Bee Populations, Forest Disturbance, and Africanization in Mexico[1]

Christine E. Cairns[2,3,6], **Rogel Villanueva-Gutiérrez**[4], **Suzanne Koptur**[5], and **David B. Bray**[2]

[2]Environmental Studies Department, Florida International University, 11200 SW 8th St, Miami, Florida 33199, U.S.A.

[3]Air, Pesticides and Toxics Management Division, U.S. Environmental Protection Agency, 61 Forsyth St. SW, Atlanta, Georgia 30303, U.S.A.

[4]El Colegio de la Frontera Sur (ECOSUR), Av. Centenario km 5.5, Chetumal, Quintana Roo C. P. 77900, Mexico

[5]Department of Biological Sciences, Florida International University, 11200 SW 8th St. Miami, Florida 33199, U.S.A.

ABSTRACT

This study documents the stingless bees' (Meliponinae) recent displacement in the Yucatan (Quintana Roo, Mexico) and the effects of human-induced ecosystem disturbance on bee diversity. Point observations of flower-visiting bees were made along transects in three communities with different degrees of human-induced ecosystem disturbance. The community with the greatest anthropogenic disturbance had lower overall species richness of stingless bees and the highest degree of dominance of the Africanized honeybee (*Apis mellifera scutellata*), while the area with the most intact ecosystem had the highest diversity of stingless bees, though *A. mellifera* was still the dominant species. We observed aggressive competitive behavior involving physical attacks by *A. mellifera* against stingless bees, indicating that Africanized honeybees are adopting new behaviors to compete better with dominant native pollinator species.

RESUMEN

Este estudio, realizado en el estado de Quintana Roo, México, tuvo como objetivo determinar las causas del reciente desplazamiento de las abejas sin aguijón (*Meliponinae*) en la región del Yucatán y los efectos de la destrucción del ecosistema sobre la diversidad de las abejas. Los métodos de investigación incluyeron observaciones de polinizadores visitando plantas a lo largo de transectos en tres comunidades con diversos grados de alteración del ecosistema. La comunidad con el mayor grado de perturbación ecosistémica tuvo menos riqueza de especies de abejas sin aguijón y un alto grado de dominancia de la abeja africanizada (*Apis mellifera scutellata*), mientras que el sitio con el ecosistema mejor conservado tuvo la mayor diversidad de abejas sin aguijón, aunque *Apis mellifera* siguió siendo la especie dominante. En varias ocasiones se observó un comportamiento agresivo involucrando ataques físicos de *Apis mellifera* contra abejas sin aguijón el cual representa un nuevo patrón de comportamiento para las abejas *Apis*. Estas observaciones indican que las abejas africanizadas están adoptando nuevos comportamientos para competir mejor con las otras especies de polinizadores dominantes.

THE AFRICANIZED HONEYBEE (APIS MELLIFERA SCUTELLATA) is a tough competitor for floral resources, capable of out-competing many native species of Neotropical stingless bees (subfamily Meliponinae) for desirable floral resources (Roubik 1978). Stingless bees have demonstrated apparent foraging shifts in order to avoid competition with the Africanized honeybee (Roubik *et al.* 1986). It has not yet been demonstrated, however, that the presence of the Africanized honeybee has any population level effects on native bee species over time in an intact ecosystem (Roubik & Wolda 2001).

Anthropogenic habitat fragmentation through agriculture, logging, urban development, and cattle ranching has been correlated with changes in native pollinator densities in various regions of the world (Janzen 1974, Williams 1986, Jennersten 1988, Gess & Gess 1993, O'Toole 1993, Vinson *et al.* 1993, Aizen & Feinsinger 1994, Kearns & Inouye 1997). Kerr *et al.* (1999) cite five specific reasons for declines in stingless bee populations in Brazil: agricultural clearing, honey collection, inadequate protected areas, habitat destruction due to timber extraction in old growth habitat, and gen-

eral deforestation. Africanized honeybee invasion has been linked to human perturbation of ecosystems and to decreased bee diversity (Aizen & Feinsinger 1994).

The State of Quintana Roo, Mexico, on the Caribbean coast of the Yucatan peninsula, is a unique place to study the effects of Africanization and habitat disturbance on changes in native stingless bee diversity due to the ancient practice of honey harvesting from wild stingless bee colonies, and domestication of the native stingless bees by Mayan indigenous people of the region. When interviewing the local people it became apparent that a dramatic population decline in native bees, especially *Melipona beecheii*, had occurred over the last two decades. Local people reported that wild hives of *M. beecheii* (Mayan name: *xunan kab*) were once very abundant in the forest, but no longer. Mayan stingless beekeepers stated that honey production dropped in the last 20 yr, and many hives absconded or died as their bees struggled to collect enough resources to maintain the hive (Cairns *et al.* 2003).

