

Invasive Africanized honey bee impact on native solitary bees: a pollen resource and trap nest analysis

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Little is known of the potential coevolution of flowers and bees in changing, biodiverse environments. Female solitary bees, megachilids and *Centris*, and their nest pollen provisions were monitored with trap nests over a 17-year period in a tropical Mexican biosphere reserve. Invasion by feral *Apis* (i.e. Africanized honey bees) occurred after the study began, and major droughts and hurricanes occurred throughout. Honey bee competition, and ostensibly pollination of native plants, caused changes in local pollination ecology. Shifts in floral hosts by native bees were common and driven by plant phylogenetics, whereby plants of the same families or higher taxa were substituted for those dominated by honey bees or lost as a result of natural processes. Two important plant families, Anacardiaceae and Euphorbiaceae, were lost to competing honey bees, but compensated for by greater use of Fabaceae, Rubiaceae, and Sapotaceae among native bees. Natural disasters made a large negative impact on native bee populations, but the sustained presence of Africanized honey bees did not. Over 171 plant species comprised the pollen diets of the honey bees, including those most important to *Centris* and megachilids (72 and 28 species, respectively). Honey bee pollination of *Pouteria* (Sapotaceae) plausibly augmented the native bees' primary pollen resource and prevented their decline. Invasive generalist pollinators may, however, cause specialized competitors to fail, especially in less biodiverse environments. No claim to original US government works. Journal compilation © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, 98, 152–160.

ADDITIONAL KEYWORDS: biodiversity – competition – mutualist networks – natural disturbance – phylogenetic community organization – pollination – tropical biosphere reserve.

INTRODUCTION

Students of evolutionary ecology often choose the interactions of flowers and bees as an intriguing theme. Those interactions, however, likely change over time, and mutualist roles are seldom clarified at the population level (Tepedino & Stanton, 1980; Roubik, 1989; Thompson, 2005; Cane & Sipes, 2006). Moreover, difficulty in documenting the enduring effects of non-native bees in natural communities emphasizes the need for adequate long-term monitoring studies, ideally both of plants and pollinators (Roubik, 1996a, b, 2001, 2009; Frankie *et al.*, 1998; Pyke, 2000; Roubik & Wolda, 2001; Goulson, 2003; Minckley *et al.*, 2003; Villanueva-Gutiérrez & Roubik, 2004). A single honey bee colony, and the hundreds of

honey bee colonies and millions of foragers having access to flowers in a natural setting, are ecologically formidable. Their foraging range of 8 km compromises the inductive value of small-scale field experiments. As a competitor or mutualist, Africanized *Apis mellifera* has little verified impact as an invasive, although a positive effect on coffee production in Central America was indicated (Roubik & Wolda, 2001; Roubik, 2002; Franco *et al.*, 2008). Africanized honey bees share floral resources with thousands of Neotropical pollinators and, 50 years after their colonization, any thematic ecological impact remained unknown (Roubik & Wolda, 2001; Villanueva-Gutiérrez & Roubik, 2004; Moure, Urban & Melo, 2007). Therefore, we designed experiments to study bee populations by documenting pollen resources and reproductive success. We used the pollen data from 'trap-nesting' (i.e. the field assay of solitary female

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bees using artificial nest tunnels; Frankie *et al.*, 1998; Tschardtke, Gathmann & Steffan-Dewenter, 1998; Roubik, 2001) to provide a detailed description of the impact of honey bees on native bees. We have documented honey bee resource use elsewhere (Villanueva-Gutiérrez & Roubik, 2004; Roubik, 2005; Villanueva-Gutiérrez *et al.*, 2009). In the present study, we quantify solitary tropical bee ecology and evaluate potential coevolution with the larger community of plants and competitors. We interpret the phenomenon of colonist pollinators and theorize that pollinator flexibility and plant species richness are mainstays of stable plant–pollinator assemblages.

