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From neglect to stardom: how the rising popularity of stingless bees threatens diversity and meliponiculture in Mexico

José Javier G. QUEZADA-EUÁN¹, William J. MAY-ITZA¹, Pilar DE LA RÚA², and David W. ROUBIK³

¹ Departamento de Apicultura Tropical, Universidad Autónoma de Yucatan, Campus Ciencias Biológicas y Agropecuarias, Km. 15.5 carr. Mérida-Xmatkuil, Mérida, Mexico

² Dpto. Zoología Y Antropología Física, Fac. de Veterinaria, Área de Biología Animal, Universidad de Murcia, 30100 Murcia, Spain

³ Smithsonian Tropical Research Institute, Luis Clement Avenue, Bldg. 401 Tupper, Balboa, Ancón, Panamá

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Abstract – Mexico is part of the Mesoamerican region where ancient bee keeping (meliponiculture, or stingless bee keeping) emerged and reached exceptional levels. Different events caused Mexican stingless bee keeping to decline. Recently, meliponiculture has modernized and is undergoing a dramatic change, rising from neglect to an alarming popularity. The increase in commerce and number of species under management fundamentally affect, and are influenced by, translocation of colonies across geographic regions. Moreover, the social networks that propel commercialization create the impression that maintaining bees as resources or pets and promoting honey and other commercial products at premium prices are inherently desirable. The ecology of pollination in nature is rarely considered, nor the ecological network of the bee populations and their many associated organisms and ecological processes. With growing numbers and types of bee keepers and bee keeping methods, changes are posing novel risks to the integrity of native species. Such emerging factors may certainly impact biodiversity of Mexican stingless bees and the sustainability of meliponiculture. We examine findings on population differentiation among Mexican bees and measures urgently needed in the short term, with possible application in other regions of the world that experience problems caused by the modern stingless bee boom.

stingless bee boom / meliponiculture / conservation / translocation / meliponini

1. INTRODUCTION

1.1. The rebirth of Mexican meliponiculture

The Meliponini or stingless bees are among the most representative bees of Mexico. Here,

stingless bees represent a relatively small portion (2.6%) of the highly diverse bee fauna (ca. 1800 species), but the economic, social, and cultural impacts they have are like nowhere else (Quezada-Euán et al. 2001; Ayala et al. 2013). A rational form of meliponiculture (stingless bee keeping including breeding and management) likely originated in the seasonally dry lowland forests within the Maya region of the Yucatan Peninsula, Northern Guatemala, and Belize, more than 1400 years ago (Kent 1984; Crane 1992; Yurrita-Obiols and Vásquez 2013). It

Corresponding author: J. J. G. Quezada-Euán,

javier.quezada@correo.uady.mx

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represented the first husbandry and reproduction of stingless bees in the world. Notably, ancient meliponiculture in Mexico relied on the rearing of only two stingless bee species, *Melipona beecheii* in the Maya region (the Yucatan Peninsula) and *Scaptotrigona mexicana* in the Nahua and Totonac regions (states of Puebla and Veracruz on the Gulf Coast). Other species were sporadically hunted for their honey, cerumen (high wax content propolis, used in most nest elements), or resin but were not reared systematically (Quezada-Euán et al. 2018). With the change of the productive systems after the European colonization, gradual abandonment of stingless bee keeping, considered archaic and scarcely cost-effective, took place (Quezada-Euán et al. 2001; Villanueva-Gutiérrez et al. 2005). By the end of the twentieth century, stingless bee keeping in Mexico was on the verge of extinction (Quezada-Euán et al. 2001; Villanueva-Gutiérrez et al. 2013). The invasion of Mesoamerica by Africanized honey bees (*Apis mellifera*) since the 1980s (Roubik 1989; Quezada-Euán 2007), together with the development of rational methods of stingless bee keeping, triggered a rebirth of meliponiculture in Mexico (González-Acereto 200; Quezada-Euán 2018). Due to defensiveness of this hybrid honey bee, apiaries had to be relocated far from human settlements (Guzmán-Novoa et al. 2020), opening a niche slowly occupied by stingless bee keeping (Quezada-Euán 2018). A successful model based on broader training efforts and a hive-on-loan approach provided stimulus for meliponiculture with *M. beecheii* in the Yucatan Peninsula (González-Acereto et al. 2006).

In twenty-first-century Mexico, diversity, gender equality, and multiculturalism, characterized by the recognition of indigenous heritage, are steadily growing (Gutiérrez-Chong 2020). Stingless bees are now indissolubly associated with Mexican indigenous societies (Gutiérrez-Chong 2020). Women are also increasingly involved, and the success of all-female managed meliponiculture projects (González-Acereto et al. 2006) has added public approval for stingless bee related initiatives. Globally, media and social networks have placed much attention on

the preservation of bees and other pollinators (Colla 2022), which has also promoted stingless bee interest in Mexico.

Stingless bee products are also in high demand. Honey, pollen, and propolis of stingless bees are considered medicinal and sometimes delicacy items, reaching high prices and creating the perception of meliponiculture as a gold mine (Quezada-Euán and Alves 2020). Today, meliponiculture is at a new peak of popularity, but that push is paradoxically moving stingless bee biodiversity toward new risks. This phenomenon could also pose a more general threat to the preservation of wildlife and the culture and traditions of indigenous peoples (Hill et al. 2019; Reyes-González et al. 2020).

2. THREATS ASSOCIATED WITH STINGLESS BEE POPULARITY

With its growing popularity, meliponiculture has experienced a dramatic shift from being neglected to holding the spotlight. Like other native bees and pollinators, Mexican stingless bees encounter a series of threats that stem from deforestation to the impact of different agrochemicals and pathogens or parasites (a review is presented in Chapter 8 of Quezada-Euán 2018). Nevertheless, the rapid growth and popularity of meliponiculture present new features, regrettably including some increased hazards. A heightened concern that we emphasize is the basic ecology of stingless bee activities, including breeding and population movement, and their potential to alter the integrity of other species, and biodiversity itself.

