Received: 5 January 2022 | Revised: 22 February 2022 | Accepted: 20 March 2022

DOI: 10.1111/btp.13100

bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION WILEY

ORIGINAL ARTICLE

Stingless bees (Apidae: Meliponini) at risk in western Mexico

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Funding information
This study was funded by Rufford Small Grants number 24084-1, from The Rufford Foundation and by the project "Saberes ambientales para la cogeneración de estrategias de manejo sustentable de socioecosistemas" UNAM (PAPIIT IN308418). The first author received a graduate studies scholarship from the Consejo Nacional de Ciencia y Tecnología (CONACyT) (489580).

Associate Editor: Jennifer Powers

Handling Editor: Michael Staab

Abstract

The current global pollinator crisis highlights the need to investigate the diversity and distribution of ecologically and socially relevant taxa such as tropical stingless bees. We analyzed the diversity and composition of stingless bee (Meliponini) communities at a regional scale in west-central Mexico using an extensive direct search along an altitudinal gradient encompassing different climate and vegetation types. Our hypothesis was that meliponine bee diversity would be greater in tropical warmer. We found a total of 14 meliponine bee species, including two new records for the region. We identified three types of bee assemblages: one in hot lowland climates with tropical dry forest vegetation, one in temperate highland climates with mixed oak-pine forest vegetation, and one in the warm ecotone with mixed subdeciduous forest vegetation between the hot and temperate zones. As expected, the lowland assemblage in the tropical dry forest vegetation had the greatest diversity (11 species). In the warm ecotone, meliponine species from temperate highlands and hot lowland habitats converged; this region should therefore be considered a high conservation priority area. Fifty percent of the meliponine bees found are endemic and have a very low incidence, suggesting that their populations may be endangered. Given the extensive and ongoing change of land use to avocado plantations in the warm ecotone and temperate highlands with mixed oak-pine forest vegetation cover, specific conservation plans should be generated to conserve the natural ecosystems and this important native pollinator group.

Abstract in Spanish is available with online material.

KEYWORDS
endangered bees, environmental factors, Meliponini conservation, Mexican endemic stingless bees, native bees

1 | INTRODUCTION

Bees are vital pollinators for an enormous variety of wild and cultivated species (Potts et al., 2016). In recent years, there has been a worldwide decrease in pollinators due to anthropogenic causes (Potts et al., 2010, 2016). However, there is very little information about the decline of bees in tropical areas of America. Stingless bees or meliponine bees (Apidae: Meliponini) are essential pollinators in tropical and subtropical areas (Michener, 2007). They are responsible for the pollination of at least 60 crops and 50% of the floral visits to wild plants in different habitats of tropical America (Heard, 1999; Michener, 2007; Slaa et al., 2006).

The Meliponini tribe is very diverse, with more than 500 species worldwide (Michener, 2007). While they display different behavioral patterns, nesting habits, and defense strategies (Roubik, 2006), all share the distinctive character of an atrophied sting (Michener, 2007). In Mexico, there are 46 species, 26% of which are endemic (Ayala et al., 2013).

At a national scale, meliponine bees in Mexico follow a typical neotropical distribution (Halffter, 1976). Most of them inhabit warm lowland areas in both dry and humid regions, though some inhabit mountainous areas up to 3000 m elevation (Ayala et al., 2013). At the state scale, however, their distribution has not been clearly established and there are areas of overlap among species with distinct biogeographical histories (Yañez-Ordóñez et al., 2008). The Pacific Coast from Guerrero to Chiapas as well as southern Veracruz are the areas that contain the greatest number of stingless bee species reported to date (Ayala et al., 2013). These authors proposed a distributional scheme for Meliponini by vegetation type composed of three groups: (1) widely distributed species associated with both tropical dry and wet forests; (2) species associated with tropical wet forests; and (3) endemic species associated with several types of vegetation. More recently, meliponines have been recorded in areas where they were previously considered absent, generating the need to further analyze the biotic and abiotic factors that shape meliponine bee assemblages, particularly at the state level, the level at which conservation actions are established (Arnold et al., 2018; Reyes-González et al., 2014, 2017).

In Mexico, studies of meliponine bees are concentrated in a few areas of the country in the Southeast (Chiapas, Oaxaca, Veracruz, and the Yucatán peninsula) (Arnold et al., 2018; Ayala, 1988, 1997; Hinojosa-Díaz, 2003; Meléndez-Ramírez et al., 2016; Reyes-González et al., 2014, 2020; Reyes-Novelo et al., 2009; Roubik et al., 1991; Vandame et al., 2013; Vergara-Briseño & Ayala, 2002), leaving regions to the west in need further study to understand the diversity, composition and distribution of Meliponini. Some recent studies in western Mexico have documented 13 Meliponini species, including two new records for the area—*Lestrimelitta chamelensis* Ayala and *Plebeia fulvopilosa* Ayala—as well as an important cultural legacy of knowledge and management associated with these native bees (Ayala et al., 2013; Reyes-González et al., 2014, 2016, 2017, 2020).