MATERIAL AND METHODS

STUDY RATIONALE

The study was timed to include the initial colonization of a large lowland biosphere reserve by feral Africanized honey bees. In the almost two-decade duration of our study (1988–2005), additional environmental factors such as drought and hurricanes were also considered. The study was divided into ‘pre’ and ‘post-*Apis*’ periods. Immigrant Africanized honey bee swarms were first seen to arrive in 1989. Detection of the colonizing feral population in the larger Yucatan peninsula places its initial arrival 2 years earlier (Ratnieks, Piery & Cuadriello, 1991; Villanueva-Gutiérrez, 1999). Detailed population studies of the immigrant bees in Panama demonstrated an increase over several years (Roubik & Boreham, 1990). The present study establishes a baseline for monitoring mutualisms and perturbations. Which bee populations are present, how is their abundance related to significant ecological events, and which floral hosts do they utilize?

PHYSICAL SETTING

Sian Ka’an Biosphere Reserve comprised the core study area, centered at 19°34’ N, 088°W. Established in 1986, it is made up of 500 000 ha containing low-stature mature forest (20 m canopy) and some marshlands, surrounded by a Maya region buffer zone in Quintana Roo state, Yucatan peninsula, Mexico. The available flora in the region are well known (Duran & Olmsted, 1990).

BEE SAMPLING PROCEDURES

Four sites, each surrounded by protected forest with a narrow access road, were used for trap nest replicates. One additional site was added in the park buffer zone in 2001 and thereafter. A transect of 80 km was used to make trap nests available for female bees, from Palmas to Vigia Chico. Sampling

extended from February of 1988 until October of 1991, including the ‘pre-*Apis*’ period (with a few feral nesting colonies established) and resumed during January 2001 to October 2005, which comprised the ‘post-*Apis*’ or complete colonization period. Pollen studies of both Africanized and European *A. mellifera* were conducted at two of the trap nest sites during 1990–91 (Villanueva-Gutiérrez & Roubik, 2004). Additional pollen in honey was identified for Africanized honey bees from 78 sites in the Yucatan peninsula during the first half of 2000 (Villanueva-Gutiérrez *et al.*, 2009).

Every 2 months, a new set of nest blocks was placed at the sites, and the existing blocks were removed to outdoor rearing cages. Nest blocks made of local pine lumber (5 × 10 × 15 cm) were drilled with 12-cm tunnels of three diameters (3, 5, and 7 mm). Twenty blocks with a total of 300 tunnels were placed at a site. Groups of two blocks were tied with wire on low tree branches or shrubs within the forest. The capped tunnels potentially held developing brood and were fitted with plastic Eppendorf tubes, glued to the wooden block (Fig. 1). Emerging adults were identified using a reference collection (Roubik *et al.*, 1990) housed at ECOSUR and the Smithsonian Tropical Research Institute.

POLLEN

Pollen reference collections and field guides were developed to allow specific identification of pollen in bee nests, which constitutes ‘melittopalynology’, an application of palynology (Erdtman, 1943; Müller & Kuhlmann, 2008). Pollen processing and identification were conducted *sensu* Palacios, Ludlow-Wiechers & Villanueva-Gutiérrez (1991) and Roubik & Moreno (1991). Nest tunnel blocks were opened with a chisel and individual nest contents collected. All pollen samples were homogenized and acetolyzed, then slide mounted. We excluded pollen that might comprise nectar sources or include contaminants by only scoring major pollen types found in each nest tunnel. If < 50 grains were found, or < 20% total grains encountered of that species, then it was not registered as major nest pollen. Nest tunnels with abundant pollen usually yielded two slides, and a mean of 740 grains was identified for a nest. A total of 1620 slides with significant nest pollen were examined. We chose not to quantify the individual volumes of pollen species (Buchmann & O’Rourke, 1991) because they did not vary over a broad range. The present study aimed to associate major pollen resources with bee populations, thus absolute pollen volume, or dietetic value, were not primary considerations.

Dominant pollens were tallied for all bee nests of a given species for yearly sample characterization.