The number of managed species has increased, together with breeder and hobbyist demand across the country. Since the demand exceeds colony supply, both the price and exploitation of wild and managed populations have increased. In Mexico, the price of a *M. beecheii* colony went from 20 USD in 2000, to near 200 USD and is increasing by the year (Quezada-Euán 2018). Some negative effects include the somewhat random improvisation of hive types

and bee keeping organization in bee yards or urban settings, the adoption of management methods that seldom consider biology, and inexperienced guidance or practitioners. These often lead to rapid demise of newly acquired colonies. In the following paragraphs, we examine such factors and their potential effects on stingless bee populations.

2.1. New managed species and inappropriate management

Over the last decade, the number of people interested in keeping stingless bees in rural and urban areas has drastically increased (Martínez-Fortún et al. 2018; May-Itzá et al. 2021). Species chosen from among the 16 or so local stingless bee species (Ayala et al. 2013; Quezada-Euan 2020) has also increased. Besides the two traditionally and indeed, historically favored *M. beecheii* and *S. mexicana*, there are more, all extracted from wild populations. Frequently, people rescue nests from trees in logged areas or from condemned buildings, which is in general good for conservation. However, demand now outstrips this method of colony harvest. Species with ample distribution across the country like *Frieseomelitta nigra*, *Scaptotrigona pectoralis*, and *Nannotrigona perilampoides* are now more commonly found in “stingless bee yards” around the Gulf of Mexico and the Yucatan Peninsula (González-Acereto 2008; Martínez-Fortún et al. 2018). Similarly, in Veracruz and along the Pacific coast, the keeping of *Tetragonisca angustula* and *Melipona solani* is increasing (Arnold et al. 2018). Species of the genus *Plebeia* are also more commonly found in meliponaries spread across Mexico (Arnold et al. 2018). Species like *Melipona fasciata*, *Melipona colimana*, and *Scaptotrigona hellwegeri* endemic to the Pacific coast are also being brought into stingless bee keeping (González-Acereto and De Araujo-Freitas 2005; Ayala et al. 2013). Colonies of those species can adapt to wooden hives. However, there are species like some in the genus *Cephalotrigona* and all those in the genus *Geotrigona* that nest underground, with

precarious thermoregulation. Experiments transferring *Cephalotrigona* to wooden hives have shown that colonies frequently dwindle and die in a few months (Zwaal 1992). Attempts to use *Cephalotrigona* species are now more frequently seen, as the genus contains the largest non-*Melipona* stingless bees in Mexico. Their colonies produce abundant and flavorful honey which makes them attractive to bee keepers (González-Acereto 2008). However, colonies are mostly killed by transfer to conventional hives.

Because methods for rapid and efficient colony multiplication are still preliminary (Menezes et al. 2013; Quezada-Euán 2018; Eleutério et al. 2022), a growing demand for popular new species necessarily relies more on wild populations and is extractive (Roubik et al. 2018), resulting in growing risk of depletion. In the early years of bumble bee commercial production, a similar situation occurred. It became necessary to develop efficient methods to rear colonies from domesticated populations and significantly diminish the depletion of wild bees (Velthuis and van Doorn 2006).

Managed populations of species like *M. beecheii* are not abundant, and wild ones have disappeared completely from some areas posing a more severe risk for their conservation (Quezada-Euán et al. 2001; Villanueva-Gutiérrez et al. 2005). Furthermore, no “queen banks” (see Vollet-Neto et al. 2018) or natural colony reserves have been established.

Many new stingless bee keepers lack any training in biology and management of the different species. Criteria used for the husbandry of honey bees are frequently applied to stingless bees, without considering their contrasting biology (Quezada-Euán and Alves 2020). Stingless bee keeping rational methods (Nogueira-Neto 1997; Venturieri 2008) are also being applied incorrectly. One example is the control of phorid flies, the most common and severe pest of stingless bees. The use of vinegar traps to control the flies (usually applied after transferring or splitting a colony) is a recommended practice only in the case of modest to high colony infestation (Ramos et al. 2003). Currently, new bee keepers use vinegar traps permanently, both within

and outside hives. It is likely that the constant acidic smell attracts the flies—the opposite of the desired effect. To repel phorids, bathroom cleaning products are also being used in plastic bag containers around bee yards. These could readily affect bee foraging or recruitment, or yield toxins that affect colonies.

Sugar syrup as carbohydrate source to colonies was recommended originally for internal feeding during periods of low nectar abundance (González-Acereto 2008). More frequently, sugar syrup is fed in exposed containers in the meliponaries. This can cause robbing between colonies and also attracts honey bees that then can start to rob stingless bee colonies. Honey bees frequently return to profitable sources of food, increasing the risk of attacks on weak or small colonies. Stingless bee keepers usually blame the honey bee for invading or attacking their colonies, but in many cases it is probably a consequence of bad management and feeding technique. Feeding with honey bee honey and pollen is also becoming common practice. The consequences of this method are not fully understood. However, finding of the etiological agent of the European foulbrood *Melissococcus plutonius* after feeding stingless bee colonies with *A. mellifera* honey and pollen, evidences the possibility of pathogen spillover from honey bees to stingless bees by means of sharing products (Teixeira et al. 2020). Unfortunately, diseases are transmitted at floral resources (Iwasaki and Hogendoorn 2022) that are usually not within the power of bee keepers to survey or manage.