Population decline of stingless bees such as *M. beecheii* may be due, in part, to human interference. Slash and burn agriculture is common in Quintana Roo, and stingless bees are susceptible to fire as their queens do not fly and cannot escape (Kerr *et al.* 1999).

The shifting agriculture (forest–fallow) landscapes may contain significant biodiversity, but are not suitable for *M. beecheii* (Finegan & Nasi 2004). This species prefers mature forest for nesting, and selects branches of mature trees with a minimum diameter of 25 cm. Selective timber harvest in Quintana Roo under a community forest management regime may deplete some of the best large-diameter nesting trees. Some of the tree species utilized by *M. beecheii* are commercially logged (Morales *et al.* 1991). Honey from wild colonies is often destructively harvested by felling nest trees. The landscape in central Quintana Roo is a human-dominated matrix of relatively intact forest, with localized areas of dynamic agriculture and commercial logging at relatively reduced levels since the mid-1980s (Bray *et al.* 2004).

Disturbance may explain why wild stingless bees are disappearing, but why have the domesticated stingless bees declined as well? Why have so many stingless beekeepers observed their domesticated hives struggling to collect resources and eventually dying during the past 20 years? The Africanized honeybee (AHB) is a fierce competitor, although there is lack of evidence to show that the AHB alone is responsible for population declines. Roubik and Wolda (2001) observed bee populations in Panama, over 17 years starting before the AHB invasion, and found no significant population effects on native bee species. Their study, however, was carried out in a nature preserve with relatively undisturbed forest. In Quintana Roo, local people reported dramatic decline in *M. beecheii* numbers after the invasion of the AHB in 1986. This was concurrent with the establishment of a community logging regime known as the Forest Pilot Plan, which zoned and preserved large blocks of forest under selective logging practices, and reduced logging levels from what they had been previously (Bray *et al.* 1993, Galletti 1998). The population decline of *M. beecheii* and other stingless bee species may, therefore, be due to a combination of factors: the stress of competition with the invasive, highly competitive AHB compounded by localized agricultural burning, timber harvesting in mature forest, and over-harvesting of honey by humans. In central Quintana Roo, where disturbance from various human activities has created a human-dominated forest matrix with patches of shifting agriculture landscapes, we expect native bee diversity to decrease with increased disturbance and Africanized honeybees to predominate in disturbed areas.

The objectives of this study were: (1) to quantify the diversity, abundance, and dominance of different bee species in three areas in central Quintana Roo, Mexico; (2) to compare actual abundance patterns among highly disturbed areas and less disturbed areas; and (3) to observe behavior patterns among bees visiting flowers to determine if direct competitive interaction was occurring between different species. Our goal was to understand bee community structure, to detect negative effects on bees most commonly exploited for honey, and to provide insight into management alternatives for the local people.

METHODS

STUDY AREA.—Three areas representing three levels of anthropogenic disturbance were chosen for the study: two traditional Mayan *ejidos* (collective land tenure systems in which the land is communally owned and managed), Kampocolche and Santa María, and the Sian Ka'an biosphere reserve. In Kampocolche (ejido territory of 5709 ha), medium stature subdeciduous forest is patch-worked with medium semievergreen forest, with a few small patches of seasonally flooded low forests (*bajos*; Miranda and Hernández 1963, Sánchez-Sánchez & Islebe 2002). Kampocolche is the most disturbed of the three study areas, having suffered a fire in the early 1960s and subsequently subjected to intensive shifting agricultural practices (Beck *et al.* 2003). Santa María (ejido territory of 9226 ha) is also a traditional Mayan farming community, 50 km south of Kampocolche. Santa María's forest is relatively intact, with medium stature semievergreen and subdeciduous patches, as well as some seasonally flooded *bajos* and grasslands or savannas (*pantanos)*. This forest has been only lightly logged since the mid-1980s; large tracts of mature forest exist, with shifting agriculture and secondary succession mainly in the central area (Beck *et al.* 2003). Santa María is therefore the "intermediate disturbance" site. The Sian Ka'an Biosphere Reserve, is a UNESCO-registered reserve of 528,000 ha extending along the eastern coast of the Yucatan, mostly composed of wetlands with some upland ecosystems. Sampling for this study was done in a small area of the northern portion of the Sian Ka'an, where the ecosystem most resembles that of the two other study communities, characterized by medium stature subdeciduous and semievergreen forest, with some patches of *bajos* as well as seasonally flooded *pantanos*. Human population is so low in this area that the forests are almost entirely intact. Although Quintana Roo forests are also periodically affected by hurricanes (Snook 1998), our study areas had not experienced hurricanes since the mid-1980s.