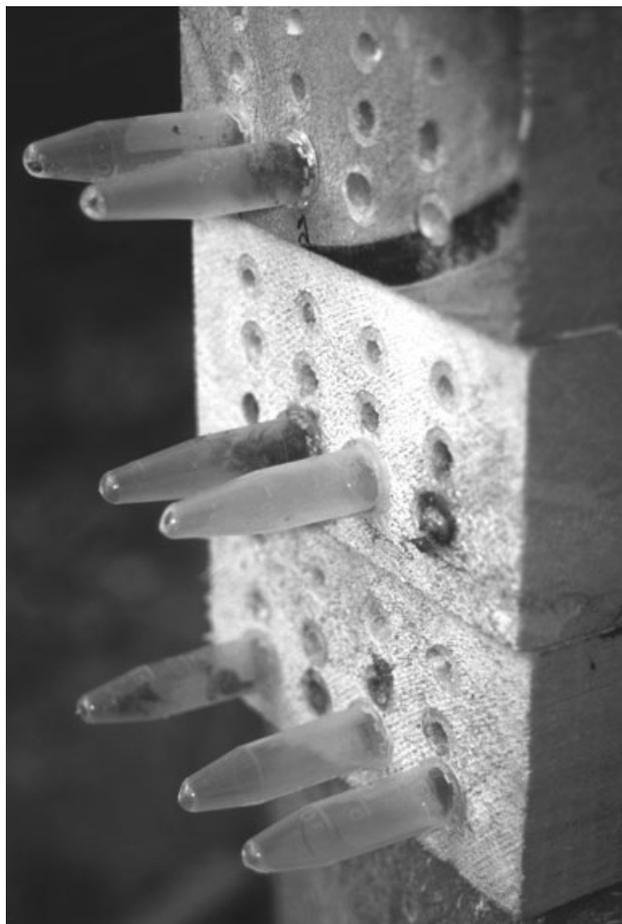


Figure 1. Trap nest blocks with tubes placed to capture emerging adults.

Pollen was identified at least to family and morphospecies. Statistical analysis used ESTIMATES (R. K. Colwell; <http://purl.oclc.org/estimates>) to calculate pollen diversity for megachilids and *Centris analis* for each calendar year. For the most abundant bees, *Centris*, similarities in dominant nest pollens were compared between all years using the Morisita–Horn (M–H) Index, and compared variation within pre- and post-*Apis* periods (one-tailed *t*-test).

RESULTS

POPULATION DYNAMICS

Trap-nesting *Megachile zaptlana* Cresson (Megachilidae) and *C. analis* (Fabricius) (Apidae) were by far the most abundant bees. The former was analysed with other megachilids because this family proved uncommon compared to *C. analis*. In pre- or post-*Apis* periods, trap-nesting megachilids included *Megachile*, *Heriades*, *Anthidiellum*, and *Anthodioctes*. Pollen utilization and annual nesting success (Figs 2, 3, 4, Table 1) varied, but the native bees peaked in 2001–

post-*Apis*. *Centris* displayed greater abundance throughout that period, compared to the first 4 years of the study. The mean abundance of combined solitary bee nests at the study sites did not diminish during the four pre-*Apis* and the five post-*Apis* years (one-tailed paired *t*-test, $P = 0.09$). On the other hand, no megachilids nested in the blocks in 1991 or 2002, and *Anthodioctes* did not appear after 1989.

A low abundance of solitary bee nests occurred in 1988 and 2005, two of the three hurricane years (Gilbert in 1988, Isidore in 2002, and Emily then Wilma in 2005; Fig. 2), whereas 1991 had the lowest rainfall and the lowest nest abundance. Another dry year, 1989, with less than the 50-year mean rainfall of 1259 mm, had low bee nest abundance (Fig. 2).