A recurrent problem is the use of oversized hives, with volumes that do not consider the natural thermoregulation or nest defense characteristics of stingless bee species. Most stingless bees are not efficient at maintaining stable temperatures in their nests and depend on the protection of cavities for adequate development (Roubik 1989; Macías-Macías et al. 2011). When cavity size increases, colony development is negatively affected, possibly as a consequence of poor thermoregulation (Quezada-Euán 1988; Quezada-Euán and González-Acereto 1994). Thus, adequate hive volume is crucial for sufficient thermoregulation and colony adjustment

(Quezada-Euán 1988; Quezada-Euán and González-Acereto 1994). Originally, the linear measures of natural nests were the basic information to estimate species-specific hive volumes for stingless bees (Portugal-Araujo 1957; Nogueira-Neto 1997; González-Acereto 2008; Venturieri 2008; Villas-Boas 2012; Quezada-Euán 2018). Nonetheless, hives are today notably increasing in size without any consideration of the natural nest volumes of different species. It is speculative but likely the anticipation of honey production has motivated this process. Hives for *M. beecheii* in the Yucatan Peninsula, with volumes of more than 20 l, are employed in some meliponaries (Quezada-Euán and Alves 2020). The risk of colony divisions, potential sensitivity to temperature fluctuation, and extra-large boxes add to colony stress. Not infrequently, many newly split colonies die after a few days and are lost to the bee keeper and to nature (JJQE and DWR, personal observations). Newer models of hives for stingless bees, made from different materials, such as plastic, plywood, and even cement, occur regularly, and their marketing is also more common on e-commerce pages and bee fairs and congresses, but species-specific recommendations are rare.

One factor that significantly contributes to distortion of management methods is inexperience (Jaffé et al. 2015; Quezada-Euán and Alves 2020). Escalating popularity and rapid growth of meliponiculture places pressure upon availability of valid information and instruction. With an increasing number of stingless bee projects supported by government and international initiatives, instructors are increasingly in demand, but qualifications are limited and seldom required. Combined effects of inexperienced instruction, deterioration of management, and a lack of continued inspection of projects, by NGOs, project managers, or government authorities, is proving destructive (Quezada-Euán and Alves 2020).

2.2. The impact of social networks

Many new stingless bee keepers are self-taught, but regularly draw on social networks

for information. Such virtual platforms are often plagued with erroneous facts and methods (Quezada-Euán and Alves 2020) but are accepted based on trust in those who claim to be experts (Iyengar and Massey 2019; Saurwein and Spencer-Smith 2020). The speed and extent to which news travels around the world on social platforms result in overwhelming and often negative viral effects (Martens et al. 2018). “New experts” are very active and exploit the advantages offered by web sites and their commercial basis. Websites offer the incentive of an economic reward to marketing professionals, after reaching a certain number of followers (Iyengar and Massey 2019). From their platforms, these marketing individuals present information in ways proven to convince users, who in turn are also more likely to believe and spread articles that agree with their beliefs or socioeconomic group (Kim et al. 2019). Emotions also count more than facts in validation of information without regard to proven facts (Higgins 2016). To make things worse, good and objective information is increasingly more often rejected or ignored by audiences who have absorbed false and misleading information (Iyengar and Massey 2019). “Don’t confuse me with new data, I have already made up my mind.” Eventually, a vast number of “likes” and materials posted allow these new “stingless bee experts” to be acknowledged as resource persons, independent of their training or experience. More seriously, government and authorities can frequently fall for them. The impact of social networks in the spread and adoption of misinformation leading to mortality of stingless bee colonies should be a major concern, although control measures are difficult (Carvalho 2022a).

2.3. Anthropogenic movement of colonies

In general, the conservation status among managed and wild populations of stingless bees is unknown. The effect of different stressors on the demography or the life and death schedules and expectations of species remains undocumented (Freitas et al. 2009; Galetto

et al. 2022). A major worry derived from stingless bee popularity is the movement of colonies across regions. This may have detrimental consequences at different levels. Until recently, stingless bee colony translocation was absent in Mexico (Quezada-Euán et al. 2001), but lately and increasingly more often, attempts are taking place for which there are no records. The number, origin, and destination of colonies are unknown. Superior honey-producing species are the most popular candidates for transport across regions, mainly those of the genera *Melipona* and *Scaptotrigona*, but also those with potential for crop pollination, like *N. perilampoides*.

Currently, Mexican regulations are vague regarding the use or transport of stingless bees among regions. In spite of being part of the wild fauna, colony movement across regions is not considered a threat to biodiversity. As stingless bees are honey producers, they are somehow considered a managed or domesticated species. Honey bee hive movement across Mexico occurs too (Guzmán-Novoa et al. 2020). However, these are two completely different kinds of bees in a fundamental and ecological way: one is native and the other is not. At the same time, one is utilized in predominantly agricultural areas, but maintains large feral populations in many habitats, while the second is primarily in rural or marginally agricultural areas and in original forest and tends to consist of relatively uncommon (and small) colonies (Roubik 2022). Serious consequences can result from the relocation of species, ranging from genetic erosion to disease spillover (Quezada-Euán et al. 2012; Chapman et al. 2018; dos Santos et al. 2021a), and therefore, demand oversight and regulation.

2.3.1. Genetic implications of anthropogenic movement of colonies

Anthropogenic movement of animals across regions can have several genetic consequences at population level. It can lead to intraspecific genetic homogenization and also interspecific

