



## REVIEW

### Economic and Cultural Values of Stingless Bees (Hymenoptera: Meliponini) among Ethnic Groups of Tropical America

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#### Abstract

Stingless honey bees — commonly known as stingless bees — have long provided food and materials to the inhabitants of tropical America. We conducted a literature search to codify available information, including non-peer reviewed ‘grey literature’, on the purported value of stingless bees to indigenous people. Among > 400 species of Neotropical stingless bees several are widely used in beekeeping. Varied cultural and economic values are associated with their use, and in some cases husbandry, as a consequence of ongoing contact between people and these social insects. Adapting new species to husbandry is being attempted in many countries. The bees remain culturally important, and beliefs associated with them are significant for different groups, beyond utilization as commodities. We find values in food, craft, religion and medicine, with cultural values ranging from utilitarian to mythological. Values transmitted across generations allow cohesion and communal identity of native organisms associated with any indigenous society. Such cultural values seem in danger of extinction, primarily due to external factors. We provide examples of successful regional strategies in averting cultural and economic loss in natural human heritage, in this case bees that provide honey and other benefits. Preserving stingless bees and the cultural heritage around them provides a good example of sustainable use of native species in human communities. Bees are important agents for conservation of the environment.

#### Introduction

A persistent interaction with the environment has shaped human experience and resultant knowledge across diverse groups and societies. Therefore, intricate links between ecosystem use, management and human cultural values have produced numerous indigenous, local knowledge systems (Gómez-Baggethun et al., 2013; Jax et al., 2013). The Millennium Ecosystem Assessment (MA) defined cultural ecosystem services as “*the nonmaterial benefits people obtain from ecosystems through spiritual enrichment, cognitive*

*development, reflection, recreation, and aesthetic experience, including, e.g., knowledge systems, social relations, and aesthetic values*” (MA, 2005). From a biological perspective, the importance of traditional knowledge often relies on its practical nature, particularly in agriculture, fisheries, health, horticulture and forestry, including the development and preservation of locally bred plants and animals.

Recently, the importance of indigenous cultural values and traditional knowledge as essential components of biodiversity models and policy has been recognized (Hill et al., 2016; IPBES (2016)). Nonetheless, for centuries if not



millennia, traditional culture has been neglected and now has great difficulty resisting the onslaught of outside influences. Cultural values are in danger of being lost at an increasingly rapid rate.

Stingless honey bees are a tropical phenomenon whose time has apparently come, evidenced by burgeoning volumes documenting their biology and use, including in beekeeping (e.g. Roubik, 2006; Vit et al., 2013; Cortopassi-Laurino & Nogueira-Neto, 2016; Heard, 2016; Jalil & Roubik, 2017; Quezada-Euán, 2018). In addition, the Americas provide one of the best examples of a link involving cultural values and traditional knowledge. It has developed over millennia, but now is disappearing from indigenous communities. Before the European era, stingless bees played an important role in the economies and traditions of American indigenous cultures (De Landa, 1566; Cobo, 1653, cited in Roubik, 2000; Schwarz, 1948; Quezada-Euán et al., 2001; Koedam, 2018). Because it was both a sweetener and a rich source of energy stingless bee honey was frequently used in trade and in traditional medicine and ceremonies (Schwarz, 1948; Weaver & Weaver, 1981). Honey and other nutritional or useful substances were removed from wild nests. But very significantly, in a few, scattered cultures, particularly the Maya, bee husbandry evolved, and bees were protected in artificial domiciles or 'hives' (De Landa, 1566; Schwarz, 1948).

Notwithstanding the untimely disappearance of organized cities after the European conquest, in particular the 'corn-culture' centers which supported permanent settlement and human populations in much of pre-Hispanic Mesoamerica (Coe & Koontz, 2013), we find evidence of a steady decline in stingless beekeeping since the 16th century. A constant reduction of natural forest due to agriculture and settlement expansion has diminished nesting, foraging and reproduction by many species of bees and other animals used by the human population, particularly in forested or rural areas. We propose that the decline in stingless beekeeping is a multifactorial problem that involves ecological, social and economic factors (Quezada-Euán et al., 2001; Villanueva-Gutiérrez et al., 2013). Moreover, native indigenous peoples are now progressively more in contact with and influenced by Western customs and media, and thereby abandon some traditions as a consequence (Stearman et al., 2008).

There is strong evidence that bees are in decline in certain manmade settings (Biesmeijer et al., 2006; Fitzpatrick et al., 2007) with a number of factors thought to play major causal roles (Kremen et al., 2002; Woodcock et al., 2017; Tsvetkov et al., 2017). Native bees are considered the most important pollinators of crops world-wide; their contribution seems difficult to replace by commercially managed pollination (Garibaldi et al., 2013; Roubik, 2018a). In the Neotropics, stingless bees may represent the main pollinators in abundance and species (Roubik, 1989, 2018b). Given the projections for human population growth to ~9 billion by 2050 (United Nations, 2004), particularly pronounced in tropical and

subtropical latitudes, and the corresponding increasing need for food, the importance of native bees to human survival and ecosystem resilience can only increase in the coming years. Traditional practices and knowledge associated with the use of native species like the stingless bees almost certainly will diminish, if gone unacclaimed, at precisely the time when they are most relevant and important.

Here we summarize and evaluate the literature, both published in peer-reviewed journals and among our judicious selection of opinions posted on the worldwide web, regarding the values and traditional practices associated with stingless honey bees and their products in tropical America. Our interest is in revealing and summarizing as much as possible, in areas where traditional knowledge, without becoming part of anthropological field research, does not attain the level of academic publication. Thus, we include a sampling of the so-called electronic 'grey literature', or that subject to rapid database searches. Our aim is not only to identify cultural values associated with these insects and to raise public awareness of the significance of preserving them as part of biocultural human heritage, but also to acknowledge their current role in agricultural and ecosystem resilience, in the face of global change.

## Materials and Methods

We searched published peer reviewed literature on traditional knowledge and the use and cultural values of stingless bees. Databases included organizational web searches, web search engines and bibliographic checking. Many documents were in Spanish and Portuguese.

The main key words were queried in three languages, Spanish, Portuguese and English, and web searches were based upon "native bee, cerumen, wax, cultivation, cultural value, exploitation, honey, meliponiculture, husbandry, myth, *Melipona*, stingless bee, *Trigona*, indigenous and traditional knowledge". We selected publications referring to the Americas. For each category, we recorded the type of web search, date, search details, search terms, hits, and output, after replicate removal. Our review also examined book information that may be obtained from governments, dissertations, web sites of individual professionals, business and industry — in print and electronic format. These are not controlled by commercial publishers (Grey Literature Report; accessed 21/03/18 <http://www.greylit.org/home>). We also contacted academic researchers, usually with advanced degrees in the subject.

When few studies were available, we focused on the methodology as the main criterion for scientific quality and inclusion in our survey. Our findings were grouped according to the main subject of the manuscript. We further categorized economic and cultural values (as described by MA, 2005), given to stingless bees by local people, by taking the number of citations for each as a measure of relative importance. We

also considered it important to distinguish between reports of species used in rational beekeeping (generally termed that performed using hives of some sort, usually those in which colonies can be propagated or fed) and those related to other cultural/medicinal use that does not involve bee management in some form. The main features and cultural values associated with stingless honey bees in Mesoamerica and South America were considered separately (Kent, 1984; Crane, 1992). We also constructed a map including species used in beekeeping on a larger scale, and a table with all species of stingless bees for which evidence of traditional use was found across the Americas, including the indigenous groups that use them, and the major economic and cultural values given to the bees and/or their products. Finally, we compiled some of the beliefs and traditions associated with stingless bees, among various indigenous peoples.