POLLEN SPECIES UTILIZATION

Pollen was scored in 350 *Centris* and 53 megachilid nests. *Centris* used 24 to 19 and megachilids 11 to 12 plant families, respectively, in pre- and post-*Apis* periods. There are 25 plant families and 859 vascular plants documented in Sian Ka'an (Duran & Olmsted, 1990; Villanueva-Gutiérrez & Cabrera, 1990). A grand total of 136 pollen species was used by the solitary bees. Major pollen genera totaled six for *Centris* and five for megachilids, constituting approximately 70% of the pollen brought to nests. The plant families were utilized with different intensities in the pre- and post-*Apis* periods (Table 1). In addition, major individual nest pollen was primarily of one or two species (Table 2). A total of 87% and then 79% of *Centris* females used one or two major pollen species during pre-*Apis*, and post-*Apis* periods, respectively (72 species, total). The megachilid females used primarily one species in both periods (28 species in total), first in 41% and then in 66% of nests (Table 2).

The lowest diversity in pollen for both *Centris* and megachilids occurred in 1989 and 1991, during droughts, and the earliest time at which feral *A. mellifera* was present, and also in 2005, which had two hurricanes. The summed richness in major pollen resources for the two native bees was related to the numbers of nests examined (Fig. 2), which suggests the bees were generalists in pollen choice. The Simpson index showed that diversity declined in the nest pollen of *C. analis* from the pre-*Apis* period (range 3.87–17.23, mean 10.5) compared to the post-*Apis* period (range 4.38–7.53, mean 5.5). Chao indices did not indicate such a decline in estimated total major pollens (Fig. 2).

Considering important pollen in a small number of nests (Fig. 3), a few genera disappeared or first appeared in particular years. Pollen use may be viewed during contrasting periods of bee abundance (Fig. 2), the hurricane years (1988, 2002, 2005) versus

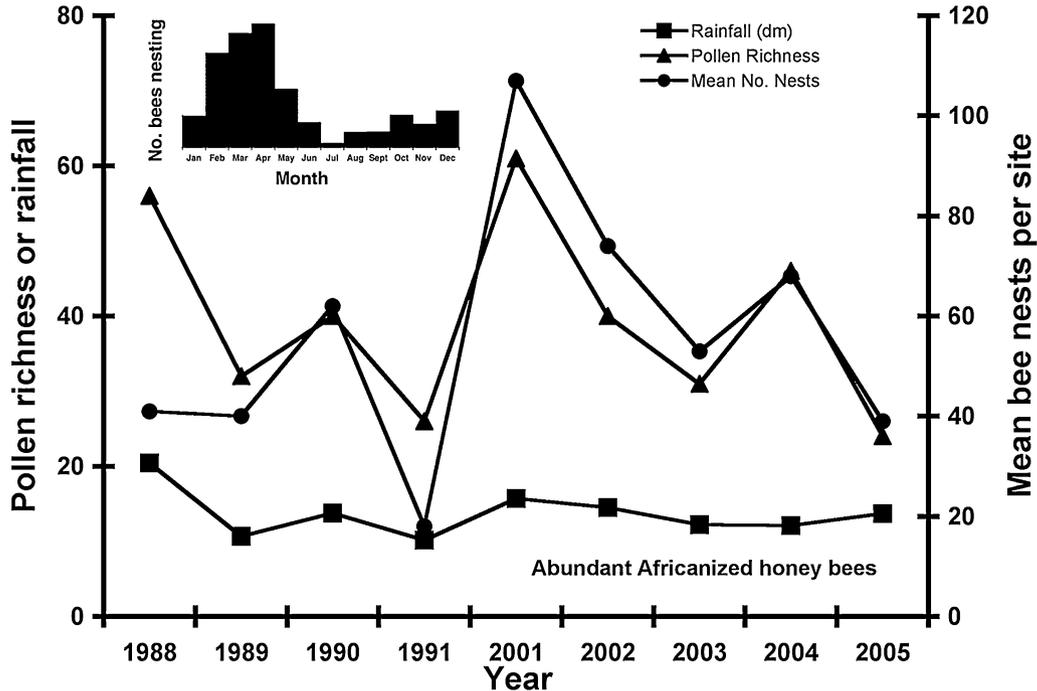


Figure 2. Mean solitary bee nests per site (combined nest blocks) over 9 years in the Sian Ka'an biosphere reserve and buffer zone. Pollen species richness is the sum of estimated pollen species number in megachilid and *Centris* nests (see Material and methods). Hurricanes occurred between August and October in 1988, 2002, and 2005. Inset: recorded monthly colonization of trap nests (3-month running means). Meteorological data are from Comisión Nacional del Agua, gerencia estatal, Quintana Roo.