As in many insects, the distribution of bees is related to various environmental variables, including altitude, latitude, temperature and humidity, and ecological disturbance (McCoy, 1990; Roubik, 1989). In general, the richest assemblages of bees are found in xeric and warm temperate zones, near the limit of the subtropics or mid-latitudes (Orr et al., 2021; Roubik, 1989). The most important drivers behind this pattern of distribution are maximal temperature of warmest month and plant species richness (Orr et al., 2021). However, social bees such as Meliponini have a pantropical distribution (Kerr & Maule, 1964; Michener, 1979), and Roubik (1989) proposed the hypothesis that this group of social bees has radiated towards the subtropics and may follow a different pattern of geographical distribution than the bees in general (Gaston, 1992; Mittelbach et al., 2007; Price et al., 1995). Therefore, in order to understand if tropical or subtropical areas in Mexico hold the vast majority of meliponinis for conservation purposes, there is a need for detailed studies at regional scales.

Despite the historical and cultural importance of meliponine bees in western Mexico, there are many knowledge gaps with respect to their ecology and distribution in this region. In this study, we evaluated the composition and diversity of the Meliponini tribe in the state of Michoacán (Figure 1) to determine whether they follow the proposed increase in diversity towards areas with warm and hot climates, which correspond to the lower altitude areas at the state level, and to establish their potential spatial distribution and habitat preferences. Using data from bee sampling, we analyzed the different types of vegetation and their associated climates along an elevational gradient in the structuring of Meliponini assemblages. This knowledge is important to implement effective conservation and maintenance strategies for these crucial and vulnerable native pollinators.

2 | METHODS

2.1 | Study area

This study was carried out in western Mexico in the south-central portion of the state of Michoacán (Figure 1). This region has an area of 38,228 km^2 and encompasses lowland areas on the Pacific coast to mountainous areas up to 2200 m in elevation in the center of the state, near the limit between the Balsas Basin and the Trans-Mexican Volcanic System. In this large region, there is a wide variety of climate types. At the higher altitudes, the climate is temperate subhumid and humid, with an average annual temperature between 12 and 18°C. The lowlands include various types of tropical climates: warm humid with an average annual temperature above 18°C; as well as warm subhumid, hot subhumid, and hot semi-arid, each of which have an average annual temperature above 22°C. The whole region has seasonal precipitation with rains in the summer. The natural vegetation is mixed oak-pine forest in the higher elevations, mixed subdeciduous forest and tropical dry forests in the lower and hotter areas, and a few xerophytic scrub areas and mangroves on the coast (CONABIO, 1998; INEGI, 2015).

2.2 | Site selection

We selected 43 sites separated from each other by at least 5 km (Figure 1). The sites were chosen based on previous reports of stingless bees in areas with natural vegetation and where local people permitted and accompanied us to sample on their lands. These sites encompass the vegetation gradient, climates, altitudinal ranges, and

