares Pires C, Imperatriz-Fonseca VL (2015) The stingless bee species, *Scaptotrigona* aff. *depilis*, as a potential indicator of environmental pesticide contamination. Environ Toxicol Chem. https://doi.org/10.1002/etc.2998

Rosa ADS, Teixeira JSG, Vollet-Neto A, Queiroz EP, Blochtein B, Pires CSS, Imperatriz-Fonseca VL (2016) Consumption of the neonicotinoid thiamethoxam during the larval stage affects the survival and development of the stingless bee, *Scaptotrigona aff. depilis*. Apidologie. https://doi.org/10.1007/s13592-015-0424-4

Rosa-Fontana A, Dorigo AS, Galaschi-Teixeira JS, Nocelli RC, Malaspina O (2020) What is the most suitable native bee species from the Neotropical region to be proposed as model-organism for toxicity tests during the larval phase? Environ Pollut. https://doi.org/10.1016/j.envpol.2020.114849

Roubik DW (1978). Competitive interactions between neotropical pollinators and Africanized honey bees. Science. https://doi.org/10.1126/science.201.4360.1030

Roubik DW (1980) Foraging behavior of competing africanized honeybees and stingless bees. Ecology. https://doi.org/10.2307/1936754

Roubik DW (1983) Experimental community studies: time-series tests of competition between African and neotropical bees. Ecology. https://doi.org/10.2307/1937803

Roubik DW (2009) Ecological impact on native bees by the invasive Africanized honey bee. Acta Biol Colomb. **14**(2):115-124.

Russo L (2016) Positive and negative impacts of nonnative bee species around the world. Insects. https://doi.org/10.3390/insects7040069

Samejima H, Marzuki M, Nagamitsu T, Nakasizuka T (2004) The effects of human disturbance on a stingless bee community in a tropical rainforest. Biol Conserv. https://doi.org/10.1016/j.biocon.2004.03.030

Sánchez D, De J Solórzano E, Liedo P, Vandame R (2012) Effect of the natural pesticide Spinosad (GF-120 Formulation) on the foraging behavior of *Plebeia moureana* (Hymenoptera: Apidae). J Econ Entomol. https://doi.org/10.1603/EC12047

Sánchez-Bayo F, Wyckhuys KAG (2019) Worldwide decline of the entomofauna: A review of its drivers. Biol Conserv. https://doi.org/10.1016/j.biocon.2019.01.020

Santos AOR, Bartelli BF, Nogueira-Ferreira FH (2014) Potential pollinators of tomato, *Lycopersicon esculentum* (Solanaceae), in open crops and the effect of a solitary bee in fruit set and quality. J Econ Entomol. https://doi.org/10.1603/EC13378

Seabrooks L, Hu L (2017) Insects: an underrepresented resource for the discovery of biologically active natural products. Acta Pharm Sin B. https://doi.org/10.1016/j.apsb.2017.05.001

Seide VE, Bernardes RC, Pereira EJG, Lima MAP (2018) Glyphosate is lethal and Cry toxins alter the development of the stingless bee *Melipona quadrifasciata*. Environ Pollut. https://doi.org/10.1016/j.envpol.2018.10.020

Shanks JL, Haigh AM, Riegler M, Spooner-Hart RN (2017) First confirmed report of a bacterial brood disease in stingless bees. J Invertebr Pathol. https://doi.org/10.1016/j.jip.2017.01.004

Simões D, Bego LR, Zucchi R, Sakagami SF (1980) *Melaloncha sinistra* Borgmeier, an endoparasitic phorid fly attacking *Nannotrigona* (*Scaptotrigona*) *postica* Latreille (Hymenoptera, Meliponinae). Rev Bras Entomol. **24**(2):137-142.

Soares HM, Jacob CRO, Carvalho SM, Nocelli RCF, Malaspina O (2015) Toxicity of imidacloprid to the stingless bee *Scaptotrigona postica* Latreille, 1807 (Hymenoptera: Apidae). Bull Environ Contam Toxicol. https://doi.org/10.1007/s00128-015-1488-6

Soroye P, Newbold T, Kerr J (2020) Climate change contributes to widespread declines among bumble bees across continents. Science. https://doi.org/10.1126/science.aax8591

Souza BA, Carvalho CA, Alves RM (2006) Flight activity of *Melipona asilvai* Moure (Hymenoptera: Apidae). Braz J Biol. https://doi.org/10.1590/S1519-69842006000400017

Souza-Junior JB, da Silva Teixeira-Souza VH, Oliveira-Souza A, de Oliveira PF, de Queiroz JP, Hrncir M (2020) Increasing thermal stress with flight distance in stingless bees (*Melipona subnitida*) in the Brazilian tropical dry forest: Implications for constraint on foraging range. J Insect Physiol. https://doi.org/10.1016/j.jinsphys.2020.104056

Stanley J, Preetha G, Chandrasekaran S, Kuttalam S (2009) Honey bees of the cardamom ecosystem and the selective toxicity of diafenthiuron to four different bee species in the laboratory. J Apic Res. https://doi.org/10.3896/IBRA.1.48.2.02