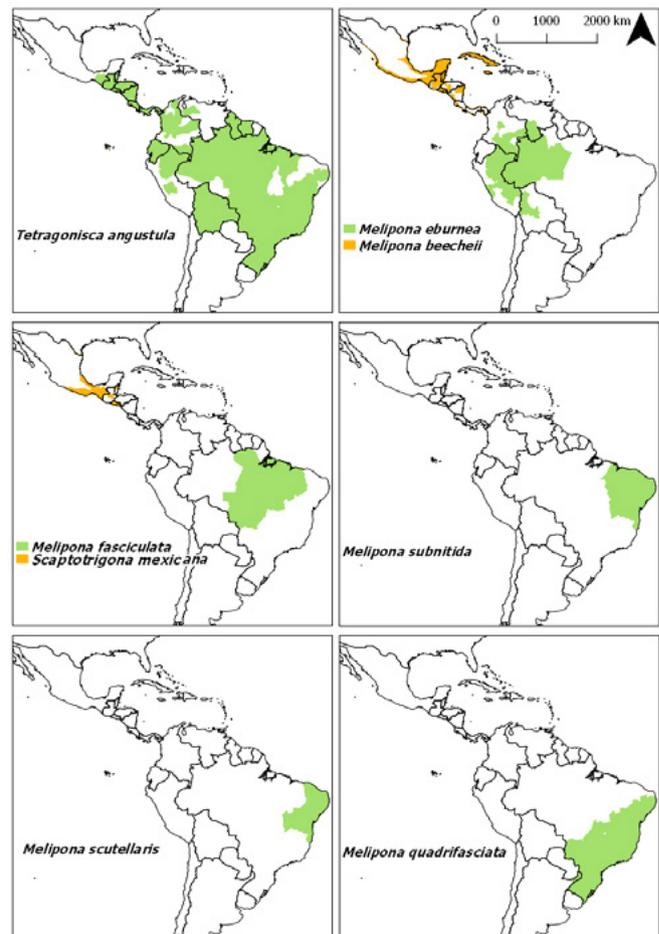
## Results

Although we conducted an extensive search of the literature, no published information could be found for many areas. In particular, when we refer to Mesoamerica it should be noted that most available literature comes from Mexico and Guatemala, some from Honduras, El Salvador, Nicaragua, Costa Rica and Panama, but no information could be obtained from Belize. In South America, information was found from Brazil, Colombia, Venezuela, Ecuador, Peru, Paraguay, Bolivia and Argentina.

One general finding was that current stingless beekeeping, most often with a local, indigenous origin, is based on only a few species. In this regard, we are not considering species of stingless bees that may be occasionally exploited, or with limited relevance in current beekeeping. Indeed, there are many reports of several species recently promoted for honey production (Yurrita-Obiols & Vásquez, 2013; Ruano-Iraheta et al., 2015; Arnold et al., 2018). In Brazil, for instance, the use of 61 species in different biomes, with their popular names, was recognized (Venturieri et al., 2012).

The most important species, geographically, in beekeeping is *Tetragonisca angustula* (Latreille) (Fig 1). However, *Melipona beecheii* Bennett, is probably the most important culturally (De Landa, 1566). Apart from these species only five or six more are used extensively in beekeeping in the Americas. Species of the genus *Melipona* seem to be particularly appreciated because of the amount and quality of their honey (Fig 1). We note that some of these species are possibly species complexes, as indicated by molecular analyses (Quezada-Euán et al., 2007; May-Itzá et al., 2012; Francisco et al., 2014; Hurtado-Burillo et al., 2016, 2017). Thus, a few more distinct bee species may be involved in indigenous beekeeping. At least 100 more species have cultural and medicinal importance. Further, the use of common names reveals that, in an analysis of 76 ethnic names for Ecuador (Vit et al., 2017), and over 50 names

used by two indigenous peoples in Amazonas state, Brazil (Oliveira et al., 2013), the species with multiple names are likely most important. In Mesoamerica *M. beecheii* has at least 20 different local names (Arnold et al., 2018; Quezada-Euán, 2018), while *T. angustula* had seven common names in Ecuador and *Melipona grandis* Guérin, in central Brazil, had eight (Table 1). Finally, in Brazil, only about 10% of the stingless honey bees have common names, while an estimate based on 12 countries, worldwide, indicates 25% of local species are utilized and have such names (Roubik et al., 2018). If common names indicate utility, or exploitation, then there is an indication here for both underexploited and perhaps potentially overexploited species (Table 1).



**Fig 1.** Geographic distribution of the main species of stingless bees used in beekeeping in Tropical America. Data from Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region. Available on line at <http://www.moure.cria.org.br/catalogue>.

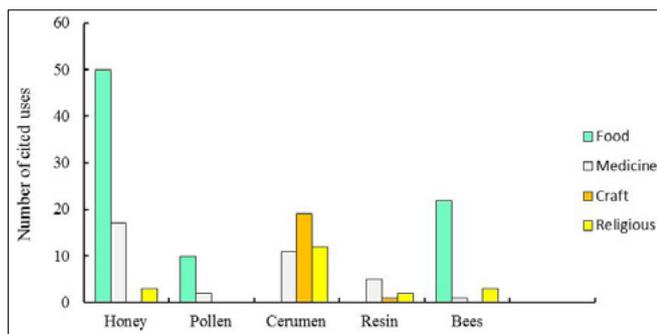
## Discussion

We identified many economic and cultural values associated with stingless bees and their products. We also found several major categories within each value type. Food, tool and craft, medicinal, economic or mythological categories predominated. The results are presented in Table 1. The most important overall value given to stingless bees is economic, as a source of food and additional income. Honey is the main

commodity in this respect, used either for local consumption or trade (Fig 2). Honey is also used to treat various illnesses and is sometimes mixed with other natural products. Other bee colony products are also used for consumption but are minor, such as the pollen, resin and brood. Resin (propolis) and cerumen are used primarily in tools and handicraft. A second economic use concerns traditional medicine practiced by shamans and midwives, which in the process become figures of authority and respect in their communities (Fig 2).

The number of ways in which stingless bees are valued contrasts between Mesoamerica and South America. Although all the surveyed native groups make extensive use of Meliponini as a source of food, the medicinal and religious values associated with stingless bees are, evidently, a more currently relevant and also an ancient feature in Mesoamerica. In contrast, the mythological significance of these insects is a common feature to indigenous peoples throughout tropical America.

Although the stingless honey bees have been extensively used and appreciated among native groups, major geographic differences are found today in the management of different stingless bees. As discussed further below, the Northern Hemisphere cultures, particularly those in large, permanent settlements, practiced husbandry, with the possibility of reproducing their colonies and maintaining them, while the Southern Hemisphere peoples relied on bees as one of the renewable resources extracted directly from the forest. To date, there is no evidence of extensive stingless bee husbandry in South America, where use has always concentrated on hunting nests mostly for honey (Brown, 2006; Rosso & Imperatriz Fonseca, 2017). People usually open and remove meliponine nest contents, leaving the damaged colonies in the wildlands (Kerr et al., 2001). There was no systematic reproduction of such colonies, and most succumb to phorid fly depredation (Roubik, 1989). The Brazilian Kayapó are perhaps an exception, practicing what is considered semi-domestication, collecting the nests and bringing them to the vicinity of their homes to remove bee products from time to time (Camargo & Posey, 1990). South American societies had no religious relationship like that in Mesoamerica, but for some indigenous peoples (Andoque, Uwa, Tupinambá, Kayapó), stingless bees were important in cosmogony and mythology (Jara, 1996; De Jong, 1999; Falchetti & Nates-Parra, 2002; Lima & Moreira, 2005; Posey & Camargo, 1985).



**Fig 2.** A summary of literature reports of the main uses given to stingless bee products by different indigenous groups of tropical America.

In the following sections we present summaries of the most important cultural manifestations related to stingless bees and their cultivation by different ethnic groups.

### Mesoamerica

The main feature in Mesoamerican stingless bee exploitation was the development of husbandry with an annual propagation of colonies, or colony “splitting”. Such a rational form of stingless beekeeping 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 & Vásquez, 2013). Unmentioned is perhaps the equally important fact that ‘corn culture’ and the potential for permanent settlements developed in the same region. As the forest was cleared for corn cultivation, and local stingless bees were overexploited, the indigenous people may have devised means for sustainably maintaining their colonies of *M. beecheii*, and perhaps other species. It is believed that due to the Maya, stingless beekeeping spread to other civilizations across Mesoamerica (Schwarz, 1948; Kent, 1984). A key aspect of husbandry in Mesoamerica was the development of hives of standard measures to accommodate colonies. Interestingly, two types of hive exist today in Mesoamerica, one, the hollow log (locally known as ‘hobon’) was extensively used in the Maya area. Another type consists of clay pots (‘mancuernas’ or ‘ollitas’) used as hives in the Mexican highlands of Puebla, Veracruz and Oaxaca (Fig 3; Weaver & Weaver, 1981; González-Acereto, 2008; Arnold et al., 2018; Quezada-Euán, 2018).