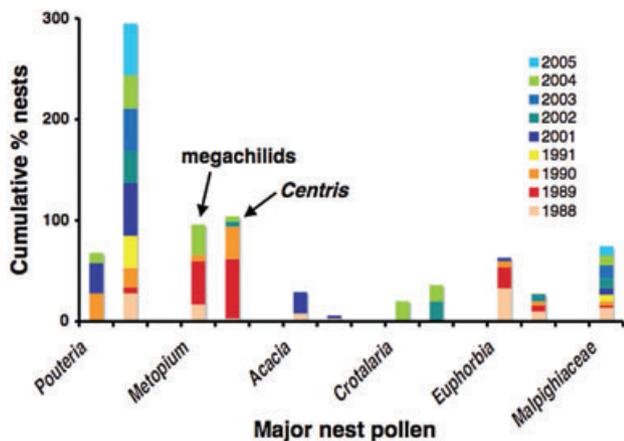


Figure 3. Yearly major pollen of megachilids and *Centris*. Malpighiaceae combines three genera and only was utilized by *Centris*.

2001 (high nest abundance), and 2001 compared to all other years. Irrespective of pollen dominance, only one genus common in nests of *Centris* in 2001 (*Cordia*) was not found in other years, and two genera were relatively frequent in megachilid nests only in that year (*Merremia*, *Peperomia*). Both megachilids

and *Centris* lost the major resource of *Metopium* almost completely subsequent to 1990 (Fig. 3). Megachilids lost *Euphorbia* in 2004, and *Centris* used *Euphorbia* (four to six nests) only in 1988 and 2002. *Pouteria* was used heavily from 2001 to 2005 by the solitary bees. Rubiaceae (unidentified genera) were intensively used by *Megachile* in 2001, as was *Acacia* in 1988 and 2001. Simpson diversity registered high values for *Centris* in a drought year (1991) and a hurricane year (1988), which is also the year of highest megachilid pollen diversity (Fig. 2).

Year to year variation was large for major pollen species utilized by *Centris* populations. From one to nine dominant pollen species were shared between years. The mean M–H similarity index for all pairs of years ($N = 35$) was 0.485. Among years exclusively in pre- or post-*Apis* periods, however, the mean was higher (0.572) than that for all other comparisons (between years of the two periods, mean M–H index = 0.411, $P = 0.019$, t -test). This test illuminates the basic differences among groups of 'Apis' years in pollen use by a native bee. During the post-*Apis* period, native bees greatly reduced visits to flowering Euphorbiaceae and Anacardiaceae (Figs 3, 4) and increasingly used Malpighiaceae, Fabaceae, Rubiaceae or Sapotaceae (Fig. 3, Table 1).