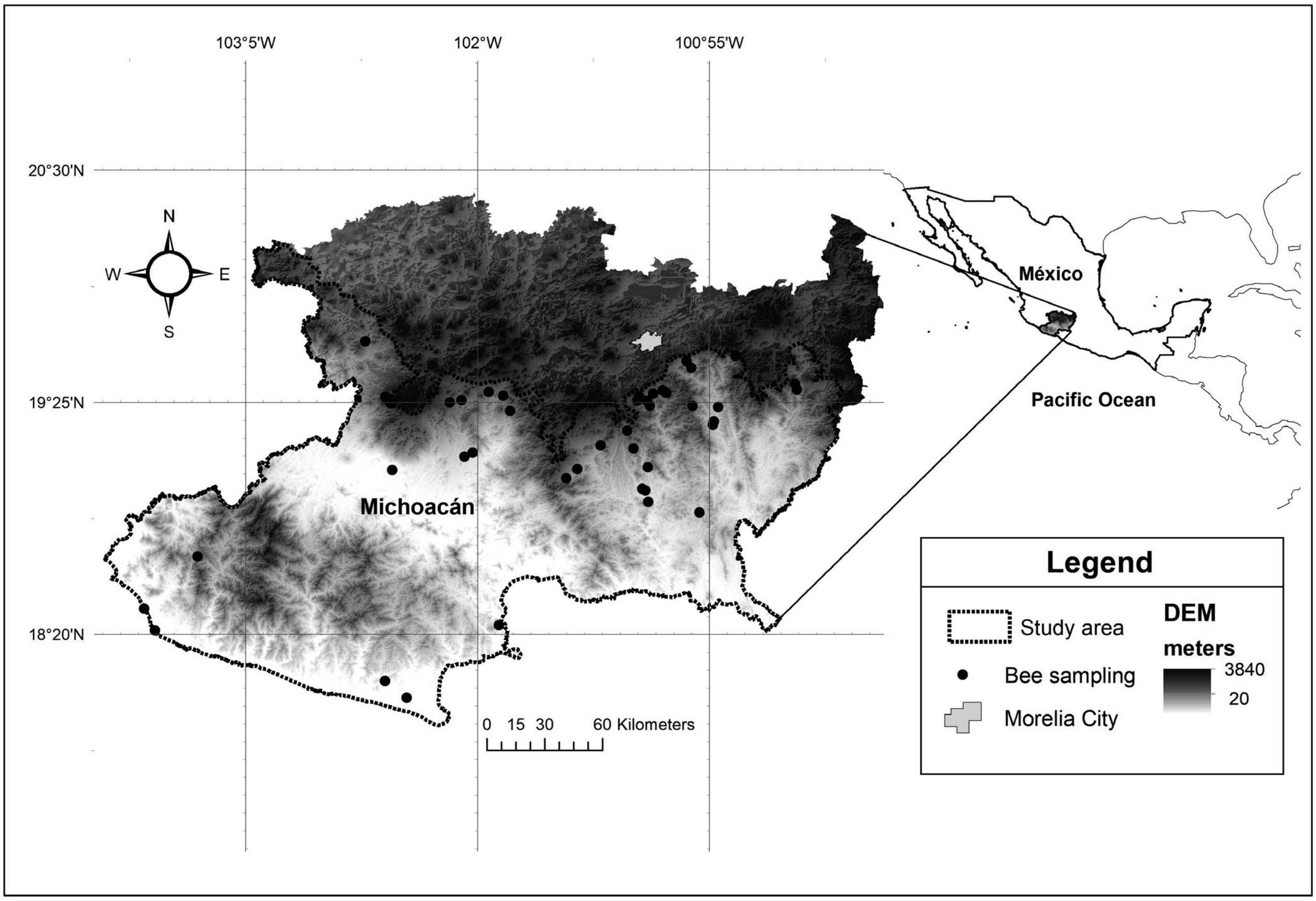

FIGURE 1 Bee sampling sites (black dots) in the western Mexican state of Michoacán. DEM: Digital Model Elevation

different geomorphic units where meliponine bees have been reported in Michoacán (Table 2).

2.3 | Bee sampling

Stingless bees were sampled by direct search, following Sutherland's (1996) proposal. At each site, two people searched for bees for a minimum of four to a maximum of six consecutive hours in an area of 2 Km^2. Searching time differences depended on the number of bee species observed, if after 4 h no more new bee species appeared, we stopped the sampling in that site. Sampling days began 8–9 am depending on weather conditions. At each location, we chose sites where flowering was evident, with water sources or salt deposits nearby. Bees were collected with entomological nets or entomological aspirators. We also considered information provided by local people about sites with bee aggregations, bee nests, and floral patches. A single sampling session was performed at each site between February 2018 and June 2019. Because meliponine bees are active throughout the year, they were sampled when plants where flowering according to the type of vegetation and on days without rain or strong winds.

One year after the systematic samplings (in October 2020), a new state record of a stingless bee was reported from a single site outside Uruapan city. This record was not included in the statistical analyses, but was included as a part of the Meliponini inventory, and its presence in the study region will be discussed.

2.4 | Bee determination

Bee specimens were identified to the species level using taxonomic keys (Ayala, 1999), and the nomenclature proposed by Camargo and Pedro (2013). The identities of determined specimens was corroborated by the expert R. Ayala in 2019 at the Universidad Nacional Autónoma de México (UNAM).

2.5 | Data analysis

We evaluated the effect of climate and vegetation on the composition of the Meliponini assemblages using a canonical ordination analysis (CCA) (Zuur et al., 2007). Five climate categories were defined following the Köppen classification modified by García at a scale of 1:1,000,000 (CONABIO, 1998): hot semi-arid [BS1(h')w], hot subhumid [Aw0], warm subhumid [(A)C(w1)], warm humid [(A)C(w2)] and temperate humid [Cw2]. Three vegetation categories were defined following Palacio-Prieto et al. (2000) and Bär et al. (2006): tropical dry forest, mixed subdeciduous forest, and mixed oak-pine forest. For each sampling site, we assigned a climate category and a vegetation type. Bee assemblages were characterized using species presence/absence data.

Species diversity of order 0 (species richness) was estimated for each climate category and vegetation type using the "Chao" asymptotic species estimator, which accounts for unobserved species based on incidence data (Chao et al., 2014). Estimation was done using the "iNEXT" function in the 'iNEXT' package for R (Hsieh et al., 2020).