FIELD METHODS AND ANALYSIS.—Fieldwork took place February–May 2002, during the dry season and peak flowering season in Quintana Roo. In each of the three areas, nine transects were sampled, each *ca* 2 km long. Transect walks started around 0700, stopping around 1200, and sometimes continued again from 1600 until sunset. Along each transect, observations were made at designated flowering patches. Patches were not uniform in composition, but defined as points of interest for flower-visiting bees: a flowering tree, a flowering shrub, or a large cluster of flowering herbs. Initial 5-min observation periods were used to determine if patches were suitable for formal observations; if no visitors were observed, the patch was omitted. In suitable patches, a smaller observation area of approximately 30×30 cm^2 was designated, and all flower visitors to that area were recorded over a 20-min period. All transects yielded between 2 and 4 data gathering points, with the exception of four transects which yielded only a single point (two in the Sian Ka'an, one each in the other two communities) and one transect which yielded six (in the Sian Ka'an).

We visited each area within the same week in order to maximize similarities in species of plants flowering each time, although it was not possible to get identical species sets in all areas. Plants observed (Appendix) were species known (Souza Novelo 1981, Suarez Molina 1981, Porter 2001, and reports from local people) to attract stingless bees and *Apis* bees.

Plant voucher specimens were deposited in the ECOSUR herbarium (CIQRO) in Chetumal, Quintana Roo, Mexico, and

determined by Odilón Sanchez, botanist at El Colegio de la Frontera Sur (ECOSUR). Insect specimens were determined by David W. Roubik, entomologist at the Smithsonian Tropical Research Institute (STRI), and deposited in the museum at CIQRO. Some specimens of non-apid bees were identified to genus level only. Field determinations of stingless bees were made with reference to identified vouchers, but to avoid field identification errors, some morphologically similar bee species were grouped into single morphospecies groups: *Plebia* spp. (*P. minimia, P. frontalis*, and *P. jatiformis*) and *Trigona* spp. (*T. corvina* and *T. fuscipennis)*. All other bees had distinguishing characteristics that made accurate field identification possible.

Chi-square analysis was used to determine distributions in the abundance of three basic categories of bees in each of the three communities: *Apis* bees, Meliponinae bees, and all other bee species. An analysis of the diversity of all bee species was done for each of the three communities, and repeated for only stingless bees. Due to differing sample sizes, a rarefaction technique was applied using EcoSim (Gotelli & Entsminger 2001). Rarefaction allows estimation of the expected species richness for a sample size smaller than that actually obtained at a given site, permitting more accurate comparisons among sites by "rarefying" samples to the lowest sample size. Standardizing data sets by number of individuals collected is one way to compare assemblages using taxon sampling curves, and is appropriate for individual-based datasets such as ours (Gotelli & Colwell 2001).

RESULTS

Two-way contingency tables revealed significant differences among the study areas in distributions of three general categories of bees: *Apis* bees, Meliponinae bees, and other bees (Table 1; $P < 0.05$). Bonferroni post-hoc test showed significant differences among all three communities. Kampocolche, the most highly disturbed community, had the highest abundance of *A. mellifera* and the lowest abundance of other bees. Santa María, the moderately disturbed community, showed the highest proportion of Meliponinae and other bees, and the lowest level of *Apis* bees. The protected area of the

Sian Ka'an showed a slightly lower percentage of Meliponinae bees, but a more even distribution over all categories than Kampocolche. Bees were less abundant in the Sian Ka'an (only 75% of the total floral visitors in our samples, vs. 91% in both Kampocolche and Santa María). Despite equal sampling effort, only 177 individual bees were observed in the Sian Ka'an, versus 495 in Kampocolche and 413 in Santa María.

Two species of bees dominated all floral resources in Kampocolche and Santa María: *A. mellifera* and *T. fulviventris*. *T. fulviventris*, a native stingless bee, is not typically domesticated for honey. In Kampocolche, *A. mellifera* was the dominant species (39% of all bees observed), whereas *T. fulviventris* comprised 34 percent of the total bees (64% of all stingless bees). In Santa María, *T. fulviventris* was the dominant species (29% of all bees, and 55% of all stingless bees), and *A. mellifera* only 22 percent of the total. In the Sian Ka'an, *T. fulviventris* was almost absent, and *A. mellifera* was still dominant (31% of all bees). *M. beecheii* (1.7% of all bees) was only observed at flowers in the Sian Ka'an. We observed a greater diversity of pollinator types in the Sian Ka'an (Fig. 1), including Lepidoptera, Diptera and other Hymenoptera (wasps and ants). Richness and abundance curves for all bee species sampled show Santa María with a higher overall diversity and greater abundance than either Kampocolche or the Sian Ka'an (Fig. 2). Considering only stingless bees, the Sian Ka'an had greater diversity than either of the other two areas, even with a substantially lower number of bees sampled (Fig. 3).