hybridization (Nascimento et al. 2000; Byatt et al. 2016; Jara et al. 2020). A number of molecular studies conducted in Mexico and other countries show that compared to other bees, wild stingless bee populations frequently show genetic differentiation (structure) within regions (Landaverde-González et al. 2017; Quezada-Euán 2018). This could be a consequence of the natural limited dispersal of reproductive swarms (Slaa 2006; Quezada-Euán 2018; Grüter 2020). Such a system of reproduction restrict the spread of colonies and queens to a few hundred meters, which may result in genetic differentiation over time (Quezada-Euán et al. 2012). Notably, studies on managed species have shown weaker genetic structure compared to wild populations (Jaffé et al. 2016; Chapman et al. 2018), suggesting that human-mediated colony movement can enhance artificial gene flow and alter the natural structure of populations, as it does for other bee species (Harpur et al. 2012; De la Rúa et al. 2013). However, in haplodiploid insects, like bees, haploid males expose deleterious genes, which are relatively rapidly eliminated (Crozier and Pamilo 1996). Thus, the introduction of novel alleles in an established population does not necessarily lead to decline or weakness, but may sometimes result in genetic improvement, depending on current selection pressures (Edmands 2007). A negative side is that in the process a loss of genetic diversity can occur. Rare or unique alleles, particular to certain populations can be lost or diluted when the source population is very small, thus potentially eroding the gene pool and the possibility of adaptation to changing environmental conditions (Allendorf et al. 2013). Any loss of genetic variation may lead to long-term risk in population stability, but this necessarily depends on selection pressures, which may be expected to increase or change, due to climate change, habitat destruction, or any of a number of other perceived threats (but see also below). Although outbreeding with geographically distant populations may increase genetic diversity, it can also lead to the breakdown of local adaptation, potentially resulting in associated fitness loss (Reed and Frankham 2003; Edmands 2007; dos Santos

et al. 2021a). Similarly, when closely related species are put in contact, hybridization can take place (Harbicht et al. 2014). We have no current information about whether this possibility exists for congeneric meliponine species in Mexico. Nonetheless, in Brazil, hybridization can occur between *M. capixaba* and *M. scutellaris* when brought together, which resulted in diminished productivity and survival of the hybrid colonies (Nascimento et al. 2000).

Reduced genetic diversity has additional negative effects on bees. A reduced diversity at the single complementary sex determination locus (*csd*) in haplodiploids can lead to endogamy, i.e., a higher frequency of “matched matings” (matings between partners carrying the same allele at the *csd* locus; Zayed 2009). Fertilized eggs that are homozygous at the *csd* locus develop into diploid males (Cook and Crozier 1995). This is a potentially serious cause of reduced fitness in bees because diploid males are inviable in mating and are produced at the expense of females (Zayed 2009). A similar problem may arise when colonies are moved to areas in which species are not native. They will not encounter wild colonies to mate with and a small number of colonies (and, thus, genotypes), in such founder populations causes a genetic bottleneck with reduced genetic diversity and the subsequent production of diploid males (Alves et al. 2011; May-Itzá et al. 2021). As a possible example, four colonies of *S. mexicana* moved from Chiapas to Yucatan where this species is not native died after a few months, after a visible reduction in the brood they produced (González-Acereto 2008). However, it is worth noting that highly endogamic stingless bee populations in Brazil have remained viable for many years (Nogueira-Neto 2002; Alves et al. 2011; Vollet-Neto et al. 2018).

Other factors may also be involved in a colony’s death when moved across geographic regions. Translocated species may fail to adapt to contrasting environmental regimes (Macías-Macías et al. 2011; dos Santos et al. 2021a). Competition for resources and displacement of less fit, or endangered species, could also occur (dos Santos et al. 2021a). Alternatively, species could become invasive (dos Santos et al. 2021a).

2.3.2. Estimates of genetic differentiation in stingless bees

Meliponine movement aided by humans suffers from the same uncertainties applicable to a still largely unknown tropical biodiversity, throughout the world. A particular situation is the high frequency of cryptic species in stingless bees (Michener 2000). Cryptic species are phenotypically similar in spite of substantial genetic differentiation (Bickford et al. 2006). Most often, haplotypes differ in mitochondrial DNA surveys of an apparently homogeneous species (Morgan-Richards et al. 2017). If not in fact different biological species, incapable of interbreeding, they can often have restricted ranges or different adaptive profiles and requirements. Thus, from a practical point of view, moving colonies from one geographic region to another may inadvertently bring two cryptic lineages or species together, with possible negative consequences.

Several studies on bees have shown that an ideal approach for the identification of cryptic species is the combination of multiple sources of information, molecular, biochemical and taxonomic (Quezada-Euán et al. 2007; Francisco et al. 2008; Eltz et al. 2011; Halcroft et al. 2016). One widely accepted method to identify possible species is the sequencing and comparison of mitochondrial DNA cytochrome oxidase fragment 1 (*cox1*) or DNA barcoding (Packer et al. 2008; Hurtado-Burillo et al. 2013). In conjunction, microsatellite markers (highly variable nuclear fragments) are often used to reveal differentiation among closely related species and their populations (Sunde et al. 2020).

Estimates of genetic differentiation, inferred from genetic distance values (Wang et al. 2001) among Mexican stingless bee populations, using barcoding and microsatellites, are presented in Table I. Differentiation is estimated by means of *Fst* parameter, a measure given for population genetic structure (Wright 1965). *Fst* values measure demographic differentiation based on genotypes, routinely used in the recognition of evolutionary lineages (Jost et al. 2018). *Fst* values greater than 0.15 can be considered valid indices that distinguish populations (Frankham

et al. 2002), but they are not conclusive evidence of speciation (Balloux and Lugon-Moulin 2002).

Estimates of *Fst* among populations of all six Mexican stingless bees studied thus far have been > 0.2 (see measures of genetic differentiation, Table I): *M. beecheii*, *M. yucatanica*, *S. mexicana*, *S. pectoralis*, *S. hellwegeri*, and *N. perilampoides*. A recent study of cleptobiotic stingless bees (*Lestrimelitta*), including molecular and biochemical markers, also revealed a species not yet reported to Mexico (Vázquez et al. 2022). Those results indicate that the diversity of Mexican stingless bees, currently estimated in 46 species (Ayala 1999), may be in need of recognizing subspecific differentiation as species indicators.