For the Maya, stingless beekeeping became part of cosmogony and mythology, being of similar importance to the cultivation of maize, a staple food for Mesoamerican civilizations (De Jong, 1999). No other culture conferred such spiritual significance upon one of the bees they coveted, the “Xunan-Kab” (the lady bee, or lady of the honey), known to science as *M. beecheii*. Evidence of the economic and religious importance of Xunan-Kab is found in Maya art and manuscripts (Crane, 1992; Zralka et al., 2014; Sotelo-Santos & Asomoza, 2018; Quezada-Euán, 2018). The most important is the CODEX of Madrid, one of the three surviving Maya codices, in which stylized images of the Xunan Kab and guardian gods are represented in various scenes, probably associated with honey harvest and colony multiplication (Zralka et al., 2014). The scenes depicted in the codex and other Maya creations reveal that many deities looked after the bees and the shelter “Na hil kab”, where their nests in hollow logs “hobones” were maintained. Some of these deities are Ah-Mucen-Kab (the descending honey god), Noh Yum Kab, Hobnil, Balam-Kab and Moc-Chí (Schwarz, 1948; De Jong, 1999). All are represented with a mixture of anthropomorphic and bee-like features, sometimes involving characteristics of other sacred animals like the jaguar (as seen on the face of Balam-Kab) (López-Maldonado, unpublished data, see supplementary material 1; Quezada-Euán, 2018). Like their Mayan ancestors, peasant farmers in the Yucatan Peninsula

and Guatemala still use hollow logs, often of the “chicle” tree, *Manilkara*, to keep colonies of *M. beecheii* (Yurrita-Obiols & Vázquez 2013; Bianco et al., 2017).

Large numbers of managed colonies were kept in Pre-Columbian Yucatan, which produced large amounts of honey supporting intense trade within and outside the region (Schwarz 1948; Calkins, unpublished data; Batún-Alpuche unpublished data, see supplementary material 1). The production of *M. beecheii* honey in the Yucatán Peninsula seems to have occurred as a large-scale cottage industry and was organized at household and neighborhood levels (Batún-Alpuche, unpublished data, see supplementary material 1). Thus, the accumulation of wealth in Maya society may have been a consequence of honey trade (Quezada-Euán et al., 2001).

In Maya mythology, it is believed that the Xunan-kab was directly given to humans by the major god “Kun’ ku” or “Yumbil dios”, therefore, the beekeepers are seen as guardians and caregivers of this creature, which in essence does not belong to them (De Jong, unpublished data, see supplementary material 1). As a tribute to the real owner of the bees, during annual rituals the beekeepers are obliged by tradition to give back part of the honey harvested from the colonies in a ceremony called the “U Hanlil-kab”, or the feast of the bees (Weaver & Weaver, 1981). Only the honey from the Xunan Kab is accepted by the gods. This has to do with the concept of the earth as a living entity composed of spirit, blood and flesh. Honey from Xunan-kab is considered “hot” (Schwarz, 1948) and is seen as a living and essential fluid from the land where the bees dwell, which men have extracted from it. It is a concept parallel to that of blood as part of the human body (De Jong, 1999). Xunan-kab honey is also associated with fertility and is applied by midwives to the abdomen during child birth, and it also purportedly increases the production of milk consumed in beverages (Schwarz, 1948; González-Acereto et al., unpublished data, see supplementary material 1). Honey of this bee is used to treat disease, which in this traditional cosmology is thought to derive from an imbalance in body temperature (Schwarz, 1948). Interestingly, the pollen is considered as feces or filth from the bees and is not used for human consumption. This is probably an idea derived from the massive infestation by phorid flies that may occur in pollen pots. During the harvest, pollen pots are discarded and buried underground (González-Acereto, 2008).

Stingless bees other than Xunan-kab are considered masculine and their honey, including that of the Western hive honeybee, *Apis mellifera* L., is regarded as “cold” (De Jong, 1999), although it is consumed and used in traditional medicine (González-Acereto et al. unpublished data, see supplementary material 1). Being considered such a sacred creature, it is not surprising that the traditional cultivation of Xunan-kab is strongly associated with various symbols related to their divine origin and the creation of the world in Maya cosmogony (Schwarz, 1948; Weaver & Weaver, 1981; De Jong, 1999; González unpublished data, see supplementary

material 1). In contrast with the wide use of honey, cerumen seems to have been mainly used in “lost wax” gold foundry outside the Mayan area, but not in candle-making, which started only after contact with Europeans (Schwarz, 1948).

In Mesoamerica, outside the Yucatan Peninsula and northern Guatemala, pre-Columbian stingless beekeeping seems only to have reached a moderate level of development, but was probably widely practiced (Calkins, unpublished data; Kent, 1984; Aguilar et al., 2013a; Arnold et al., 2018). To the north, remnants of this activity are still found in the Mexican states of Puebla and Veracruz on the east coast, and on the Pacific coast in the state of Guerrero. Indigenous Nuhua groups practiced stingless beekeeping in those regions but not with Xunan-kab. Because *M. beecheii* is found from the tropical regions of Mexico to Costa Rica (Quezada-Euán et al., 2007; Roubik & Camargo, 2012), but colonies were kept and multiplied only in the Yucatan Peninsula (Foster, 1942), we may ponder the reasons why this particular species was more prolific, or managed with greater success in some regions and not in others. Along the highlands of eastern Mexico, the Totonaco and Nuhua peoples still keep and propagate colonies of *Scaptotrigona mexicana* (Guérin) “P isil-nek-mej” or “Taxcat” in clay pots (Schwarz 1948; García-Flores et al., unpublished data, see supplementary material 1). Similarly, in the highlands of Oaxaca on the Pacific coast, the Mixteco, Zapoteco, Chontal and Chinanteco cultivate *Plebeia fulvopilosa* Ayala, in clay pots (Arnold et al., 2018). In contrast, the Zapoteco and Mixteco on the Pacific and the Zoque and Popoluca of the Gulf Coast rarely cultivate *M. beecheii*, *Melipona fasciata* Latreille, *Melipona solani* Cockerell, *Scaptotrigona pectoralis* (Dalla Torre), *S. mexicana*, *T. angustula* and *Frieseomelitta nigra* (Cresson), in hives. These indigenous people keep nests of those species either in their original trunks close to their homes, or mostly hunt them in the wild (Vásquez-Dávila unpublished data, see supplementary material 1; Arnold et al., 2018). On the Pacific coast the Tlapaneco keep *M. fasciata* in log hives (González-Acereto, 2008); this is probably the bee mentioned in the account of stingless beekeeping in western Mexico provided by Dixon (1987). There is some evidence of *Nannotrigona perilampoides* (Cresson) being used along the Mexican Pacific coast (Bennett, 1964). There are very few records concerning indigenous stingless bee keeping in southern Mesoamerica, and it possibly did not play an important role in the religion of native people (Aguilar et al., 2013a).

### South America

Unlike Mesoamerica, where most traditional knowledge is related to a few bee species, South American native people used a wide range of species, but in contrast to Mesoamerica and Mexico, we found no reference to bee husbandry in Pre-Columbian times. Most indigenous groups exploited the bees in their natural environment and/or in their natural nests kept near their homes.



**Fig 3.** Indigenous stingless bee husbandry in Mesoamerica involves the use of specially made hives: hollow logs or ‘hobones’ in the Mayan area, and clay pots or ‘mancuernas’, in the highlands of Puebla, Veracruz and Oaxaca (Photos courtesy of Humberto Moo and Margarita Medina).

Before Europeans, indigenous peoples in South America knew stingless honey bees (Espinosa, 1529, cited in Samper Pizano, 2003; Gumilla, 1741; Castellanos, 1852; Acuña, 1986; Crane, 1999; Medrano & Rosso, 2010). One South American locale in which a primitive form of meliponiculture was practiced was on the slopes of the Sierra Nevada de Santa Marta, in northeastern Colombia (Patiño, 1965-1966, cited in Patiño, 1990) — perhaps under the influence of the Maya (Oviedo & Valdés, 1959, cited in Crane, 1999). A secondary center of stingless beekeeping likely existed in northern Venezuela (Sanoja & Vargas 1974, cited in Patiño, 1990). According to Rivero Oramas (1972) the oldest references on stingless bees in Venezuela, from 1612-1613, are those of Fray Pedro Simon. Although references to ancient forms of stingless beekeeping were found for these regions, it is not clear if it was practiced by native people before the Spanish conquest.

In Colombia the bee species used by indigenous peoples are at least partly known. The Nukak, traditional nomadic peoples of the northwestern Amazon, harvested products of around 43 native bee species (Cabrera & Nates-Parra, unpublished data, see supplementary material 1). Within the mythology of the Uwa (Sierra Nevada del Cocuy, Colombia), the bees are considered important as beings that made life evolve in the universe, and honey is associated with fertility and procreation (Falchetti & Nates-Parra, 2002). According to Jara (1996), for the Andoke tribe, honey is considered a food crop (and female in gender, like the cassava) while the stingless bees themselves represent the male gender. The Andoke evidently failed to recognize male versus female bees.