Our observations revealed a new competitive behavior of the AHB. Eight aggressive interactions between *A. mellifera* and stingless bees were observed by CEC at flowers and water resources. The physical contact involved a brief but forceful high-speed tackle by the aggressor AHB. The attacked bee was displaced from the flower or water resource.
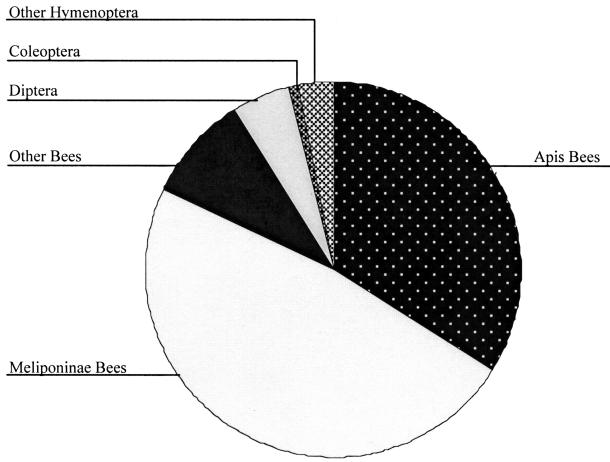
DISCUSSION

RICHNESS, ABUNDANCE, AND HABITAT DISTURBANCE.—Low richness measures for all bees in the Sian Ka'an and the distribution of pollinator types suggest that there were fewer bee species in the
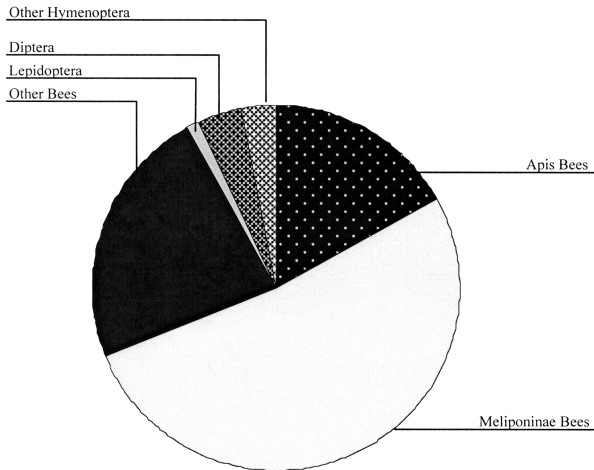
TABLE 1.   *Proportion of bees of three groups in three communities of Quintana Roo, Mexico.*

			Community			
			Kampocolche	Santa María	Sian Ka'an	Total
Bee Group	*Apis mellifera*	Count	192	90	55	337
		% within community	38.79	21.79	31.07	31.06
	Meliponinae	Count	262	215	89	566
		% within community	52.93	52.06	50.28	52.17
	Other bees	Count	41	108	33	182
		% within community	8.28	26.15	18.64	16.77
Total		Count	495	413	177	1085
		% within community	100.00	100.00	100.00	100.00