3 | RESULTS

We collected 1347 specimens of stingless bees corresponding to fourteen species, representing 30% of all of the meliponine species found in Mexico. Two of the species were first records for Michoacán—*Plebeia manantlensis* Ayala and *Plebeia moureana* Ayala. *Plebeia manantlensis* was collected in a disturbed temperate zone near an urban area one year after concluding our systematic bee sampling. *Plebeia* was the genus with the highest diversity (four species), followed by *Melipona* with two species. Our data showed a few very common species (*Frieseomelitta nigra* Cresson, *Nannotrigona perilampoides* Cresson and *Partamona bilineata* Say), which accounted more of 50% of all records (Table 1). We also found two very rare species, *Melipona lupitae* Ayala, and *P. moureana*, which were present at only one and two sites, respectively.

3.1 | Meliponini assemblages

The canonical ordination analysis showed that both vegetation type and climate accounted for differences across sites; the first two axes comprised 21.3% of the variance in assemblage composition (Figure 2). We identified three different meliponini assemblages: (1) *Hot lowlands*, characterized by tropical dry forest vegetation and hot subhumid and hot semi-arid climates located in between 0 and 1300 m elevation; (2) *Temperate highlands*, characterized by mixed oak-pine forest vegetation with temperate subhumid and warm humid climates at elevations above 1701 m; and (3) *Warm ecotone*, between those two zones, located between 1301 and 1700 m asl with a warm subhumid climate and natural vegetation dominated by mixed subdeciduous forest (Bär et al., 2006), where bee species from both temperate and tropical dry forest coexist.

3.2 | Habitat preferences and species distributions

The *Hot lowlands* assemblage found in tropical dry forest vegetation included eleven meliponine bee species, six of which are restricted to the tropical dry forest and hot climates. This was the habitat where *P. moureana* was found, constituting a new record for Michoacán (Table 1). The *Temperate highlands* assemblage consisted of five species; two of them (*Melipona fasciata* Latreille and *Plebeia fulvopilosa* Ayala) inhabited mixed oak-pine forests and a temperate climate. In the third assemblage, the *Warm ecotone*, we recorded seven species: two species that were also found in the *Hot lowlands* assemblage, two species that were also found in the *Temperate highlands* assemblage, and three species that were present in all habitats, which in this study we refer to as *generalists* (*Geotrigona acapulconis* Strand, *N. perilampoides* Cresson and *P. bilineata* Say; Table 1). The *Warm ecotone* is thus very important, since bee fauna of the two contrasting assemblages converged there, and two of the generalists (*N. perilampoides* and *P. bilineata*) occurred only in restricted locations of high humidity in ravines and along the coast in the *Hot lowlands* assemblage. Each assemblage contained a mixture of common species and rare characteristic species (Table 1). Figure 3 shows the areas inhabited by each of the three assemblages of stingless bees.

Species richness estimation with the Chao asymptotic index indicated that sampling completeness was high for the Meliponini species from the study area overall (Table 2, Figure 4). This was also the case for the three vegetation types, for which completeness was ≥0.9. However, when considering the different climate zones separately, sampling completeness was low for the Warm humid climate and very low for the Hot semi-arid, suggesting a significant underestimation of species number for these climatic zones (Table 2, Figure 4).

4 | DISCUSSION

4.1 | Meliponini assemblages

Climate and vegetation are environmental variables that strongly determine the species distribution and assemblages, as is the case for Meliponini in western Mexico. Canonical ordination analysis delimited two contrasting vegetation types (tropical/temperate), associated with different groups of meliponine species (Figure 2). Other studies of Meliponini diversity in the southern Mexican states of Chiapas and Oaxaca grouped meliponines into five assemblages by vegetation type (Arnold et al., 2018). Yurrita et al. (2017) analyzed the potential distribution of the genus *Melipona* using bioclimatic and topographic variables in Central America and Mexico and found three areas of high diversity: southern Central America, inland Central America, and south-central Mexico. Given the biological restriction of stingless bees to tropical and subtropical environments, analyzing their presence in relation to bioclimatic variables (temperature, humidity, and vegetation) is essential to understand how native bees, and insects in general, may respond to climate change and anthropogenic disturbances. This is especially critical for taxa from tropical areas, which are simultaneously the most diverse and most vulnerable to extinction due to global warming (Deutsch et al., 2009; Schowalter, 2011). This is the case for Meliponini and the other native bees, since they are bioindicator organisms of intensive climatic changes and other ecological perturbations (Reyes-Novelo et al., 2009).