In the Vaupés state of Colombia, Rosso and Parra (2008), Estrada (2012) and Rosso-Londoño (unpublished data, see supplementary material 1), documented indigenous

traditional knowledge related to stingless bees, especially within the ethnic groups Tatuyo, Syriano and Bara. Among these societies there is detailed knowledge of at least 25 ‘ethnospecies’ of stingless bees, used in traditional medicine, food, tool making and musical instruments and as bait for fishing, among other things. For these societies, as for the Maya, the pollen was not used because it was considered dirty (bee excrement) (Rosso-Londoño, unpublished data, see supplementary material 1). Nates-Parra and Rosso-Londoño (2013) recorded nearly 50 common names used for the stingless bees, as did Posey and Camargo (1983) among the Kayapó of Brazil, with wide variation between regions and informants.

One of the oldest references to stingless bees in South America is that written by Hans Staden in 1577, the “Warhaftig Historia” (Engels, 2009). The report describes three species and nests, probably *Melipona quadrifasciata* Lepelletier, *Scaptotrigona postica* (Latreille) and *T. angustula* used by the Tupinambá, who lived in the coastal region of Santos, State of São Paulo, Brazil. Another study from Lima and Moreira (2005) reports that the Tupinambá associate the stingless bees with their cosmology. They have named constellations with bee names such as the “Seichu-jurá” or “jirau-de-abelha”, “Seichu” or “Eichu”, meaning Master Bee or Queen Bee.

Noteworthy among South American indigenous groups are the Kayapó from the eastern Amazon forest, who developed a solid tradition on knowledge of stingless bees (Posey, 1983; Camargo & Posey, 1990; Melatti, 2007). The stingless bees compose part of their cosmology and social organization models, while maintaining importance in food and medicine. When hunting colonies, the Kayapó recommend leaving part of the colony and nest intact after harvesting honey, as an offering to “Bep-kororoti”, a powerful shaman. Although

it was perhaps unintentional, by following that practice, a colony could recover, and again provide honey for the Kayapó (Posey, 1986). The Kayapó group can identify 56 species of “stingless bees” (note that Posey, 1986, included bees of taxa other than Meliponini), in strong correlation with scientific classification, and they recognize the nest architecture of each in detail, as well as the different stages of bee development (Posey, 1983). In addition, the Kayapó developed an ability to locate bee nests by listening for the noise made by bees performing nest ventilation, which they recognized for each bee species. Aggressive bees like *Oxytrigona* and the exotic colonist *A. mellifera* were managed with smoke of a liana (*Tanaecium nocturnum* (Barb. Rodr.) Bureau & Schumann, Bignoniaceae), which narcotized the bees, so that honey could be taken (Camargo & Posey, 1990). The Kayapó people have a semi-domesticated system of beekeeping. Some wild nests are taken to the village, while others are harvested in their natural environment, and small forest clearings are made to encourage nesting there by certain stingless bee species. No other Amazonian tribe is reported to maintain stingless bees in the manner of the Kayapó.

The Kayapó associate honey, wax, and bees with the heavens and rains because of the fondness that “Bepkororoti” has for honey. They burn the cerumen to produce a smoke that is believed to attract storm clouds and rain, as well as to repel evil spirits, purge houses from lingering ancestral spirits, and protect children from witchcraft. The cerumen has multiple uses, such as (when melted) a glue to attach feathers to an arrow, and to strengthen and lubricate bow strings (Posey, 1983; Stearman et al., 2008). A most impressive and symbolic use of cerumen is for the “me-kutom”, a hat worn by young men about to receive ceremonial names upon reaching adulthood. Cerumen for the hat is inherited and kept in the family for generations (Posey, 1983).

Other groups like the Enawenê-Nawê from the southwestern Amazon, Mato Grosso State, also have an excellent classification system and recognize 48 species of stingless bees (Santos & Antonini, 2008). The Pankararé from the northeastern “Caatinga” savannah (steppe), Bahia State, name 23 folk species (Costa-Neto, 1998) and the Kaiabi, also from Mato Grosso State and Guarani M’Byá from the Atlantic Forest, southwestern and southern Brazil, recognize 27 and 13 species, respectively (Ballester unpublished data, see supplementary material 1; Rodrigues unpublished data, see supplementary material 1).

The Kawaieté people that live in Xingu River Basin in Brazil have names and knowledge for 37 stingless bee species, identify 28 forest trees they use for nesting and 19 plants for feeding (Villas-Bôas, 2012).

Bees are also important in the cosmology and diet (honey, pollen and larvae) of the Guarani from the Atlantic Forest. They call the bees “mother of the Gods” (Nogueira-Neto 1997; Rodrigues unpublished data, see supplementary material 1).

To the Pankararé from the arid zones of northeastern

Brazil, all “bees” (bees and wasps are placed in a single category) are believed to be enchanted organisms, protected from human exploitation by guardian spirits of plants and animals called “encantados” (Costa-Neto, 1998). Eleven species provide 13 raw materials used for remedies to treat or prevent 16 illnesses (Costa-Neto, 1998). The Pankararé classify the “abeias” (bees) according to their behavior as either “angry” or “gentle”. They also divide the “abeias” into three ethno-families, depending on the presence of a sting (Costa-Neto, 1998; Castro et al., 2017).

The knowledge on bees held by Brazilian indigenous tribes is passed on orally from one generation to another and has likely influenced many involved in stingless beekeeping. Indeed, widely used stingless bee names, such as “Jataí, Uruçu, Tiúba, Mombuca, Irapuá, Tataíra, Jandaíra, Guarupu, Manduri” have indigenous linguistic origins (Lenko & Papavero, 1979; Nogueira-Neto, 1997; Villas-Bôas, 2012).

The Kaingang tribes from southern Brazil believe that stingless bee honey has two strongly contrasting values. Honey and raw vegetables are “cold” foods. They are only allowed to widows or widowers who, if they eat meat or any cooked food, are at risk of suffering from an internal heating, followed by death (Lévi-Strauss, 2004b). Nevertheless, other groups of Kaingang prepare a fermented manioc beverage in two different ways, with or without stingless bee honey, and the type sweetened with honey is considered more intoxicating, and if imbibed while fasting, may induce vomiting. It is thus called a “hot” food.

Lévi-Strauss (2004b) reports that among certain northern Tupi Indians, honey occupies a central place in ceremonial life and religious thought. Like their relatives from the Tembê tribe, the Guajajara from Maranhão state, northeastern Brazil, celebrate honey in their principal festivals. It is also reported that the Umutina believe man was created from wild fruits and honey (Lévi-Strauss, 2004 a, b).

The cerumen of native bees also played a central role in Amerindian cultures that practiced metallurgy. Golden ornaments like jewelry used the cerumen of stingless bee nests to fashion their model, and a mold was made into which molten gold was poured, after the cerumen or “lost wax” had been melted away (Falchetti, 1999). Another product widely used was “propolis”, or pure collected plant resin. In Colombia the propolis of “brea bees”, *Ptilotrigona occidentalis* (Schulz), called “canturron”, served for the elaboration of “embil”, a name given the torches used by Chocoan people (Patiño, 2005). The ‘canturron’ is also used by other local communities (Valle de Cauca and Antioquia, western Colombia) for waterproofing boats and for the healing of minor wounds (Galvis, 1987; Nates-Parra, 2005). In Argentina, especially in Misiones and Yungas, there is evidence of stingless honey bee product use in traditional medicine, along with many plants (Zamudio & Hilgert, 2011, 2012; Flores et al., 2015). The stingless bees were well known by different cultures in northern Argentina before the arrival of Europeans;

the traditional knowledge of stingless bees in Argentina is reflected in the many and accurate names by which different species have been known by diverse ethnic groups, such as the Guaraní, Guaycurú, Toba, Wichí, and Quichua people, as well as the criollos. The more exploited species of stingless bees in northern Argentina are *Tetragonisca fiebrigi* (Schwarz) ('yatei', 'rubiecito'), *Scaptotrigona jujuyensis* (Schrottky) ('negrito', 'tapezua', 'yana') and *T. aff. angustula* ('rubiecito', 'mestizo') and some *Plebeia* (Schwarz) species (Roig-Alsina et al., 2013).

In Bolivia, *T. angustula* are called "señorita bees", and there are indigenous communities (Yuqi, Ayoreo, Sirionó) that use this bee for food and medicine. The Ayoreo possess an extraordinary knowledge of bees and honey. They report 16 species of bees such as "ajidabia" (*T. angustula*) and "cuteri" (*Scaptotrigona polysticta* Moure), and classify honey by flavor and texture, acknowledging different properties. For example, acid honey causes diarrhea, so they don't eat it. The acid and sour taste were due to the origin, that is to say, certain flowers — a biologically correct observation (Szabó & Stierlin, 2005). Currently, the Sirionó keep various species of stingless bees in hives as a state-supported production project. Honey is used as food, especially to give strength to children and to make drinks like "mead" and "hichi". The cerumen is used as glue in the making of arrows (Lehm & Lehm, 2004).