a. Kampocolche

Other Hymenoptera

Coleoptera

Diptera

Other Bees

Meliponinae Bees

Apis Bees

b. Sta. María

Other Hymenoptera

Diptera

Lepidoptera

Other Bees

Apis Bees

Meliponinae Bees

c. Sian Ka'an

Other Hymenoptera

Diptera
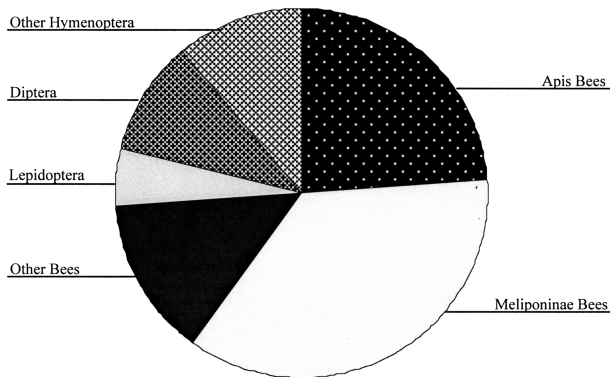
Lepidoptera

Other Bees

Apis Bees

Meliponinae Bees

FIGURE 1.   Relative abundance of insect pollinators observed at flowers at three sites in Quintana Roo, Mexico. Data are the percentage of individuals in all observations made at each site. The three sites are presented in the order from most disturbed (Kampocolche) to least disturbed (Si'an Ka'an).
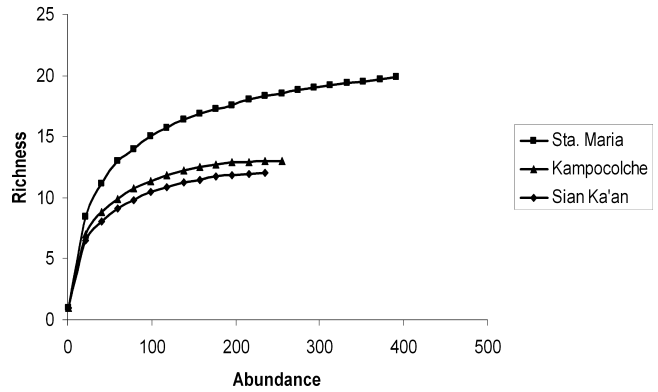
All Bees

FIGURE 2.   Rarefaction curves of species abundance (number of individuals) by richness in three communities, considering all bee species observed.

Sian Ka'an, with individuals more evenly distributed among those species. The bee fauna of the Sian Ka'an had lower density than the other two sampling areas. Other researchers have consistently found that the abundance of bees in the Sian Ka'an area is low. Many solitary bees are ground nesting, and much of the Sian Ka'an's soils are too poor and thin for ground-nesting species; therefore, the conditions in the Sian Ka'an favor tree nesting bee species, including most stingless bee species as well as *Apis* bees (David Roubik, pers. comm.).

Species distribution patterns indicated greater dominance by *A. mellifera* in Kampocolche, and this was where we observed the most competitive interactions at flowers. Santa María displayed the highest diversity and abundance of bees overall, with a greater presence of other bee families such as Anthophoridae and Halcitidae. The patchwork of landscapes in Santa María, including a mix of mature forest, lowlands, and various levels of secondary vegetation, may allow for a wider variety of foraging and nesting opportunities. *Apis mellifera* and *T. fulviventris* were the dominant species in Santa María, and stingless bee diversity and evenness was lower than in the protected area.

Though *A. mellifera* was dominant in the protected area where overall bee numbers are lowest, evenness and richness of stingless bee species were higher in this intact ecosystem than in the more disturbed sites. Despite observing fewer bees in the Sian Ka'an, we observed stingless bee species there that were not seen in either Santa María or Kampocolche, including *M. beecheii* and *Scaptotrigona pectoralis*. The higher abundance of stingless bees in the communities of Kampocolche and Santa María was largely due to the overwhelming presence of *T. fulviventris*, almost to the exclusion of other stingless bee species. *T. fulviventris* is a ground-nesting species, which could explain its enhanced presence in the logged (disturbed) communities.

COMPETITIVE INTERACTIONS.—While *A. mellifera* bees compete with other bees for shared resources, they were not known to show active aggression against other bees at flowers (Roubik 1978, 1980,
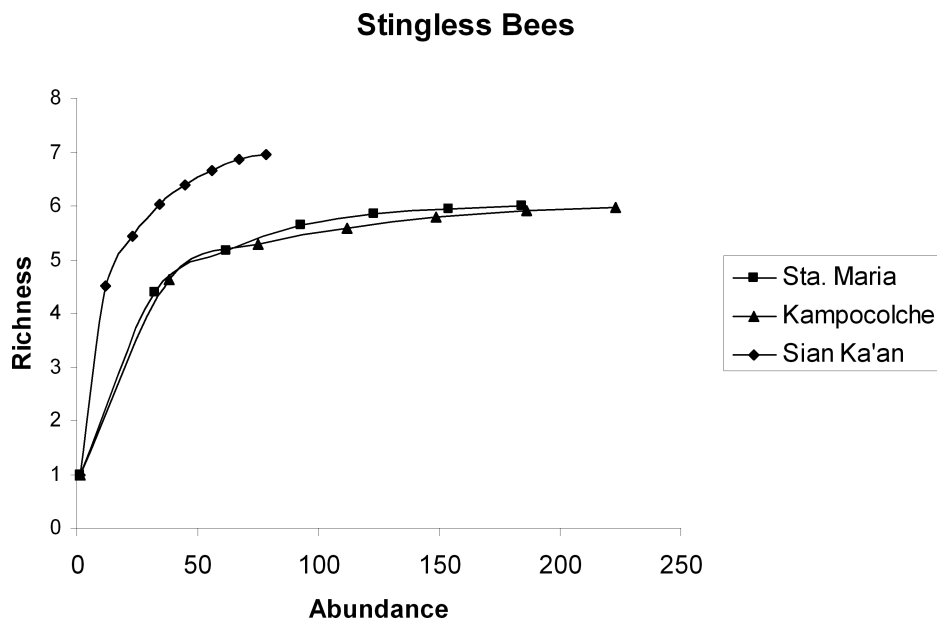
Stingless Bees

FIGURE 3.   Rarefaction curves of species abundance by richness in three communities, considering stingless bee species only.