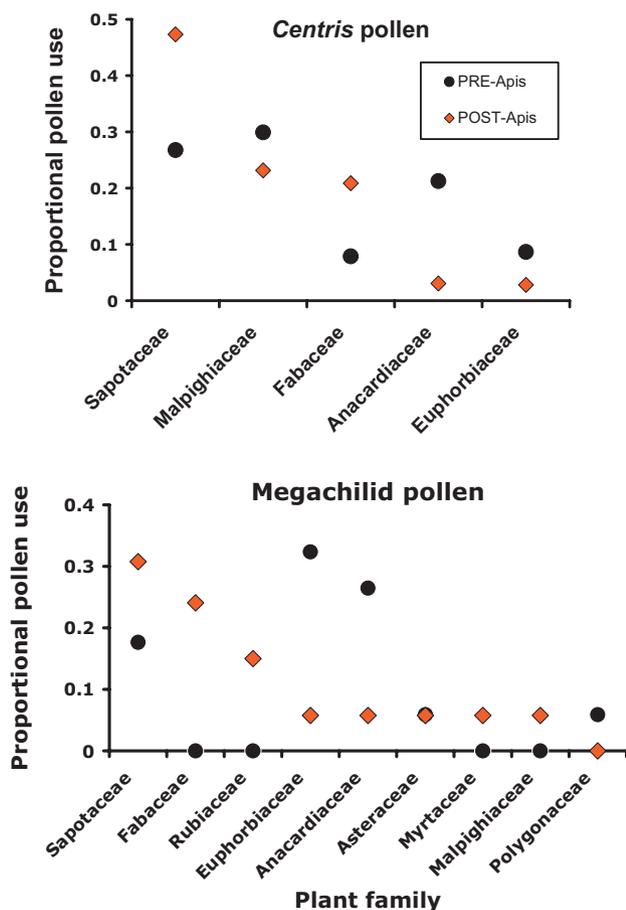


Figure 4. Dominant pollen taxa in nests of solitary bees, ranked by utilization after honey bee invasion. Sample sizes were 350 *Centris* and 53 megachilid nests.

Pollen selection at the plant family level remained steady over the pre- and post-*Apis* intervals for megachilids (one-tailed paired *t*-test, $P = 0.43$) but not for *Centris* (paired *t*-test, $P = 0.05$). Both bees initially utilized 17–18% of local taxa in their preferred families, but *Centris* had a mean of 26% utilization in the post-*Apis* period, reflecting a more complete use of legumes in particular, a large taxonomic group in Sian Ka'an (Duran & Olmsted, 1990), and more species of Malpighiaceae were utilized.

DISCUSSION

The present study indicates broad and complementary changes in both the plant and the bee community, which are attributable to invasive honey bees. An analysis of pollinator populations might be couched in the rubric of pollen hosts and evolved floral preferences (Proctor, Yeo & Lack, 1996; Cane & Sipes, 2006; Minckley & Roulston, 2006), and it may appear contradictory that apparently significant com-

petition with an invasive bee led to no general population decline. We hypothesize that: (1) native bees can adjust behaviorally or physiologically (Müller & Kuhlmann, 2008) and alter their choice of flowers and (2) honey bees, as pollinators, augment the local bee resource base. A generalist bee should tend to use resources in the proportion that they are encountered. Although we did not document plant abundance in the Sian Ka'an area, we believe that the native bees provided comparable information. Moreover, those native bee populations did not decline, although some megachilids, previously scarce, were not found in the later years of the survey. The data obtained in the present study cannot discriminate the cause of possible decline among the rare trap-nesting bees. The abundance of the colonizing Africanized honey bee may itself decline after several years (Roubik & Boreham, 1990) but, during the later part of the study, there was certainly an established feral population, which was absent in the pre-*Apis* period. Bee populations, including *C. analis*, fluctuate considerably in abundance (Roubik, 2001). Furthermore, three long-term Neotropical forest studies suggest that food is not the limiting factor (Andrewartha & Birch, 1954; Roubik, 2009) for a variety of social and solitary bees. We found that drought and heavy rain or hurricane damage can have severe effects on bee populations, even when artificial nest sites are available, although we are unable to determine precisely how long the effects last.

Pollen previously important in the reproduction of native bees was consumed by honey bees. At least 171 plant species were used by Africanized *A. mellifera* (Villanueva-Gutiérrez & Roubik, 2004), and 250 pollen species were found in honey sampled throughout the Yucatan peninsula in the major honey production season, during the first 6 months of 2000 (Villanueva-Gutiérrez *et al.*, 2009). That figure is in agreement with the general estimate of 25% of the local flora suggested for honey bee resource exploitation in wildlands (Roubik, 1989), and the honey study coincided with the nesting activity of solitary bees (Fig. 2, inset). Tropical bees in more rainy forest also experience nesting peaks during the major flowering season in the dry or dry to wet season transition (Roubik, 1989; Thiele, 2005).