Interestingly, mountain ranges seem to have acted as barriers for genetic flow among different populations of stingless bees from Mexico. In particular, the mountain range of Sierra Madre del Sur seems important in this regard. In the case of *M. beecheii*, the most popular stingless bee in Mexico, two genetically distinct groups or lineages separated by the Sierra Madre del Sur, have been confirmed. One lineage includes populations from the Yucatan Peninsula and northern Guatemala and another those from southern Guatemala down to Costa Rica (Quezada-Euán et al. 2007; May-Itzá et al. 2012). Notably, both lineages are largely in agreement with the two subspecies, *M. beecheii beecheii* and *M. beecheii fulvipes*, proposed by Schwarz (1932). Although significant differentiation has been found among southern populations of *M. beecheii*, no studies have been conducted on the northern populations along the Mexican Gulf (Tabasco, Veracruz, and Puebla), nor the Pacific Coast (Oaxaca to Sinaloa) where this species is native (Yurrita et al. 2017). However, substantial phenotypic differences in size and pigmentation can be found between workers of *M. beecheii* from the Yucatan Peninsula and Puebla (Figure 1), which may have a genetic basis.

A sympatric species of *M. beecheii* is *M. yucatanica*. This species is found in Mexico and Guatemala (Ayala 1999) and likely farther south (DWR, pers. obs.). The populations of *M. yucatanica* from the Yucatan and Guatemala show

Table 1 Estimations of genetic differentiation among geographic populations of different Mexican stingless bee species

Species	Geographic populations	marker	Estimation of genetic differentiation	Reference
<i>Melipona beecheii</i>	Yucatan Peninsula with Costa Rica	Microsatellites <i>Cox1</i>	$F_{st}=0.280$ populations differed by 1.2%	Quezada-Euán et al. (2007)
<i>M. beecheii</i>	Yucatan Peninsula and northern Guatemala with southern Guatemala Salvador, Nicaragua, Costa Rica	<i>ITS1</i> Correlation between genetic and geographic distance	Kimura Genetic distance (Yucatan vs. Costa Rica)=0.017 $R=0.369, P<0.05$	May-itzá et al. (2012)
<i>M. yucatanica</i>	Yucatan Peninsula with Guatemala	Microsatellites <i>Cox1</i>	$F_{st}=0.492$ populations differed by 2.2%	May-Itzá et al. (2010)
<i>Scaptotrigona hellwegeri</i>	Mexico: Jalisco with Guerrero	Microsatellites	$F_{st}=0.273$	Quezada-Euán et al. (2012)
<i>S. mexicana</i>	Mexico: Gulf coast and Northern Chiapas with Pacific coast of Chiapas	Microsatellites	$F_{st}=0.23$	Hurtado-Burillo et al. (2016)
<i>S. pectoralis</i>	Mexico: Yucatan Peninsula, Chiapas and Veracruz	Microsatellites	$F_{st}=0.228-0.294$	Hurtado-Burillo et al. (2016)
<i>Nannotrigona perilampoides</i>	Mexico: Yucatan Peninsula, Gulf Coast and Pacific Coast	16S rDNA	AMOVA=80% variation between the two populations	Urueña et al. (2022)

significant differentiation (May-Itzá et al. 2010). Both lineages seem isolated, as in the case of *M. beecheii*, by the mountain barrier of the Sierra Madre del Sur (May-Itzá et al. 2012).

Another socioeconomically important group of species in Mexico includes stingless bees in the genus *Scaptotrigona*. Populations of *S. hellwegeri* from contrasting environments of the Pacific Coast of Mexico, distant only 470 km, showed significant phenotypic and genetic differences (Quezada-Euán et al. 2012). Populations from the Gulf Coast and southern Chiapas of the widely used *S. mexicana* showed significant genetic and morphological differences too (Hurtado-Burillo et al. 2016). Interestingly, when investigating the genetic structure of *S. mexicana*, Hurtado-Burillo et al. (2016) found

possible genetic introgression between populations from the north (Peten), and south of Chiapas (Figure 2), a Mexican state where the two genetic lineages are found, only separated by the Sierra Madre del Sur (Hurtado-Burillo et al. 2016, 2017). It is not clear if introgression in this case was human-mediated, as such a widely kept honey producer is expected to be moved, and exchange of colonies between relatively close regions is a possibility. Similarly, *S. pectoralis* shows evidence of genetic structure among populations from the Yucatan Peninsula and the Gulf coasts of Mexico with those on the Pacific coast of Chiapas (Hurtado-Burillo et al. 2017).

The effect of the mountain range of the Sierra Madre del Sur as a barrier for gene flow among stingless bee populations in Mexico was further



Figure 1. Phenotypic differences between workers of *Melipona beecheii* from the Yucatan Peninsula (Mérida, Xmatkuil) and Puebla (Teziutlán, Coyopul) on the Mexican Gulf Coast. Genetic analyses are underway to compare these populations.

confirmed by recent analyses of *N. perilampoides*, the most widely distributed species of stingless bee in the country (Urueña et al. 2022). This species produces little honey but has shown ready adaptation and efficiency in the pollination

of peppers and tomatoes in greenhouses (Cauch et al. 2004), proving a good alternative, especially in tropical areas (Palma et al. 2008). Molecular data (based on the sequence variation of the 16S ribosomal gene) and morphometrics

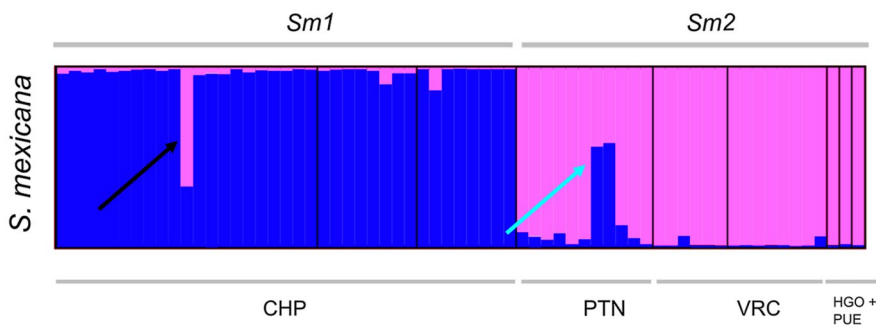


Figure 2. Results of a Bayesian clustering showing evidence of genetic introgression between populations of *S. mexicana* (taken from Hurtado-Burillo et al. 2016). Two genetic lineages were found in this species: *Sm1* (blue) and *Sm2* (pink). Each area delimited by black lines represents a population. Within each area, one colony is represented with a colored vertical bar according to the probability of belonging to the *Sm1* or *Sm2* lineage. Most colonies in the southern Chiapas population (CHP, 3 localities sampled) belong to the *Sm1* lineage, except for one (in population 1) marked with a black arrow that has a significant probability of belonging to the *Sm2* lineage. Likewise, most colonies in the northern populations of the Sierra Madre: Petén (PTN), Veracruz (VRC), plus Hidalgo and Puebla (HGO+PUE) belong to the *Sm2* lineage. However, the blue arrow indicates two colonies in the Petén population with a high probability of belonging to *Sm1* lineage.