1982, 1991; Menezes & Camargo 1991; Aizen &Feinsinger 1994, Villanueva-G. *et al.* 2003). We assumed that competition between *Apis* bees and other bees was strictly exploitation competition. Interference competition often involves physical interactions, and may evolve under conditions where exploitation competition becomes severe (Gotelli 2001). Our observations indicate that *Apis* bees changed their behavior to compete better with native, dominant species. In Panama (Roubik *et al.* 1986), there was a "general lack of competitive effect" due to resource shifting by stingless bees. Such resource shifting may not be possible in these forests of Quintana Roo, for local people have discovered that honey of the *Apis* bee is highly lucrative, and many people in this region are keeping domesticated AHBs, increasing their populations. A concomitant decrease in fallow periods of shifting agriculture systems over the last 20 years from an average of 16–25 to 5–10 yr (Villanueva Mukul 1997) also decreased floral resource availability.

AFRICANIZATION AND STINGLESS BEE DECLINE.—It appears that competition with the AHB is having a variable impact on native bee species, and that anthropogenic disturbances may be compounding the effect. In an environment where human activities create pressure on native species, the addition of a highly competitive new subspecies may have changed the dynamics of interactions in native bee communities. Native species less adept at interference competition (*e.g.*, *M. beecheii*) and not adapted to disturbed environments are becoming increasingly rare, while those that excel at interference competition and are better adapted to disturbed environments (some *Trigona* spp.) are persisting and perhaps increasing. In areas where ecosystems are still mostly intact, anthropogenic forest disturbance has not compounded the effects of Africanization; the distribution of stingless bee species is more even, with higher richness. Some stingless bee species, including *M. beecheii* and *Trigonisca*

buyssoni, now have population numbers so low they were barely detected by our sampling, and four other stingless bee species known to be present in the region were absent in our samples.

Our research documented a decline of stingless bees in this area of central Quintana Roo, particularly of the once-economically important *M. beecheii*. We suggest that both habitat change and increased competition with an invasive species may have contributed to this decline. Selective logging affects several important nesting tree species for stingless bees, and other changes in the vegetation mosaic may also have contributed to the decline of *M. beecheii*. We acknowledge that this study was limited in time and scope, and that further research is needed to determine the significance of the competitive interactions that we observed. The observations of our informants (Cairns *et al.* 2003) were substantiated by this ecological study: the *xunan kab* are now very difficult to find. The precise mechanisms that have led to this decline warrant further study.

ACKNOWLEDGMENTS

LITERATURE CITED

AIZEN, M. A., AND P. FEINSINGER. 1994. Habitat fragmentation, native insect pollinators, and feral honeybees in Argentine Chaco Serrano. Ecol Appl. 4: 378–392

BECK, C. T., E. A. ELLIS, AND C. CRUZ CÁCERES. 2003. Mapeo Participativo para el Manejo Forestal Comunitario y Planificación del Uso de Suelo y las Dinámicas de Cobertura del Suelo en dos Comunidades Maya en Quintana Roo, México. In D. B. Bray, N. A. Canto, V. S. Jiménez (Eds.). Investigaciones en Apoyo de una Economía de Conservación en la Zona Maya de Quintana Roo: Informes Sobre Proyectos de Investigación Colaborativa entre Instituciones Académicas en Mexico, los EEUU, y la Organización de Ejidos Productores Forestales de la Zona Maya (OEPFZM)/Unión Nacional de Organizaciones Regionales Campesinas Autónomas (UNORCA). OEPFZM/UNORCA, Felipe Carillo Puerto, Quintana Roo.

BRAY, D. B., M. CARREÓN, L. MERINO, AND V. SANTOS. 1993. On the road to sustainable forestry. Cultural Survival Q. 17: 38–41.

———, E. A. ELLIS, N. ARMIJO-CANTO, AND C. T. BECK. 2004. The institutional drivers of sustainable landscapes: A case study of the "Mayan Zone" in Quintana Roo, Mexico. Land Use Policy 21: 333–346.

CAIRNS, C. E., D. B. BRAY, AND R. VILLANUEVA-G. 2003. Las Fuerzas Impulsoras Detrás del Descenso de la Meliponicultura en el Estado de Quintana Roo. In D. B. Bray et al. (Eds.). Investigaciones en Apoyo de una Economía de Conservación en la Zona Maya de Quintana Roo. The Institute of Sustainability Science, Latin American and Caribbean Center, Florida International University, Miami, FL.