In the upper Amazon of Ecuador, the Achuar people collect bee nests to consume their larvae and obtain honey "mishik" from *T. angustula* "wapaa yumir". Pot-honey is used to treat throat inflammation (Descola, 1996; Guerrini et al., 2009). The Kichwa people are recognized for their knowledge of stingless honey bees. They are able to describe and to differentiate honey types without previous sensory training. This suggests Ecuadorian native Kichwa maintain a sensory legacy by teaching new generations how to identify different honeys by taste (Vit et al., 2017).

Although we cannot claim there is clear documentation of ancient cultures in the hot, seasonal savanna-forest of

northeastern Brazil, there are many cave paintings, dated over 20 millennia in age (Lahaye et al., 2013; see Hoffman et al., 2018). One of them is probably related to harvest of bee brood or other material from an aerial nest of *Trigona* (Fig 4). This fact indicates that further study is required to fill many gaps and clarify our knowledge of the archeology of bee use and management in the Americas.

### Status and perspective of indigenous knowledge related to stingless bees in tropical America

Stingless bees have been widely used across tropical America. Many were documented here, but probably many more remain undocumented. Native groups have developed and still maintain strong traditions and myths based upon their perception of these insects.

In spite of the varied evidence of a rich heritage associated with stingless bees, it could be at risk of disappearing. In Yucatan, a steady decline of stingless beekeeping is occurring, probably as a consequence of deforestation, changes in the economic system and the introduction of honeybees (Quezada-Euán et al., 2001; Villanueva-Gutiérrez et al., 2005a, b; González-Acereto et al., 2006; Villanueva-Gutiérrez et al., 2013). In South America, a similar situation has occurred; there was a rich background of knowledge of various native tribes that is disappearing in the younger generation across the region (Stearman et al., 2008).

It seems in many countries traditional knowledge associated with these species is disappearing. One of the important factors for the decline of traditional knowledge is the decline of the indigenous peoples themselves. Geographic displacement, encroachment and the erosion of their culture occur as outside elements have caused the breakdown of their customs and traditions (Lyver et al., 2014).

Nonetheless, different educators and groups of producers across the Americas have been aiming at rescuing stingless bees through their inclusion in beekeeping. A mainstay of this activity concerns dissemination of methods to efficiently maintain and reproduce colonies, which reduces the impact of hunting wild populations (González-Acereto et al., 2006; Quintal & Roubik, 2013; Hill et al., 2016). Attempts are also made to improve the quality and marketability of products for better economic rewards and also by increasing the value of colonies from additional services such as commercial pollination (Quezada-Euán et al., 2001; Vit et al., 2013; Roubik et al., 2018). Stingless beekeeping is showing signs of recovery for various indigenous groups. People outside these communities are also getting involved in stingless beekeeping and commercialization of bee products (González-Acereto et al., 2006).

Across the Americas, there are numerous examples of projects to promote stingless beekeeping and for the recovery of this 'threatened' activity (Ferrufino & Aguilera, 2006; González-Acereto et al., 2006; Meriggi et al., unpublished data, see supplementary material 1; Pérez & Salas, 2008;



**Fig 4.** An ancient cave image from the Serra da Capivara, Northeast Brazil, probably related to hunting stingless bee honey. Courtesy of Acervo da Fundação Museu do Homem Americano.

Rosso & Parra, 2008; Venturieri, 2008a, 2008b; Infante et al., unpublished data, see supplementary material 1; Estrada 2012; Gómez unpublished data, see supplementary material 1; Aguilar et al., 2013b; Herrera-González et al. unpublished data, see supplementary material 1; Villanueva-Gutiérrez et al., 2013; Arnold et al., 2018). Countries like Brazil are developing a vigorous following of meliponiculture, especially in the Northeast and North regions (Villas-Bôas, 2012; Jaffé et al., 2015). *Melipona scutellaris* Latreille, *M. quadrifasciata*, *Melipona rufiventris* Lepeletier, *Melipona subnitida* Ducke, *Melipona compressipes* (Fabricius), *T. angustula* and *Scaptotrigona* spp. are the most common bees maintained in Brazilian meliponaries (Rosso unpublished data, see supplementary material 1; Jaffé et al., 2015). In Rio Grande do Sul, an extensive work was done to improve meliponiculture techniques (Witter et al., unpublished data, see supplementary material 1) and *Melipona bicolor schencki* Gribodo, *Plebeia* spp., and *Scaptotrigona* spp. are important species for honey production and pollination. In el Gran Chaco, the honey extracted from stingless bee colonies often caused destruction of the colony and the tree sheltering it (Arenas, 2003; Meriggi et al., unpublished data, see supplementary material 1, Medrano & Rosso, 2010), but meliponiculture is now encouraged as a tool to preserve nature in the Argentinian part of this region. This was followed by the implementation of modern techniques to raise and manage stingless bees (Meriggi et al., unpublished data, see supplementary material 1). The government and nongovernmental organizations have promoted meliponiculture projects in different provinces (CEDIT, 2005; Baquero & Stamatti, 2007; Gennari unpublished data, see supplementary material 1).

Key elements for the recovery of stingless bees have been the development of a market for their products and “extension” courses and instruction. Many young people of surviving ethnic groups have lost the connection to their ancestors or even have no knowledge of the bees. Training offered to indigenous peoples can also make honey hunting sustainable by preventing colony destruction (González-Acereto, 2008; Perichon, 2013). Most importantly, a respect for the local habits and traditions is essential to preserve ancestral knowledge and management techniques that may help in preserve both stingless bees and beekeeping (Lyver et al., 2014; Jaffé et al., 2015; Quezada-Euán, 2018). There are many examples in which outsiders try to change traditional systems and take advantage of indigenous communities depriving them from their land and resources. There should be a way to regulate such interactions, protecting the latter (Rosso & Imperatriz-Fonseca, 2017).

The lesson to be learned is that the traditional knowledge and heritage can survive as long as they are linked to the economics and well-being of local people (González-Acereto et al., 2006; Villanueva-Gutiérrez et al., 2013; Hill et al., 2016), as they are the ones in direct interdependence with them. We suggest that it is essential, for the future

preservation of stingless bees and the cultural heritage that surrounds them, to consider the different aspects of indigenous local knowledge in the development of policies for conservation of the bees. They are needed in the global effort to support programs for the development of indigenous peoples. Traditional knowledge can strengthen the capacity of human societies to address disturbances and to maintain ecosystem services under conditions of uncertainty and change (Berkes & Turner, 2006; Gómez-Baggethun et al., 2013). There is hope that stingless bees can recover from an apparent imminent extinction and go on to become important agents for the conservation of the environment and human heritage.

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### Supplementary Material

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**Table 1.** Economic and cultural values associated with stingless bees by different ethnic groups of tropical America.

Scientific name	Local Name	Country	Indigenous groups	Product used	Value (E = Economic, C = Cultural)	Refs.
<i>Cephalotrigona capitata</i> (Smith) 	Ei tapexua	Brazil	Guarani M'Byá	Honey, cerumen	<b>C: Food</b> <b>C: Craft:</b> cerumen used for art crafts.	Rodrigues (unpublished data, supplementary material 1)
<i>Cephalotrigona zexmeniae</i> (Cockerell) 	Ta 'ah Cab Ehoal	Mexico	Maya	Honey, cerumen	<b>E: Food</b> <b>E: Craft</b> Making of figurines to magically protect crops.	González-Acereto (2008)
<i>Friesella schrottkyi</i> (Friese) 	Ei mirí 'i	Brazil	Guarani M'Byá	Honey, larvae, pollen,	<b>E: Food</b> – honey, pollen, larvae <b>C: Religious &amp; medicinal</b> honey is used in new-born children mouth as bactericide.	Rodrigues (unpublished data, supplementary material 1)
<i>Frieseomelitta</i> sp. 	Mykrwät	Brazil	Kayapó	Honey, pollen, brood	<b>E: Food</b> – honey, larvae, pupae and pollen	Posey (1983)
<i>Frieseomelitta nigra</i> (Cresson) 	Sak Xic	Mexico	Maya	Honey	<b>E: Medicinal</b> Diluted to treat pterygium. Mixed with resin of the same bee to treat wounds.	González-Acereto (2008)
<i>Frieseomelitta silvestrii</i> (Friese) 	Abeia-brancao-fundinho-branco	Brazil	Pankararé	larvae, pollen (food) cerumen,	<b>E: Food</b> – larvae and pollen <b>C: Medicinal</b> cerumen used to treat influenza.	Costa-Neto (1998)
<i>Frieseomelitta varia</i> (Lepelletier) 	Mehnodjanh	Brazil	Kayapó	Honey, cerumen,	<b>E: Food</b> – honey <b>C: Medicinal</b> cerumen has medicinal use Smoke from cerumen used for curing/healing.	Posey (1983)