TABLE 1 Percent species incidence and habitat preference of meliponine bees in Michoacán

Percent Incidence	Species	Preference habitat		Climate	Vegetation type
2.3%	*Melipona lupitae* Ayala	Hot lowlands		Hot semi-arid, Hot subhumid	Tropical dry forest
7%	*Plebeia frontalis* Friese				
4.7%	*Plebeia moureana* Ayala[a]				
9.3%	*Trigona fulviventris* Guérin				
14%	*Trigonisca pipioli* Ayala				
46.5%	*Frieseomelitta nigra* Cresson				
20.9%	*Scaptotrigona hellwegeri* Friese	Hot lowlands	Warm ecotone	Hot subhumid, Warm sub-humid	Tropical dry forest, mixed subdeciduous forest
11.6%	*Lestrimelitta chamelensis* Ayala				
7%	*Geotrigona acapulconis* Strand[b]	Hot lowlands, Warm ecotone, Temperate highlands		All climates	All vegetation types
30.2%	*Nannotrigona perilampoides* Cresson[b,c]				
30.2%	*Partamona bilineata* Say[b,c]				
16.3%	*Melipona fasciata* Latreille	Temperate highlands	Warm ecotone	Warm humid, Temperate humid	Mixed oak-pine forest
14%	*Plebeia fulvopilosa* Ayala				

[a]New record for Michoacán.

[b]Generalist species: present in all vegetation and climate types.

[c]Restricted to coastal zones and ravines in the hot lowlands.

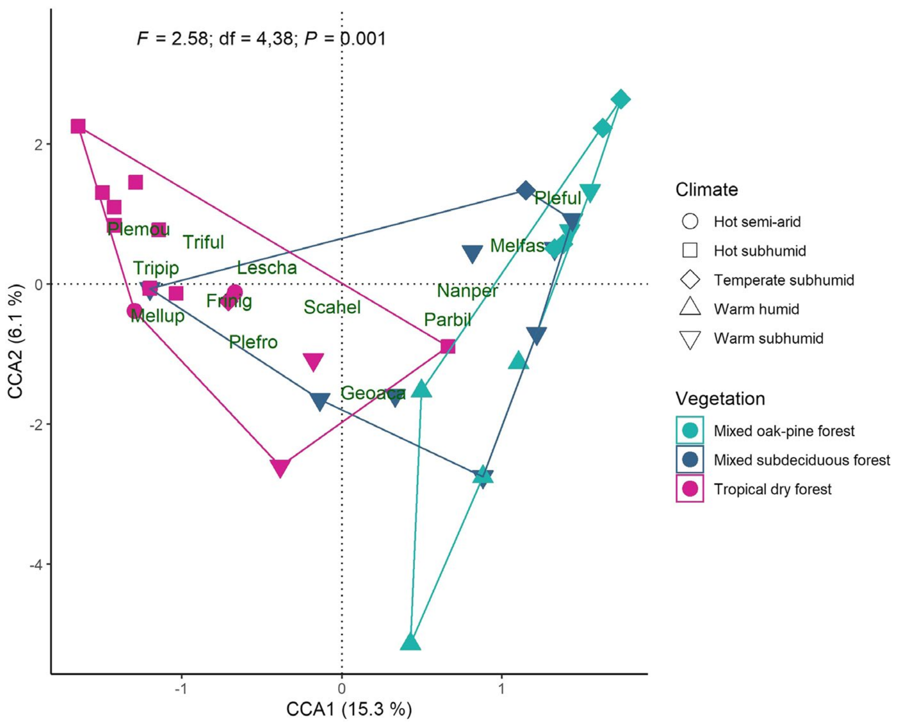

FIGURE 2 Canonical ordination analysis showing Meliponini assemblage differentiation among vegetation and climate types. Within the figure, sh ort for the scientific names of stingless bees are shown

4.2 | Habitat preferences and species diversity

As proposed in our hypothesis, the most diverse Meliponini assemblage was found in the tropical dry forest. This ecosystem is widely distributed and is known for having higher availability of food resources and nesting sites for tree-nesting bees than other habitat types (Roubik, 1989). One finding to highlight is that we recorded two species (*N. perilampoides* and *P. bilineata*) in the tropical dry forest that had been previously reported as absent from this habitat (Ayala, 1999). We recorded them along the coastline and in some ravines, so they appear to be colonizing the wettest part of tropical dry forests in addition to the temperate forests