(Figure 3) confirm that populations of *N. perilampoides*, East to the Sierra Madre del Sur (Tabasco, Veracruz, and Yucatan) show significant differences from those in the West (Jalisco and Nayarit) (Urueña et al. 2022).

The findings on genetic differentiation in Mexican stingless bees, and from other latitudes, support the notion that geographic isolation is a major cause of speciation in Meliponini (Quezada-Euán et al. 2012; Jaffé et al. 2016). This fact alone leads us to conclude that the mobilization of colonies across geographic, contrasting regions is a potential threat for the genetic identity of the different lineages that have evolved separately and are adapted to their specific environments.

2.3.3. Risk of pathogen spillover

In addition to population genetic considerations, the anthropogenic movement of stingless bee colonies to different geographic regions carry the risk of disease and/or pathogen dissemination. It is well documented that translocating bees or their colonies can introduce novel pathogens and should be an important criterion to evaluate this practice (Otterstatter and Thomson 2008; Muñoz et al. 2014; Goulson and Hughes 2015). The transmission is primarily or wholly at flowers the bees visit for nectar and pollen (Iwasaki and Hoogendorn 2022).

Accumulating evidence suggests pathogen spillover from honey bees to stingless bees. In Mexico, deformed wing and black cell viruses have been found in *S. mexicana* (Guzmán-Novoa et al. 2015). More recently, Fleites-Ayil et al. (2021) also identified the presence of both viruses in *M. beecheii* from the Yucatan Peninsula. The possibility of *Nosema* infection, a microsporidian parasite originally found in honey bees, spreading to Mexican *M. colimana*, provides an additional warning sign of pathogen spillover to native bees in Mexico (Macías-Macías et al. 2020). So far, studies on stingless bee pathogens are scarce, and there may be yet

unknown infectious agents present in different species or populations. Noteworthy, stingless bee colonies are home to varied and complex microbiota (de Paula et al. 2021), as well as species-specific relationships with rich mite fauna (da Costa et al. 2021), which could have direct implications for the transport of hives and non-naturally occurring species to different regions. A precautionary principle, which we believe applies across the gamut of stingless bee ecology in the present age, to stop the movement of colonies to areas where they are exotic, would be the best option to avoid potentially disastrous consequences (Vandame and Palacio 2010; Quezada-Euán et al. 2012; dos Santos et al. 2021a).

2.4. Threats associated to the growth of urban meliponiculture

Recently, hobbyists are showing increasing interest in keeping stingless bees. Notably, most hobbyists are found in urban areas where many stingless bee species are naturally absent. Nevertheless, cities may harbor many colonies living in walls like those of the genera *Nannotrigona* and *Scaptotrigona* (DWR Pers. Obs.). Moving colonies to urban areas could have negative consequences. If there are no other colonies of the same species, urban areas may become artificial islands where colonies may fail as a consequence of low genetic diversity. Additionally, cities may lack a sufficient supply of food or resin for nest building, needed by colonies to prosper. Only partial information is available on the performance of stingless bee colonies in urban areas and the results are not uniform (Hamid et al. 2016; Kaluza et al. 2018). May-Itzá et al. (2021) conducted a study in Mexico on the stingless bee *N. perilampoides* naturally present in urban and rural areas and found that males had smaller body size and higher frequency of diploidy in the city of Mérida, compared with rural areas. Thus, the movement of stingless bee colonies to urban areas could be another risk for colony survival and deserves further study.