**Table 1.** Economic and cultural values associated with stingless bees by different ethnic groups of tropical America. (Continuation)

<p><i>Geotrigona leucogastra</i> (Cockerell)</p> 	Abeja de la tierra	Ecuador	Kichwa community	Honey	<b>E: Food</b> – honey	Vit et al. (2017)
<p><i>Melipona</i> sp.</p> 	Bísara, Bichara, Bįjara	Colombia	Uwa	honey	<b>E: Food</b>	Falchetti and Nates Parra (2002)
	Ei ruyu or akā-moto	Brazil	Guarani M'Byá	Honey, cerumen	<b>E: Food</b> – honey; <b>C: Craft:</b> cerumen used for art crafts.	Rodrigues (unpublished data, supplementary material 1)
<p><i>Melipona beecheii</i> Bennett</p> 	Xunan Kab Kolel Kab Pool Kab Paisil Kab	Mexico (Yucatan Peninsula)	Maya	Honey	<p><b>E: Medicinal:</b> treat conjunctivitis Mixed with herbs and deer flesh for women fertility. Mixed in a drink with leaves of the tree <i>Guazuma ulmifolia</i> and applied on the abdomen of women during labor</p> <p><b>C: Religious:</b> beverage <i>Balché</i>. In ceremonies for good crops and rain (U Hanlil Kab)</p> <p><b>C: Mythology:</b> Vital fluid of the land.</p>	González-Acereto et al., (unpublished data, see supplementary material 1)
				cerumen	<b>E: craft:</b> Candle making in honor of the death.	Weaver and Weaver (1981) González (unpublished data, see supplementary material 1)
				The bees	<b>C: Mythological:</b> Gods: <i>Ah Mucen Cab</i> -The great divine bee. Bees related to the creation of the world (Chilam Balam)	De Jong (1999)
	Yum chab	Mexico (Tabasco)	Chontal	Honey	<b>E: Food</b>	González-Acereto (2008)
	Ajachab	Mexico (Chiapas)	Tzeltal and Zoque	Honey	<b>E: Food</b>	Vásquez-Dávila and Hipólito-Hernández (unpublished data, see supplementary material 1)
	oy měj tsin měj pa'ak tsin pa'ak	Mexico (Oaxaca)	Mixe	Honey	<b>E: Food and medicinal</b>	Vásquez-Dávila (unpublished data, see supplementary material 1)
	busdoo	Mexico (Oaxaca)	Zapoteco	Honey	<b>E: Food and medicinal</b>	Arnold et al. (2018)
	Criolla Colmena grande	Guatemala		Honey	<b>E: Food and medicinal:</b> Wounds, gastritis, post-partum.	Arnold et al. (2018)
Jicote gato	Costa Rica		Honey	<b>E: Food</b>	Enriquez et al. (unpublished data, see supplementary material 1)	
					Herrera-González et al. (unpublished data, see supplementary material 1)	

**Table 1.** Economic and cultural values associated with stingless bees by different ethnic groups of tropical America. (Continuation)

 <p><i>Melipona bicolor</i> Lepeletier</p>	Guaryuka	Brazil	Guarani M'Byá	Honey, propolis (batumen)	<p><b>E: Food</b> – Honey</p> <p><b>C: Medicinal:</b> Propolis (extracted from the batumen) used as infusion as contraceptive for men and woman.</p>	Rodrigues (unpublished data, supplementary material 1)
 <p><i>Melipona compressipes</i> (Fabricius)</p>	Ngày-re Tiubá	Brazil	Kayapó	Honey, cerumen	<p><b>E: Food</b> – honey;</p> <p><b>E: Craft &amp; Medicinal</b> cerumen has utilitarian and medicinal use</p> <p><b>C: Religious:</b> cerumen has ceremonial use</p>	Posey (1983) Kerr et al. (2001)
 <p><i>Melipona fasciata</i> Latreille</p>	Colmena real	Mexico	Tlapaneco	Honey	<b>E: Medicinal</b>	González-Acereto (2008)
	Tinzuca	Guatemala		Honey	<b>E: Food</b>	Enriquez et al. (unpublished data, see supplementary material 1)
 <p><i>Melipona fulva</i> Lepeletier</p>	To beroa	Colombia	Tatuyo	Honey, larvae  cerumen	<p><b>E: Food:</b> honey, larvae and for fishing bait</p> <p><b>E: Craft:</b> cerumen</p>	Estrada (2012) Rosso-Londoño (unpublished data, see supplementary material 1)
 <p><i>Melipona fuscopilosa</i> Moure &amp; Kerr</p>	Isabitto	Venezuela  Paria Grande (Estado Amazonas)	Uothuja (Piaroa)	Honey,  Pollen  cerumen,	<p><b>E: Food:</b> honey</p> <p><b>E: Medicinal :</b> <b>Honey :</b> Treatment of cataracts <b>Pollen:</b> Treatment of spots on the skin, facial cleaning</p> <p><b>E: Craft:</b> cerumen has utilitarian use <b>C:</b> cerumen has ceremonial use</p>	Vit et al. (2011)  Infante et al. (unpublished data, supplementary material 1)
 <p><i>Melipona grandis</i> Guérin</p>	bunga negra abeja de la tierra	Ecuador	Kichwa	honey	<b>E: Food</b>	Vit et al (2017)
 <p><i>Melipona mandacaia</i> Smith</p>	Mandassaia  Kagnàrà-krà-tik Kagnàrà-udja-ti Kagnàrà-ti	Brazil	Pankararé  Kayapó	Honey  Honey, larvae, pollen,  cerumen	<p><b>C. Religious &amp; Medicinal:</b> honey has medicinal use for snake bites.</p> <p><b>E: Food</b> – honey, larvae and pollen;</p> <p><b>E: Craft:</b> cerumen has utilitarian use;</p> <p><b>C: Religious &amp; Medicinal:</b> cerumen has ceremonial and medicinal use.</p>	Costa-Neto (1998)  Posey (1983)

**Table 1.** Economic and cultural values associated with stingless bees by different ethnic groups of tropical America. (Continuation)

<i>Melipona marginata</i> Lepeletier 	Mandori	Brazil	Guarani M'Byá	Honey, cerumen	<b>E: Food</b> – honey. <b>C: Craft:</b> cerumen used for art crafts.	Rodrigues (unpublished data, supplementary material 1)
<i>Melipona nebulosa</i> Camargo 	Niti dobea	Colombia	Bará	Honey, larvae  cerumen	<b>E: Food:</b> honey, larvae and for fishing bait  <b>E: Craft:</b> cerumen.	Estrada (2012)  Rosso-Londoño (unpublished data, see supplementary material 1)
<i>Melipona quadrifasciata</i> Lepeletier 	Ei raviju	Brazil	Guarani M'Byá	Honey,  cerumen	<b>E: Food</b> – Honey  <b>C: Religious;</b> cerumen has ceremonial and religious use <b>C: Craft:</b> cerumen used for art crafts.	Rodrigues (unpublished data, supplementary material 1)
<i>Melipona</i> cf. <i>rufescens</i> Friese <i>Melipona eburnea</i> Friese 	To dobea	Colombia	Bará	Honey, larvae  cerumen	<b>E: Food:</b> honey, larvae and for fishing bait  <b>E: Craft:</b> cerumen	Estrada (2012)  Rosso-Londoño (unpublished data, see supplementary material 1)
<i>Melipona rufiventris</i> Lepeletier 	Ngây-kumrenx	Brazil	Kayapó	Honey,  cerumen	<b>E: Food</b> – honey; <b>E: Craft &amp; Medicinal:</b> cerumen has utilitarian and medicinal use <b>C: Religious:</b> cerumen used for “me-kutom” (ceremonial use).	Posey (1983)
	Quigüeté	Bolivia	Yuquí,	Brood Cerumen ( <i>iriti</i> )	<b>E: Food:</b> immature <b>E: Craft:</b> Cerumen has utilitarian use: elaboration of arrows	Stearman et al. (2008)
	Ere reu	Bolivia	Tacana community	Honey	<b>E: Food:</b> Honey	Gomez et al. (2003) <a href="https://www.researchgate.net/profile/Robert_Wallace7/publication/269398245_Investigacion_colaborativa_un_pilar_para_la_conservacion_de_la_biodiversidad_a_nivel_del_paisaje_basada_en_comunidades_locales/links/54b680b80cf24eb34f6d267f/Investigacion-colaborativa-un-pilar-para-la-conservacion-de-la-biodiversidad-a-nivel-del-paisaje-basada-en-comunidades-">https://www.researchgate.net/profile/Robert_Wallace7/publication/269398245_Investigacion_colaborativa_un_pilar_para_la_conservacion_de_la_biodiversidad_a_nivel_del_paisaje_basada_en_comunidades_locales/links/54b680b80cf24eb34f6d267f/Investigacion-colaborativa-un-pilar-para-la-conservacion-de-la-biodiversidad-a-nivel-del-paisaje-basada-en-comunidades-</a>
<i>M. r. flavolineata</i> Friese	<i>Quigüeguá</i>	Bolivia	Yuqui	Brood Cerumen ( <i>iriti</i> )	<b>E: Food:</b> immature <b>E: Craft:</b> Cerumen has utilitarian use: elaboration of arrows	Stearman et al. (2008)