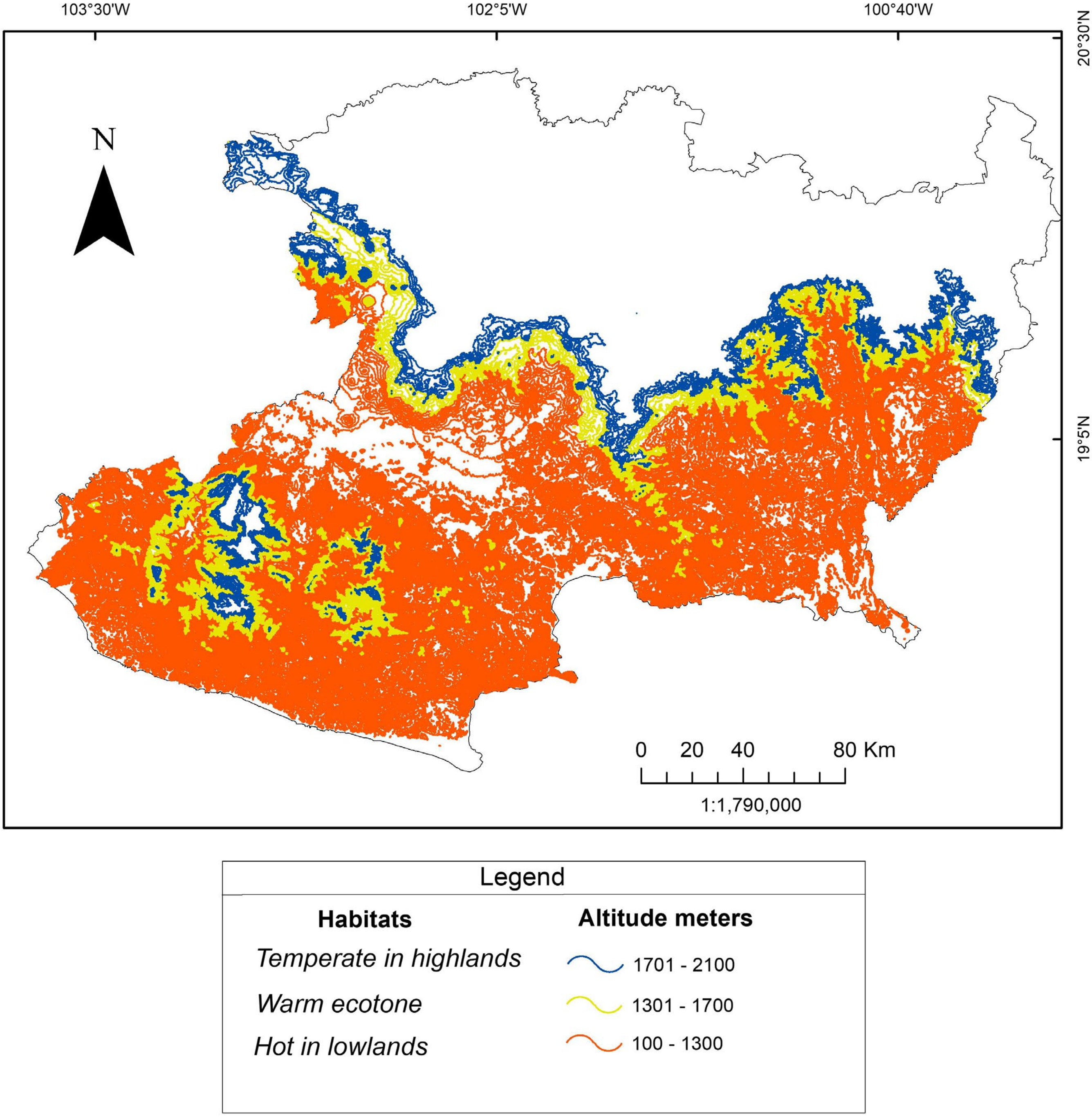

FIGURE 3 Meliponini assemblage distribution in Michoacán

where they had been previously recorded (Reyes-González et al., 2016).

On the other hand, in the temperate habitat we found fewer species within a narrow spatial zone (Figure 4). The species found in temperate habitats are highly prized in traditional and technical meliponiculture in this region of Mexico (Reyes-González et al., 2016, 2020).

In the warm ecotone assemblage there was a higher richness of generalist species. When considering characters thay may allow those species to be habitat generalists (i.e., thrive in different environments), one potentially important shared character is that these three species are flexible in their nesting sites and do not depend on trees for nesting (Table S1). However, there is another species that does not dependent on the trees for nesting yet has restricted distributions (e.g., *T. fulviventris*), so this question warrants further study to determine which meliponine characteristics most limit their distributions.

The most common species recorded in this study (*F. nigra* and *N. perilampoides*) are known for having a large distributional range and nesting in different environments, including hollow trunks, directly in the soil, between rocks, and in artificial structures (concrete walls or metal tubes) (Roubik, 1983; A. Reyes-González