Apis may have forced competitors to switch some of their food plants, and virtual abandonment of two major pollen families by native bees was not the result of abiotic factors such as weather or hurricanes. No consistent rainfall or temperature changes that we are aware of occurred in the study biosphere reserve. The forest trees were not expected to cease flowering, nor was plant succession likely to offer new resource species. The native bees did not select novel pollen in hurricane or drought years (Fig. 3). By con-

Table 1. All families and genera of major nest pollen, and proportional use of local plant taxa at the family level, by solitary bees in a Yucatan Biosphere Reserve, including potentially 859 species in 25 families*

<i>Centris</i> pollen use (major taxa) 1988–91	Percent family*		<i>Centris</i> pollen use (major taxa) 2001–05
	Pre- <i>Apis</i>	Post- <i>Apis</i>	
Malpighiaceae: <i>Bunchosia</i> , <i>Heteropterys</i> <i>Hiraea</i> , <i>Malpighia</i>	29	57	Malpighiaceae: <i>Bunchosia</i> , <i>Byrsonima</i> , <i>Heteropterys</i> , <i>Hiraea</i> , <i>Malpighia</i>
Sapotaceae: <i>Pouteria</i> , <i>Chrysophyllum</i>	36	36	Sapotaceae: <i>Pouteria</i> , <i>Bumelia</i>
Anacardiaceae: <i>Metopium</i>	25	25	Anacardiaceae: <i>Metopium</i>
Fabaceae: <i>Acacia</i> , <i>Caesalpinia</i> , <i>Diphysa</i> , <i>Lonchocarpus</i>	5	13	Fabaceae: <i>Acacia</i> , <i>Bauhinia</i> , <i>Caesalpinia</i> , <i>Crotalaria</i> , <i>Diphysa</i> , <i>Lonchocarpus</i> , <i>Piscidia</i> , <i>Senna</i>
Euphorbiaceae: <i>Chamaesyce</i> , <i>Euphorbia</i> (Totals: 22 families, 56 genera, from 79 nests)	6	9	Euphorbiaceae: <i>Euphorbia</i> (Totals: 19 families, 56 genera, from 271 nests) (lost Bombacaceae, Combretaceae, Flacourtiaceae, Malvaceae, Moraceae, Rubiaceae, Turneraceae)
Megachilid pollen use (major taxa) 1988–91			Megachilid pollen use (major taxa) 2001–05
Asteraceae: <i>Eupatorium</i> , <i>Viguiera</i>	6	6	Asteraceae: <i>Viguiera</i>
Sapotaceae: <i>Pouteria</i>	9	9	Sapotaceae: <i>Pouteria</i>
Anacardiaceae: <i>Metopium</i>	25	25	Anacardiaceae: <i>Metopium</i>
Fabaceae: <i>Acacia</i> , <i>Caesalpinia</i>	11	9	Fabaceae: <i>Acacia</i> , <i>Piscidia</i>
Euphorbiaceae: <i>Euphorbia</i>	6	6	Euphorbiaceae: <i>Euphorbia</i>
(Totals: 12 families, 18 genera, from 21 nests)	7	14	Rubiaceae: unidentified (<i>N</i> = 2) (Totals: 15 families, 30 genera, from 32 nests)

*Duran & Olmsted (1990), Villanueva-Gutiérrez & Cabrera (1990); pollen genera were recorded once or more for megachilids, twice or more for *Centris*.

Table 2. Solitary bee nest pollen (major species only, see Methods) during 1988–91 (pre-*Apis*) and 2001–05 (post-*Apis*) in the Sian Ka'an Biosphere Reserve, Yucatan, Mexico

Study period	Number of major pollen species and solitary bee					
	<i>Centris</i> (% nests)			Megachilids (% nests)		
	1	2	≥ 3	1	2	≥ 3
Pre- <i>Apis</i>	51	36	13	45	40	15
Post- <i>Apis</i>	34	43	23	66	20	14

Sample sizes: 350 *Centris* and 53 megachilid nests.

trast, they switched to plant taxa of the same families or orders (Jensen *et al.*, 2007) within their major reproductive peaks (always the dry season, from December to June), when Africanized honey bees competed for flowers. Those responses suggest that bees avoid resource competition with honey bees. Trees, shrubs, and vines comprised almost all major pollen genera used by the native bees, implying that these are forest bees and are not primarily adapted to disturbed or open habitats. However, the use of *Cecropia* as the major pollen source, linked to hurricane damage, and the frequent use of grasses and sedges,

is evident for Africanized *A. mellifera* (Whigham *et al.*, 1991; Villanueva-Gutiérrez & Roubik, 2004; Roubik, 2009).