**Table 1.** Economic and cultural values associated with stingless bees by different ethnic groups of tropical America. (Continuation)

 <p><i>Melipona scutellaris</i> Latreille</p>	Uruçu	Brazil	Pankararé	Honey	<b>C: Medicinal:</b> snake bites, rabid dog bites, impotence.	Costa-Neto (1998)
 <p><i>Melipona seminigra</i> Friese</p>	Ngài-ny-tyk-ti	Brazil	Kayapó	Honey, cerumen	<b>E: Food</b> – honey; <b>E: Craft &amp; Medicinal:</b> cerumen has utilitarian and medicinal use <b>C: Ceremonial:</b> Bee parts used for hunting magic; <b>C: Ceremonial:</b> cerumen has ceremonial use.	Posey (1983)
 <p><i>Nannotrigona perilampoides</i> (Cresson)</p>	Trompetilla  bees beú	Mexico	Nahua  Zapoteco	Honey	<b>E: Food</b>	Padilla-Vargas et al. (unpublished data, see supplementary material 1)  Arnold et al. (2018)
 <p><i>Oxytrigona tataira</i> (Smith)</p>	Kagnàrà·krā-kamrek	Brazil	Kayapó	Honey, brood pollen,  cerumen,	<b>E: Food</b> – honey, larvae and pollen; <b>E: Craft:</b> cerumen has utilitarian use <b>C: Religious &amp; Medicinal:</b> cerumen has ceremonial use and medicinal use; <b>C: Cultural:</b> Cut entire tree to take kamrek honey.	Posey (1983)
 <p><i>Paratrigona</i> sp.</p>	Yvy ei	Brazil	Guarani M'Byá	Honey, brood	<b>E: Food</b> – honey and larvae	Rodrigues (unpublished data, supplementary material 1)
 <p><i>Partamona</i> sp.</p>	Ngày-càk-ñy Kukoire·ka	Brazil	Kayapó	Honey  Cerumen	<b>E: Food</b> – honey; <b>C: Cultural:</b> cerumen in magic to make enemy weak. Nests preserved in termite mounds.	Posey (1983)
 <p><i>Partamona bilineata</i> (Say)</p>	Cho'ch  Kuitanehtsin	Mexico	Maya  Nahua	Honey	<b>E: Medicinal</b> – mixed with the blood of the bird <i>Crotophaga sulcirostris</i> is used to treat diphtheria  <b>E: Food</b>	Quezada-Euán et al. (2001)  Padilla-Vargas et al. (unpublished data, see supplementary material 1)
 <p><i>Partamona cupira</i> (Smith)</p>	Cupira	Brazil	Pankararé	Honey	<b>E: Medicinal:</b> honey has medicinal used, for throat inflammation treatment.	Costa-Neto (1998)

**Table 1.** Economic and cultural values associated with stingless bees by different ethnic groups of tropical America. (Continuation)

<i>Plebeia</i> sp. 	Xalneksin  besinbea	Mexico	Nahua  Zapoteco	Honey	<b>E: Food</b>	Padilla-Vargas et al. (unpublished data, see supplementary material 1)  Arnold et al. (2018)
	Ei mir~i	Brazil	Guarani M'Byá	Honey	<b>E: Food</b> – honey; <b>E: Medicinal:</b> honey is used in new-born children mouth as bactericide	Rodrigues (unpublished data, supplementary material 1)
<i>Plebeia mosquito</i> (Smith) 	Mosquito-preto	Brazil	Pankararé	Honey	<b>E: Medicinal:</b> Honey has medicinal use, eaten and massaged for throat ache and oral mycosis.	Costa-Neto (1998)
<i>Ptilotrigona occidentalis</i> (Schulz) 	Canturrona Brea bees	Colombia	Afro descendant communities western Colombia	Resin called 'canturrón'	<b>E: Medicinal:</b> Minor wounds.  <b>C: Cultural:</b> Elaboration of the embil, name of the torches that the chocoan people used for lighting. Waterproofing boats	Galvis (1987) Nates-Parra (2005) Patiño (2005)
<i>Scaptotrigona hellwegeri</i> (Friese) 	Abeja Bermeja	Mexico	Pacific coast of Mexico	Honey	<b>E: Food</b>	González-Acereto (2008)
<i>Scaptotrigona mexicana</i> (Guérin) 	Pisil Nek mej Taxkat  Congo	Mexico	Nahua,  Totonaco	Honey  Propolis	<b>E: Food</b>  <b>E: Medicinal</b> Respiratory illnesses.	González-Acereto (2008)  Padilla-Vargas et al. (unpublished data, see supplementary material 1)
	Congo	Guatemala		Honey	<b>E: Food</b>	Enriquez et al. (unpublished data, supplementary material 1)
<i>Scaptotrigona pectoralis</i> (Dalla Torre) 	Kan ts'ak  Alazán	Mexico  Guatemala	Maya	Honey	<b>E: Food</b>	González-Acereto (2008)  Enriquez et al. (unpublished data, see supplementary material 1)
<i>Scaptotrigona polysticta</i> Moure 	suro, cuteri	Bolivia	Ayoreo	Honey Pollen (gebora) larvae  Cerumen	<b>E: Food:</b> Honey, pollen, larvae  <b>E: Craft:</b> cerumen has utilitarian use.	Stearman and Szabó (2005)  <a href="http://amazoniabolivia.com/amazonia_bo.php?id_contenido=304&amp;opcion=detalle_des">http://amazoniabolivia.com/amazonia_bo.php?id_contenido=304&amp;opcion=detalle_des</a>

**Table 1.** Economic and cultural values associated with stingless bees by different ethnic groups of tropical America. (Continuation)

<p><i>Scaura longula</i> (Lepeletier)</p> 	Mehnōā-tyk	Brazil	Kayapó	cerumen, resin	<p><b>E: Medicinal:</b> cerumen has medicinal use; <b>C: Cultural:</b> Resin used for jaguar hunting Magic</p>	Posey (1983)
<p><i>Tetragona</i> sp.</p> 	Kedari	Colombia	Nukak	Honey, larvae	<b>E: Food</b>	Cabrera and Nates-Parra (1999)
	O-i Ton-my Ri	Brazil	Kayapó	cerumen, resin	<p><b>E: Craft:</b> cerumen has utilitarian use <b>E: Medicinal:</b> cerumen has medicinal use; <b>C: Cultural:</b> Bee thought to be “stupid” and weak</p>	Posey (1983)
<p><i>Tetragona clavipes</i> (Fabricius)</p> 	ajavitte	Venezuela Paria Grande (Estado Amazonas)	Uothuja (Piaroa)	Honey	<b>E: Food:</b> honey	Vit et al. (2011)
	wáno	Venezuela Colombia	Yukpa-Yuko people	Honey, larvae cerumen	<p><b>E: Food:</b> honey and larvae <b>E: Craft:</b> cerumen has utilitarian use: waxing thread used to bind arrows <b>E: Economic:</b> bait by fishermen.</p>	Ruddle (1973)
	Ei pytā	Brazil	Guarani M’Byá	Honey, Cerumen, larvae (brood)	<p><b>E: Food</b> – honey <b>E: Medicinal:</b> larvae mixed with plant root used as fertility stimulant; Honey mixed with cerumen passed on children mouth (bactericide).</p>	Rodrigues (unpublished data, supplementary material 1)
<p><i>Tetragona goettei</i> (Friese)</p> 	Mehn-xi-we’i	Brazil	Kayapó	Honey, cerumen	<p><b>E: Food</b> <b>E: Craft:</b> cerumen has utilitarian use <b>C: Religious &amp; Medicinal:</b> cerumen has ceremonial and medicinal use.</p>	Posey (1983)
<p><i>Tetragona quadrangula</i> (Lepeletier)</p> 	Menire-udja Menire-udga	Brazil	Kayapó	Honey, cerumen	<p><b>E: Food</b> – honey <b>E: Craft:</b> cerumen has utilitarian use <b>E: Medicinal:</b> cerumen <b>C: Religious</b> cerumen has ceremonial and medicinal use.</p>	Posey (1983)