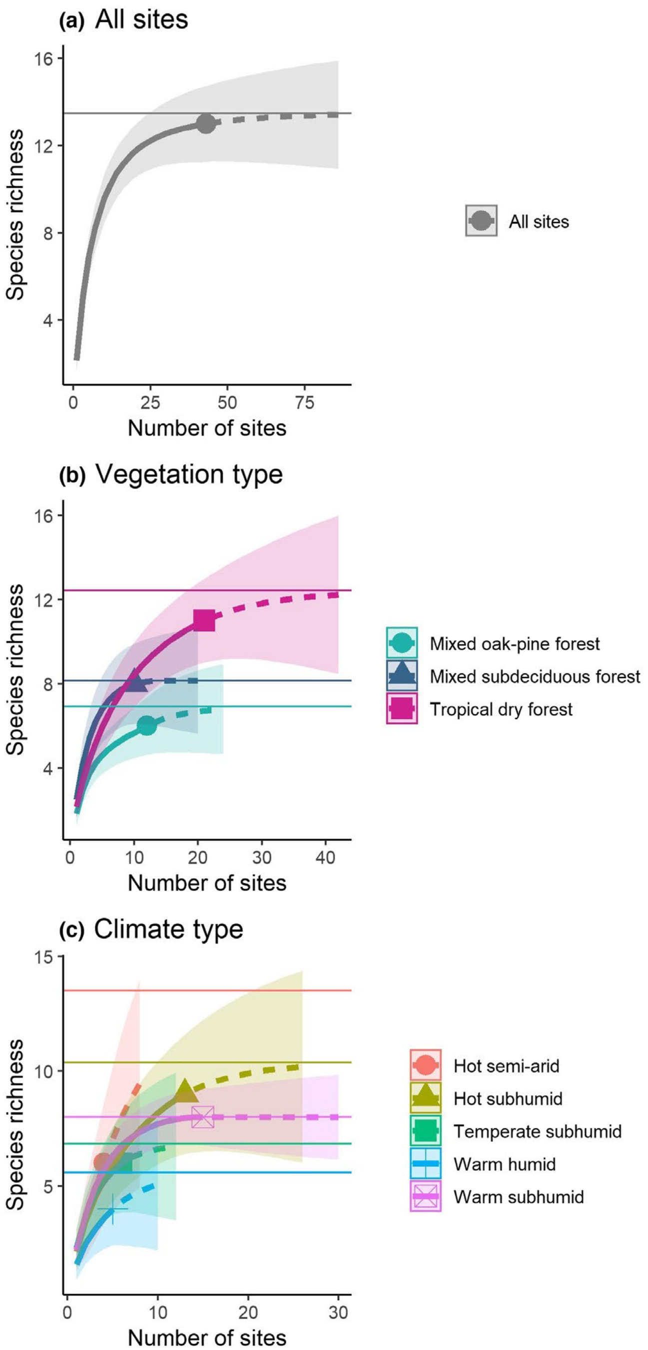

FIGURE 4 Species richness estimates of Meliponini bees in Michoacán state as a function of number of sites for the whole study (a), by vegetation type (b), and by climate type (c). The curves are rarefaction (continuous) and extrapolation (dashed) estimates of species richness, along with their 95% confidence intervals (shaded areas). Continuous horizontal lines represent asymptotic estimates of species richness based on the Chao estimator

Pers. Obs.). In a Meliponini revision for Mexico, Ayala (1999) mentioned that these two species are the most widely distributed in the country. *Nannotrigona perilampoides* can reach as far north as Chihuahua, at 29° latitude (Bennett 1964), and in this study we found that it can also be present in mountain sites of the Balsas Basin and along the Pacific coast, adding new distribution sites for this species.

The meliponine bee richness reported in this study represents a sizeable fraction (30%) of the total species recorded in Mexico. Thus, even though Michoacán does not have the highest diversity of meliponine bee species in the country (up to 30 species have been reported in Southeastern Mexico; Arnold et al., 2018; Yañez-Ordóñez et al., 2008), it is a relevant region for this group. We found seven endemic species of meliponine bees in western Mexico: *G. acapulconis*, *L. chamelensis*, *M. fasciata*, *M. lupitae*, *P. fulvopilosa*, *P. manantlensis* and *S. hellwegeri*. This is a significant number of endemic species for this region, representing more than 50% of the total 13 endemic meliponine species reported in Mexico (Ayala et al., 2013). It should also be noted that four of the species mentioned above are locally used in meliponiculture (González-Acereto, 2008; Reyes-González et al., 2014). Ayala (1999) considered that this region, at the intersection of the Balsas Basin with the Trans-Mexican Volcanic System, is an important area for bee endemisms produced by vicariant events during the Pleistocene.

The new records of *P. manantlensis* and *P. moureana* are interesting in that they are respectively the largest and smallest bees of the genus *Plebeia* in Mexico (Ayala, 2016). Very little is known about the ecology of these two species, and these new records increase the number of species for Michoacán. On the other hand, an important endemic meliponine bee, *Cephalotrigona eburneiventer* Schwarz, was missing from our study but had been reported previously for Michoacán (Ayala, 1999; Ayala et al., 2013). This absence motivates further investigation.