Tapia-González JM, Morfin N, Macías-Macías JO, De la Mora A, Tapia-Rivera JC, Ayala R, Contreras-Escareño F, Gashout HA, Guzman-Novoa E (2019) Evidence of presence and replication of honey bee viruses among wild bee pollinators in subtropical environments. J Invertebr Pathol. https://doi.org/10.1016/j.jip.2019.107256

Teixeira ÉW, Ferreira EA, da Luz CFP, Martins MF, Ramos TA, Lourenço AP (2020) European Foulbrood in stingless bees (Apidae: Meliponini) in Brazil: old

disease, renewed threat. J Invertebr Pathol. https://doi.org/10.1016/j.jip.2020.107357

Toledo-Hernández RA, Ruíz-Toledo J, Toledo J, Sánchez D (2016) Effect of three entomopathogenic fungi on three species of stingless bees (Hymenoptera: Apidae) under laboratory conditions. J Econ Entomol. https://doi.org/10.1093/jee/tow064

Tomé HVV, Barbosa WF, Corrêa AS, Gontijo LM, Martins GF, Guedes RNC (2015a) Reduced-risk insecticides in Neotropical stingless bee species: Impact on survival and activity. Ann Appl Biol. https://doi.org/10.1111/aab.12217

Tomé HVV, Barbosa WF, Martins GF, Guedes RNC (2015b) Spinosad in the native stingless bee *Melipona quadrifasciata*: Regrettable non-target toxicity of a bioinsecticide. Chemosphere. https://doi.org/10.1016/j.chemosphere.2014.11.038

Tomé HVV, Martins GF, Lima MAP, Campos LAO, Guedes RNC (2012) Imidacloprid-induced impairment of mushroom bodies and behavior of the native stingless bee *Melipona quadrifasciata anthidioides*. PLoS ONE. https://doi.org/10.1371/journal.pone.0038406

Tomé HVV, Ramos GS, Araújo MF, Santana WC, Santos GR, Guedes RN, Maciel CD, Newland PL, Oliveira EE (2017) Agrochemical synergism imposes higher risk to neotropical bees than to honeybees. R Soc Open Sci. https://doi.org/10.1098/rsos.160866

Tschoeke PH, Oliveira EE, Dalcin MS, Silveira-Tschoeke MC, Sarmento RA, Santos GR (2019) Botanical and synthetic pesticides alter the flower visitation rates of pollinator bees in Neotropical melon fields. Enviro Pollut. https://doi.org/10.1016/j.envpol.2019.04.133

Ueira-Vieira C, Almeida LO, de Almeida FC, Amaral IMR, Brandeburgo MAM, Bonetti AM (2015) Scientific note on the first molecular detection of the acute bee paralysis virus in Brazilian stingless bees. Apidologie. https://doi.org/10.1007/s13592-015-0353-2

Valdovinos-Núñez GR, Quezada-Euán JJ, Ancona-Xiu P, Moo-Valle H, Carmona A, Ruiz Sanchez E (2009) Comparative toxicity of pesticides to stingless bees (Hymenoptera: Apidae: Meliponini). J Econ Entomol. https://doi.org/10.1603/029.102.0502

van Lenteren JC, Bolckmans K, Köhl J, Ravensberg WJ, Urbaneja A (2018) Biological control using invertebrates and microorganisms: plenty of new opportunities. BioControl. https://doi.org/10.1007/s10526-017-9801-4

Venturieri GC (2009) The impact of forest exploitation on Amazonian stingless bees (Apidae, Meliponini). Genet Mol Res. https://doi.org/10.4238/vol8-2kerr031

Vijayakumar K, Jayaraj R (2013) Infestation of *Pyemotes* sp. (Acari, Pyemotidae) on *Tetragonula iridipennis* (Hymenoptera: Meliponinae) colonies. Int J Life Sci Edu Res. (IJLSER). **1**:120-122

Vijayakumar K, Muthuraman M, Jayaraj R (2013) Infestation of *Carpoglyphus lactis* (Linnaeus) (Acari: Carpoglyphidae) on *Trigona iridipennis* (Apidae: Meliponinae) from India. Sch J Agric Sci. **3**(1):25-28

Villanueva GR, Roubik DW, Colli-Ucán W (2005) Extinction of *Melipona beecheii* and traditional beekeeping in the Yucatán peninsula. Bee World. https://doi.org/10.1080/0005772X.2005.11099651

Wilms W, Imperatriz-Fonseca VL, Engels W (1996) Resource partitioning between highly eusocial bees and possible impact of the introduced Africanized honey bee on native stingless bees in the Brazilian atlantic rainforest. Stud Neotrop Fauna Environ. https://doi.org/10.1076/snfe.31.3.137.13336

Wilms W, Wiechers B (1997) Floral resource partitioning between native *Melipona* bees and the introduced Africanized honey bee in the Brazilian Atlantic rain forest. Apidologie. https://doi.org/10.1051/apido:19970602

Xavier VM, Message D, Picanço MC, Bacci L, Silva GA, Benevenute, JDS (2010) Impact of botanical insecticides on indigenous stingless bees (hymenoptera: Apidae). Sociobiology. **56**:1-13