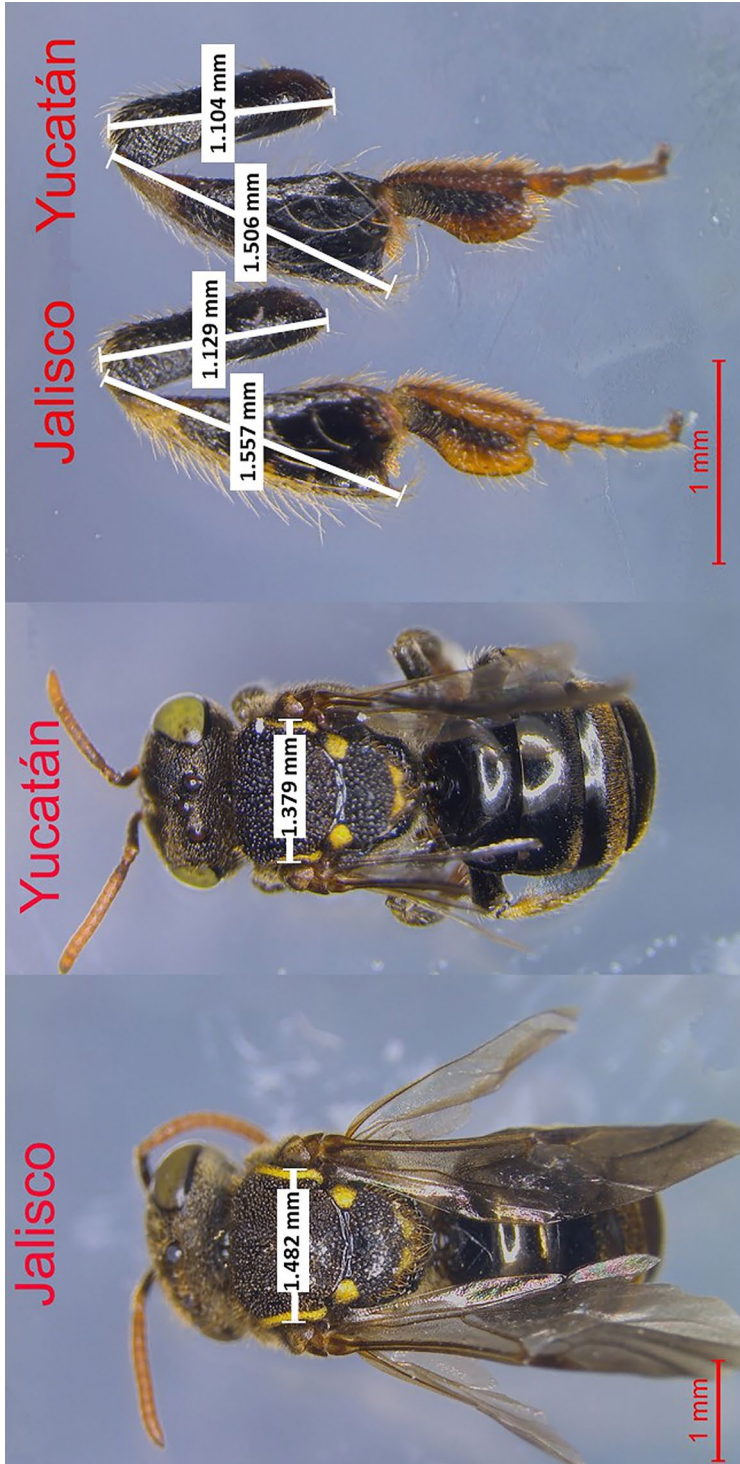


Figure 3. Phenotypic differences between workers of *N. perilampoides* from the Yucatán Peninsula and Jalisco on the Pacific Coast. Numbers indicate measurements (mm) of the intertegular distance (on the left), plus tibial and femur length (on the right).

3. CONCLUSIONS AND FILLING GAPS

3.1. Legislation and education aspects

It is important that although public and policymakers are presently more willing to support or become part of preservation initiatives, they can perceive that potential threats can arise from apparently good purposes and need to be more analytical towards them.

A first step to quantify the magnitude of the problem caused by stingless bee popularity is the keeping of records. Presently, there are no figures on the number of projects, colonies, species, destinations, etc. Federal and local governments must introduce a system to keep track of such information, especially the outcome of rescuing initiatives. Accordingly, meliponiculture projects should be subject to long-term evaluation by both cultural and biological authorities. Equally problematic is the lack of certification of technicians involved in meliponiculture, or the courses offered. Using the example of Brazil, the first country in the world to issue laws on stingless bee keeping and its products, a legal initiative seeks to regulate the professions of technologists/specialists in apiculture and meliponiculture, and is under revision (dos Santos et al. 2021a, b; Carvalho 2022b).

Validated information on meliponiculture methods and the biology of stingless bees should be made readily available through official peer-reviewed platforms. Government platforms are ideal channels to broadcast information once this is certified by recognized practitioners and experts. Some relevant management handbooks and books are already available on the biology of Mexican stingless bees, produced by acknowledged specialists from universities and scientific centers across the country and in other countries. Such information can be used to produce accessible handbooks on good practices of stingless bee management and their products. It could be central to promote good practices in bee keeping and agriculture (Quezada-Euán 2018; Roubik et al. 2018). Informative campaigns to raise awareness among the public on the risks for bees and the potential illegality of engaging

in open or clandestine trade could also be important deterrents (Carvalho 2022a). These could be firm steps of authorities towards combating disinformation and reduce the dependence on social networks as the main source of knowledge (Carvalho 2022a, b).

It is also important to regulate the extraction of colonies from the wild and the illegal trade across regions (Carvalho 2022a). Federal and local governments should promote control legislation and impose penalty fees to discourage such practices, as is currently enforced for other wild species. Colonies for trade should be certified to derive only from managed populations; likewise, certified meliponaries should be their only source. The poaching, translocation, and unauthorized commercialization of colonies is one aspect that may require novel ecological policies accompanied with legal sanctions. Suitable artificial domiciles could be a good alternative to obtain colonies of stingless bees and reduce poaching (Oliveira et al. 2013).

The consequences of stingless bee exploitation in urban environments needs to be more thoughtfully assessed before extensively promoting urban meliponiculture. It is important to investigate how often colonies suffer the consequences of genetic isolation or lack of sufficient food and materials for their nests.

3.2. Regulation of colony movement considering patterns of genetic differentiation

Regulation of colony movement across regions may prove more difficult, especially when delimiting important legal boundaries. A first form of control could be the requirement of official permission to sell and move colonies across regions. Ideally, trained official inspectors in association with government or university identification laboratories could implement an initial filter that could stop prohibited exchange of species (endangered, not sufficiently studied, or with signs of sanitary problems). Currently, Brazil legislates to try to control movements based on the political

boundaries among states (dos Santos et al. 2021b; Carvalho 2022b). In Mexico, a distributional map for the Meliponini has been proposed by Ayala et al. (2013; Figure 4). The map indicates boundaries for their natural distribution supported from sampling records and collected specimens residing in museums (Figure 4; Ayala et al. 2013). The basic information on that map can be complemented with information on the genetic status of different populations of the most important bee keeping species to propose a preliminary scheme to regulate the movement of stingless bee colonies in Mexico.