FINEGAN, B., AND R. NASI. 2004. The biodiversity and conservation potential of shifting cultivation landscapes. In G. Schroth, G. A. B. da Fonseca, C. A. Harvey, C. Gascon, H. L. Vasconcelos, A. N. Izac (Eds.). Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, Washington, D.C.

GALLETTI, H. A. 1998. The Maya forest of Quintana Roo: Thirteen years of conservation and community development. In R. B. Primack, D. Bray, H. A. Galletti, and I. Ponciano (Eds.). Timber, Tourists, and Temples: Conservation and Development in the Maya Forest of Belize, Guatemala, and Mexico, pp. 33–46. Island Press, Washington, D.C.

GESS, F. W., AND S. K. GESS. 1993. Effects of increasing land utilization on species representation and diversity of aculate wasps and bees in the semi-arid areas of Southern Africa. In J. LaSalle, and I. D. Gauld (Eds.). Hymenoptera and Biodiversity, pp. 83–114. C.A.B. International, Oxon, UK.

GOTELLI, N. J. 2001. A Primer of Ecology. Sinauer Associates, Inc., Sunderland, MA.

———, AND R. K. COLWELL. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecol. Letters 4: 379–391.

———, AND G. L. ENTSMINGER. 2001. EcoSim: Null Models Software for Ecology. Version 7.0. Acquired Intelligence Inc. & Kesey-Bear. http://homepages.together.net/~gentsmin/ecosim.htm.

JANZEN, D. H. 1974. The deflowering of Central America. Nat. Hist. 83: 49–53.

JENNERSTEN, O. 1988. Pollination in Dianthus deltoides (Caryophyllaceae): Effects of habitat fragmentation on visitation and seed set. Conserv. Biol. 2: 359–366

KEARNS, C. A., AND D. W. INOUYE. 1997. Pollinators, flowering plants, and conservation biology. BioScience 47(5): 297–307

KERR, W. E., G. A. CARVALHO, AND V. A. NASCIMENTO. 1999. The probable consequences of the destruction of Brazilian stingless bees. In C. Padoch, J. Márcio Ayres, M. Pinedo-Vaszuez, and A. Henderson (Eds.). Váreza: Diversity, Development and Conservation of Amazonia's Water Floodplains, pp. 395–403. New York Botanical Garden Press, NewYork.

MENEZES PEDRO, S. R., AND J. M. F. DE CAMARGO. 1991. Interactions on floral resources between the Africanized honey bee Apis mellifera L and the native bee community (Hymenoptera: Apoidea) in a natural "cerrado" ecosystem in southeast Brazil. Apidologie 22: 397–415

MIRANDA, F., AND X. HERNÁNDEZ 1963. Los tipos de vegetación de México y su clasificación. Boletín de la Sociedad Botánica de México 28: 29–179.

MORALES, S. M., E. C. LOPEZ, E. C. NANEZ, J. G. ACERETO, AND V. GONZALEZ C. 1991. Meliponicultura Maya: Perspectivas Para Su Sostentibilidad. Reportes de Sostentibilidad Maya No. 2, University of California, Riverside, California.

O'TOOLE, C. 1993. Diversity of native bees and agroecosystems. In J. LaSalle and I. D. Gauld (Eds.). Hymenoptera and Biodiversity, pp. 169–196. C.A.B. International, Oxon, UK.

PORTER, L. 2001. Landscape and ecology of apiculture in the Maya area of La Montana, Campeche, Mexico. Ph.D. Dissertation presented to the School of Forest Resources and Conservation, University of Florida, Gainesville.

ROUBIK, D. W. 1978. Competitive interactions between neotropical pollinators and Africanized honey bees. Science 201: 1030–1032.

———. 1980. Foraging behavior of competing Africanized honey bees and stingless bees. Ecology 61(4): 836–845.

———. 1982. Ecological impact of Africanized honeybees on native neotropical pollinators. In P. Jaisson (Ed.). Social Insects in the Tropics, pp. 233–247. Presses de L'Univeriste Paris XIII, Paris, France.

———. 1991. Aspects of Africanized honey bee ecology in tropical America. In M. Spivak, D. J. C. Fletcher, and M. D. Breed (Eds.). The African Honey Bee. Westview Press, Boulder, CO.