**Table 1.** Economic and cultural values associated with stingless bees by different ethnic groups of tropical America. (Continuation)

<i>Tetragonisca angustula</i> (Latreille) 	uux pa'ak	Mexico (Oaxaca, Chiapas)	Mixe, Zapoteco, Tzeltal,	Honey	<b>E: Food</b>	Arnold et al. (2018)
	Chumelo	Guatemala		Honey	<b>E: Food</b>  <b>E: Medicinal:</b> Cataracts	Enriquez et al. (unpublished data, see supplementary material 1)
	Angelita Wapasa yumiri	Colombia Ecuador, Alto Amazonas	Achuar	Honey Honey called "mishik" larvae	<b>E: Medicinal</b> Respiratory and ocular illnesses (conjunctivitis, pterygium) <b>E: Food:</b> Honey and larvae treat throat inflammation with pot-honey	Nates-Parra and Rosso-Londoño (2013) Descola, (1996) Guerrini et al. (2009)
	Señorita	Bolivia	Yuracaré Tacana community	Honey	<b>E: Food:</b> Honey <b>E: Medicinal:</b> Honey: Treatment of cataracts, gastritis, anemia.	Camacho, 2012. <a href="http://www.opinion.com.bo/opinion/articulos/2012/0413/noticias.php?id=51805">http://www.opinion.com.bo/opinion/articulos/2012/0413/noticias.php?id=51805</a> Gomez et al. 2003
	Señorita, Ajidabia	Bolivia	Ayoreo	Honey Pollen (gebora) larvae Cerumen	<b>E: Food:</b> Honey, pollen, larvae  <b>E: Craft:</b> cerumen has utilitarian use.	Stearman and Szabó (2005)  <a href="http://amazoniabolivia.com/amazonia_bo.php?id_contenido=304&amp;opcion=detalle_des">http://amazoniabolivia.com/amazonia_bo.php?id_contenido=304&amp;opcion=detalle_des</a>
	Jatei	Brazil	Guarani M'Byá	Honey, brood  cerumen, resin, pollen	<b>E: Food</b> – honey, brood <b>E: Medicinal:</b> Honey, resin, pollen and cerumen have medicinal use (flue, stomach diseases, rheumatism, parasitosis) <b>E: Craft:</b> cerumen used to make candles and art crafts <b>C: Religious:</b> Honey mixed with corn to prepare "tambojape", a special bread for the baptism ceremony	Rodrigues (unpublished data, supplementary material 1)
<i>Trigona</i> sp. 	Mumia	Colombia	Bará	Honey, larvae  cerumen	<b>E: Food:</b> honey, larvae and for fishing bait  <b>Craft:</b> cerumen.	Estrada (2012)
<i>Trigona</i> sp. 	Ngoi·tenk	Brazil		Resin	<b>E: Medicinal:</b> Resin is mixed with a leaf to treat rheumatism	Rodrigues (unpublished data, supplementary material 1)

**Table 1.** Economic and cultural values associated with stingless bees by different ethnic groups of tropical America. (Continuation)

	Ngoi-tenk	Brazil	Kayapó	Honey, cerumen	<b>E: Food</b> – honey <b>E: Craft:</b> cerumen utilitarian use <b>C: Religious &amp; Medicinal:</b> cerumen has ceremonial and medicinal use.	Posey (1983)
<i>Trigona amalthea</i> (Olivier) 	Udjy	Brazil	Kayapó	Resin; bees	<b>E: Craft:</b> resin used in artifacts <b>C: Cultural:</b> Bee parts mixed with urucu ( <i>Bixa orellana</i> ) for hunting magic.	Posey (1983)
<i>Trigona branneri</i> Cockerell 	Mehñiy-tyk	Brazil	Kayapó	Honey, cerumen	<b>E: Food</b> – honey <b>E: Craft:</b> cerumen has utilitarian use <b>E: Medicinal:</b> cerumen has medicinal use;	Posey (1983)
<i>Trigona chanchamayoensis</i> Schwarz 	Imre-ti-re	Brazil	Kayapó	Honey, pollen, brood	<b>E: Food</b> – honey, brood and pollen	Posey (1983)
<i>Trigona cilipes</i> (Fabricius) 	Mehnorā-kamrek	Brazil	Kayapó	Cerumen, resin	<b>E: Medicinal:</b> cerumen has medicinal use; <b>C: Cultural:</b> skinny eyes like jaguar	Posey (1983)
<i>Trigona corvina</i> Cockerell 	Wuti be´	Colombia	Nukak	Honey, larvae, cerumen	<b>E: Food:</b> honey and larvae for food. <b>E: Craft:</b> The cerumen is used in the manufacture of musical instruments, hammocks and blowpipe	Cabrera and Nates-Parra (1999)
<i>Trigona dallatorreana</i> Friese 	Tu	Colombia	Nukak	Honey	<b>E: Food</b>	Cabrera and Nates-Parra (1999)
	Kukraire	Brazil	Kayapó	Pollen	<b>E: Food</b> – pollen	Posey (1983)
<i>Trigona ferricauda</i> Cockerell 	Wuti butu	Colombia	Nukak	Honey, larvae	<b>E: Food</b>	Cabrera and Nates-Parra (1999)

**Table 1.** Economic and cultural values associated with stingless bees by different ethnic groups of tropical America. (Continuation)

<p><i>Trigona fulviventris</i> Guérin</p> 	Pyka-kam	Brazil	Kayapó	Honey, cerumen, resin	<p><b>E: Food</b> – honey</p> <p><b>E: Craft:</b> cerumen has utilitarian use</p> <p><b>C: Religious &amp; Medicinal:</b> cerumen in ceremonial and medicinal use.</p>	Posey (1983)
<p><i>Trigona fuscipennis</i> Friese</p> 	Djô	Brazil	Kayapó	Honey, cerumen	<p><b>E: Food</b> – honey</p> <p><b>E: Craft:</b> cerumen has utilitarian use</p> <p><b>C: Religious:</b> cerumen ceremonial use.</p>	Posey (1983)
<p><i>Trigona pallens</i> (Fabricius)</p> 	Myre	Brazil	Kayapó	Honey, cerumen	<p><b>E: Food</b> – Honey</p> <p><b>E: Craft:</b> cerumen has utilitarian use</p> <p><b>C: Religious &amp; Medicinal:</b> cerumen has ceremonial and medicinal use.</p>	Posey (1983)
<p><i>Trigona silvestriana</i> (Vachal)</p> 	Chiichiyá	Bolivia	Yuqui	Cerumen	<p><b>E: Craft:</b> Cerumen has utilitarian use: elaboration of arrows</p>	Stearman et al. (2008)
<p><i>Trigona spinipes</i> (Fabricius)</p> 	Mehñykamrek	Brazil	Kayapó	Honey, brood, pollen cerumen	<p><b>E: Food</b> – honey, brood and pollen</p> <p><b>E: Craft:</b> cerumen has utilitarian use</p> <p><b>C: Religious &amp; Medicinal:</b> cerumen has ceremonial and medicinal use;</p> <p><b>C: Cultural:</b> cerumen burned; smoke causes dizziness</p>	Posey (1983)
	Arapuá		Pankararé	Honey	<p><b>C: Religious &amp; Medicinal:</b> honey has medicinal use, eaten for diabetes treatment</p>	Costa-Neto (1998)
	Ei irapua		Guarani M'Byá	Honey, pollen,	<p><b>E: Food</b> – honey and pollen are eaten</p>	Rodrigues (unpublished data, supplementary material 1)
<p><i>Trigona trinidadensis</i> Vachal</p> 		Venezuela Colombia	Yukpa-Yuko people	Honey, larvae cerumen	<p><b>E: Food:</b> honey and larvae</p> <p><b>E: Craft:</b> cerumen has utilitarian use: waxing thread used to bind arrows</p> <p><b>E: Economic:</b> bait by fishermen.</p>	Ruddle (1973)
<p><i>Trigona williana</i> Friese</p> 	Kajawo dawa	Colombia	Nukak	Honey, larvae	<p><b>E: Food</b></p>	Cabrera and Nates-Parra (1999)