First, considering that for most studied species (Table I) orographic barriers seem to reduce gene flow and have thus defined genetic lineages, three regions could be proposed within the overall distribution stingless bees in Mexico (Figure 4). These three regions are naturally characterized by

contrasting climatic and biogeographic features (Morrone 2019): the Yucatan Peninsula, the Gulf Coast, and the Pacific Coast (Figure 4). Noteworthy, results on the genetic structure of different species of stingless bees (Table I) seem to follow a pattern largely in agreement with those three regions (Figure 4). Other orographic barriers in southern Mexico (and perhaps within the Pacific and Gulf regions) could be included as additional landmarks to set up legislative boundaries for the movement of colonies.

Some useful guidelines, strictly considering only genetic diversity information, can be derived from Figure 4, as a beginning for protection of stingless bee population integrity in Mexico:

- 1) Stingless bees should not be transported to regions where they are not naturally present (white zones on Figure 4).



Figure 4. A comprehensive map on the genetic diversity of stingless bees used in meliponiculture in Mexico. Black lines represent the borderlines of the different political states in the country. The regions of the Pacific Coast, Gulf Coast, and the Yucatan Peninsula represent the natural distribution of Meliponini in Mexico, as given by Ayala et al. (2013). Colors indicate separation of these regions by major orographic/climatic barriers (Morrone 2019). Recognized species are indicated with different symbols and different colors of the same symbol indicate findings of significant population differentiation (data from Table I). The mountain system of the Sierra Madre in the south of Mexico is indicated with a brown line in the state of Chiapas and represents a major barrier linked to separation among populations. Specific localities and number of samples analyzed can be consulted from references in Table I.

- 2) Colonies for trade shall originate from managed populations or trapped swarms (Oliveira et al. 2013). Wild colony extraction should be strictly regulated.
- 3) Exchange of colonies among the three regions where stingless bees are native in Mexico (Pacific Coast, Gulf Coast, and Yucatan Peninsula) should not be allowed.
- 4) Species within the Pacific region should have legal permission to be moved only within each political state. The reduced information currently available on the different species, the high frequency of endemism and the diversity of biogeographic provinces (Ayala et al. 2013; Morrone 2019) increase the possibility of there being in existence intraspecific genetic lineages for which no information is available.
- 5) A similar strict criterion can apply to the Gulf coast; if anything, movement of colonies should only be permitted within states.
- 6) In addition, colonies of the same species should not be moved within the same state when they stem from different biogeographic provinces (see Morrone 2019). This is especially true for the Gulf and Pacific coasts with diverse habitats and altitudes.
- 7) In the case of the Yucatan Peninsula (states of Yucatan, Quintana Roo, and Campeche), the similar environment (although differences are indicated between the north and south, Morrone 2019), and the genetic results already available, suggests that it could be relatively safe to move colonies among those three states.
- 8) The southern state of Chiapas represents a singular situation. At least three biogeographic provinces are found in the state (Morrone 2019). Regulations to avoid moving colonies to either side of the central mountain chain of the Sierra Madre should be strict.
- 9) Specific regulations for widely used species could consider that:
 - a) Banning colony movement of *M. beecheii* across states outside the Yucatan Peninsula could be wise, even before more information is available.
 - b) Exchange of colonies of *S. mexicana* between the Gulf and Pacific regions should be prohibited, as they represent genetically different lineages.
- 10) The movement of *S. pectoralis* colonies between the three major regions should be restricted pending work on more populations.
- 11) Exchanging stingless bees between Mexico and other countries should not be allowed.

This preliminary proposal is made here with the justification that is available. More data and evidence are needed to better define species and population differentiation.

3.3. Further aspects to consider

Currently, it is not possible to clearly define if species or populations in Mexico are at risk and if it would be necessary to establish measures for their protection. Thus, the need for taxonomic studies that can decipher data supporting the existence of subspecies or cryptic species is most relevant for conservation purposes and should be encouraged (Ayala et al. 2013). New omic-approaches are promising methods that can improve speed and accurate estimations of genetic diversity within and among populations. The use of relatively inexpensive methods such as geometric morphometrics can provide a rapid means to identify colonies and their origin (Francoy et al. 2011). Construction of extensive data base with samples of the different regions could allow development of official methods for automated identification from photographs (Francoy et al. 2011; Quezada-Euán et al. 2015). However, more studies are necessary to determine the congruence between such morphology-based tools and the genetic status of populations of different species (Francoy et al. 2011).

A consideration in the proposal is sanitation and disease control (Vandame and Palacio 2010; Colla 2022). However, little information is available, and

the investigation of stingless bees and other native bees should seek added support. In the short term, it seems important to conduct routine sanitary inspection as part of the requirements for permission regarding colony transport across regions.

There is an urgent need to develop methods for non-destructive and efficient colony reproduction to curtail dependence on wild populations (Quezada-Euán 2018; Eleutério et al. 2022). In parallel, it is necessary to adopt public policies that ensure the regularity of multidisciplinary scientific research that incorporates traditional indigenous knowledge in the conservation of stingless bee biodiversity (Hill et al. 2019; Reyes-González et al. 2022).

Finally, conservation of the diversity of stingless bees relies on preserving their natural habitats. The present levels of deforestation in Mexico are compromising the diversity and abundance of native bees in general and the resiliency of food production (Ashworth et al. 2009). In Mexico, a decrease in the number and diversity of nectar producing plants could also have a negative impact on the potential honey production and economic sustainability of meliponiculture (Quezada-Euán 2018).

Similar scenarios to those of the Americas may be occurring in areas of the world where stingless bees are native and where their popularity is also increasing. It is crucial to have information from these regions in order to generate worldwide support and make global changes regarding this problem.

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AUTHOR CONTRIBUTIONS

JJGQE and DWR conceived and designed the MS. Material preparation, data collection, and analyses were performed by all authors. The first draft of the manuscript was written by JJGQE, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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AVAILABILITY OF DATA AND MATERIAL

All data are available upon request from the corresponding author JJGQE.

CODE AVAILABILITY

Not applicable.

DECLARATIONS

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