———, AND H. WOLDA. 2001. Do competing honey bees matter? Dynamics and abundance of native bees before and after honey bee invasion. Population Ecol. 43: 53–62

———, J. ENRIQUE MORENO, C. VERGARA, AND D. WITTMANN. 1986. Sporadic food competition with the African honey bee: Projected impact on neotropical social bees. J. of Trop. Ecol. 2: 97–111.

SÁNCHEZ-SÁNCHEZ, O., AND G. A. ISLEBE. 2002. Tropical forest communities in southeastern Mexico. Plant Ecol. 158: 183–200.

SNOOK, L. K. 1998. Sustaining harvests of mahogany (Swietenia macrophylla King) from Mexico's Yucatán forests: Past, present, and future. In R. B. Primack, D. Bray, H. A. Galletti, and I. Ponciano (Eds.). Timber, Tourists, and Temples: Conservation and Development in the Maya Forest of Belize, Guatemala, and Mexico. Island Press, Washington, D.C.

SOUZA NOVELO, N. 1981. Plantas Melíferas y Políniferas que Viven en Yucatán. In Fondo Editorial de Yucatán, Merida, Yucatán, Mexico.

SUAREZ MOLINA, V. M. 1981. Flora Melífera y Polinífera de la Península Yucateca o de Fácil Propagación en la Región. In Fondo Editorial de Yucatán, Merida, Yucatán, Mexico.

VILLANUEVA-G., R., D. W. ROUBIK, W. COLLI-UCÁN, AND S. FOSYTHE. 2003. La meliponicultura, una tradición maya que se pierde. Proceedings of

the III Mesoamerican seminar on stingless bees, Tapachula, Chiapas. ECOSUR and Universidad Autónoma de Chiapas, Mexico.

VILLANUEVA MUKUL, E. 1997. La Zona Milpera de Yucatan: Perspectivas para su desarrollo sustentable. *In* L. Pare and D. Bray *et al.* (Eds.). Semillas Para el Cambio en el Campo; Medio ambiente, Mercados y Organizacion Campesina. Universidad Nacional Autonoma de Mexico (UNAM)México cityMexico.

VINSON, S. B., G. W. FRANKIE, AND J. BARTHELL. 1993. Threats to the diversity of solitary bees in a neotropical dry forest in Central America. *In* J. LaSalle and I. D. Gauld (Eds.). Hymenoptera and Biodiversity, pp. 169–196. C.A.B. International, Oxon, UK.

WILLIAMS, P. H. 1986. Environmental change and the distributions of British bumble bees (*Bombus* Latr.). Bee World 67: 50–61.

APPENDIX. *Plant species and locations of sampling: Sian Ka'an Biosphere Reserve (SK), Santa María (SM) or Kampocolche (K).*

Species	Family	Location(s) sampled
Metopium brownei (Jacq.) Urb.	Anacardiaceae	SK, SM, K
Ehretia tinifolia L.	Boraginaceae	SM
Bursera simaruba (L.) Sarg.	Burseraceae	SK
Cecropia peltata	Cecropiaceae	SK
Cochlospermum vitifolium (Willd.) Spreng	Cochlospermaceae	SM, K
Bucida buceras L.	Combretaceae	SM
Cirsium mexicanum DC.	Compositae	SM
Eupatorium pycnocephalum Less.	Compositae	SM, K
Melanthera aspera (Jacq.) Small	Compositae	SM

APPENDIX.   *Continued.*

Species	Family	Location(s) sampled
Pluchea odorata (L.) Cass.	Compositae	SM
Ipomoea anisomeres B. L. Rob. & Bartlett.	Convolvulaceae	SM
Croton sp. 1	Euphorbiaceae	K
Croton sp. 2	Euphorbiaceae	K
Bauhinia divaricata L.	Fabaceae	SM
Caesalpinia gaumeri Greenm.	Fabaceae	K
Lonchocarpus hondurensis Benth.	Fabaceae	SM
Lysiloma latisiliquum (L.) Bentrh.	Fabaceae	SK
Piscidia piscipula (L.) Sarg.	Fabaceae	SK, K
Vigna elegans (Piper) Maréchal Mascherpa & Stainier	Fabaceae	SM
Byrsonimia bucidaefolia Standl.	Malpighiaceae	SK
Malpighia glabra	Malpighiaceae	SM, K
Gymnopodium floribundum Rolfe	Polygonaceae	SK, K
Talisia olivaeformis (Kunth) Radlk.	Sapindaceae	K
Pouteria reticulata (Engel) Eyma ssp. reticulata	Sapotaceae	K
Sideroxylon salicifolium (L.) Lam.	Sapotaceae	SK, K
Avicennia germinans (L.) L.	Verbenaceae	SK
Vitex gaumeri Greenm.	Verbenaceae	SK, SM
Vitis vitifolia	Vitaceae	K