Our sampling effort, calculated with Chao2, indicates that we were able to document the presence of all meliponine bees species for the region. However, this was not the case for the hot semi-arid climate; Chao2 estimated that this habitat should contain twice the number of species we recorded, suggesting that further sampling is needed in those areas. Rare species (singletons and doubletons) included *M. lupitae* and *P. moureana*; however, due to our sampling protocol, we are not certain if they are originally rare or if their population size has been reduced by human habitat perturbation. It is worth noting that *P. manantlensis* and *M. lupitae* were only collected in one site. *Melipona lupitae* Ayala was provided by a local resident, who collected it in a recently harvested nest. This bee was not observed or collected in our field samplings and had not been reported since the 1980s (R. Ayala, personal communication). This suggests that their populations have been greatly reduced, perhaps to the point of regional extinction, as meliponines bees are social insects that are active year-round (Roubik, 1989). The ecology, behavior and habits of these two species are completely unknown. Particularly, *P. manantlensis* is reported as an endemic "mountain" species for localities in western Mexico only very close to the Pacific coast and isolated from other mountain systems (Ayala et al., 2013). Therefore, its presence in a temperate environment in the center of the state of Michocán in the upper part of Balsas basin is an interesting record.

TABLE 2 Meliponini richness estimators for different vegetation types and climate zones in Michoacán

Variable	Categories	Sites	Species diversity	Estimated species (Chao)	Sampling completeness
	All observed species	43	13	13.48	0.99
Potential vegetation	Tropical dry forest	21	11	12.42	0.94
	Mixed subdeciduous forest	10	8	8.15	0.98
	Mixed oak- pine forests	12	6	6.91	0.92
Climate	Hot subhumid Aw0; Aw1	13	9	10.38	0.91
	Hot semi-arid BS1(h')w	4	6	13.5	0.52
	Warm humid (A)C(w2)	5	4	5.6	0.80
	Warm subhumid (A)C(w1)	15	8	8	1.00
	Temperate subhumid C(W1); C(W2);	6	6	6.83	0.90

4.3 | Meliponini conservation in western Mexico

In addition to their ecological importance, meliponine bees are economically and socioculturally valuable. They have been managed since prehispanic times in a practice called meliponiculture, which is a very important component of culture and spirituality in indigenous cultures of Mesoamerica (Quezada-Euán et al., 2018). In this practice, several bee products are harvested and consumed (pot-honey, pollen, wax), which are important sources of medicinal inputs, food, and material for diverse uses (Crane, 1992; Quezada-Euán et al., 2018).

The results of the Meliponini assemblage composition and habitat preferences in Michoacán provide important information for understanding current distribution ranges to inform conservation and sustainable management strategies. Apart from the tropical area, the ecotone between mixed oak-pine forest and tropical dry forests is an important area for Meliponini conservation, since a large majority of stingless bees from different habitats coincide in this narrow strip. However, both the ecotone and temperate forest habitats are severely fragmented and transformed by human activities, mainly timber extraction and intensification of agriculture by large avocado plantations (Mas et al., 2017). There is an urgent need to implement conservation measures in this region to maintain and restore the integrity of the temperate forest and preserve the nesting and feeding habitats of native meliponine bees.

A complementary study involving local perception about meliponine bees in the area found that local people perceive a decreasing trend for these insects due to human interventions. Some species have been very rare since the 1980s, mainly due to human actions including land use change and predation of wild nests by local residents (Reyes-González et al., 2020) and suggested that there is a regional decline in Meliponini populations, as reported for other regions of tropical America (Brosi, 2009; Freitas et al., 2009). Therefore, it is important to make additional and continuous sampling efforts using mixed techniques (pan-traps, aerial nets, Van Somer Rydan traps, nest census, etc.) to obtain a more general picture that may provide an adequate and timely conservation strategy for this group of insects. Conservation actions that should be implemented immediately include providing information on the importance of these insects to the local communities to prevent looting of wild stingless bee nests and to prevent the destruction of forest areas, especially in places where stingless bees nest (i.e. trees, barren grounds, etc.). Such actions are fundamental to contribute to ameliorating the current global pollinator crisis.

ACKNOWLEDGEMENTS

The authors are grateful to Ricardo Ayala at Instituto Biología UNAM for his suggestions for collecting bees and his support in the taxonomic determination. This paper is part of the PhD thesis of the first author at the *Posgrado en Ciencias de la Sostenibilidad* of the Universidad Nacional Autónoma de México (UNAM). Thanks to the students and all informants who participated in our study for sharing their knowledge, hospitality and assistance with field work.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHOR CONTRIBUTIONS

A.R.-G., L.P.-B., M.I.R. & E.dV. contributed to the study conception and design. Bee sampling, material preparation, data collection and analysis were performed by A.R.-G. Data analysis was done by A.R.-G., E.dV. and F.M. The first draft of the manuscript was written by A.R.-G., and all authors commented and edited on previous versions of the manuscript. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.4mw6m90cq (Reyes-Gonzalez et al., 2022).

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How to cite this article: Reyes-Gonzalez, A., Mora, F., Porter-Boland, L., Ramírez Ramirez, M. I., & del-Val, E. (2022). Stingless bees (Apidae: Meliponini) at risk in western Mexico. *Biotropica*, *00*, 1–10. https://doi.org/10.1111/btp.13100