All bee genera (*Megachile*, *Centris*, *Apis*) preferred the pollen of Anacardiaceae (*Metopium browneii*), and Sapotaceae (*Pouteria*) (Villanueva-Gutiérrez, 1999; Villanueva-Gutiérrez & Roubik, 2004) in the Sian Ka'an biosphere. Euphorbiaceae included nine species in Sian Ka'an, which were used by honey bees from November until July (Villanueva-Gutiérrez, 1999). In this family, *Croton* was a prominent diet item of the honey bees in both the dry and early wet seasons, but

not of considerable annual importance (Villanueva-Gutiérrez & Roubik, 2004). Anacardiaceae is among the principal pollen resources used by Africanized honey bees in lowland Panama (Roubik, 1988) as well as in the Sian Ka'an area. Only one pollen species recorded for solitary bees (Turneraceae) was not used by *Apis* (Villanueva-Gutiérrez, 1994, 1999). Competition for food was therefore common, but its result, judging by the persistence and abundance at least of *C. analis*, provides evidence of a dynamic balance in resource exploitation, pollination, and populations.

The resilience of bees that experience periodic disasters such as hurricanes (Cane, 1997) or droughts, which may also coincide with heavy community-wide flowering (Appanah, 1993), signifies that some bees and their major resources are adapted to fluctuating environments. Bees that use artificial trap nests may be among the more adaptable or flexibly foraging species (Tylianakis, Klein & Tscharnkte, 2005), and those investigated in the present study have wide geographic distribution (Moure *et al.*, 2007). Solitary tropical bees are not well known. Only pollen specialists have been studied in some depth, which nonetheless use several plants, with high concentrations of single species (Bullock *et al.*, 1991; Martins & Borges, 1999). This does not differ greatly from the generalist bees examined here, and repeated sampling demonstrated that preliminary nest data yielding one or two major resource genera was misleading. Enquiry into coevolutionary relationships between bees and flowering plants would clearly benefit from both geographic and basic pollen host information (Thompson, 2005).

Because the bees were relatively specialized on Sapotaceae (genus *Pouteria*) and were the same size, and because *A. mellifera* is likely several orders of magnitude more abundant than the two solitary bees (Roubik, 1989; Ratnieks *et al.*, 1991), the invasive bee has probably enhanced reproduction of this essential pollen source. *Pouteria* require 3–8 years to produce fruit, after establishment as seedlings (International Centre for Underutilised Crops, 2004). The hermaphrodite flowers have no specialized pollination mechanisms, and their increasing use by *Megachile*, *Centris*, and *Apis* likely augmented pollination. The abundance of *Pouteria* may have increased beginning in the 1990s. The invasive bee is part of a competing pollinator assemblage; thus, the increased use of *Pouteria* by native bees may be due to an even more considerable increase in this resource.

Peaks in yearly flowering tend to differ among woody plant families and genera (Appanah, 1993; Wright & Calderón, 1995) but, at the same time, they also guide bee selection among alternate resources, when they share a given floral season. The conservative manner whereby native bees altered their

foraging ecology derives from plant and possibly coevolutionary bee phylogenetics (Jensen *et al.*, 2007; Wang *et al.*, 2009). The rosid orders Fabales and Malpighiales were noteworthy pollen sources, but megachilids 'crossed over' to use an asterid to replace a major rosid resource after honey bees were their competitors. *Centris analis* obligately uses floral oils of Malpighiaceae to mix with its pollen brood provisions; elsewhere in Mexico, it utilizes different asterids (Asteraceae, Solanaceae) but no Sapotaceae, and *Megachile* often uses Asteraceae and Fabaceae in the Neotropics (Quiroz *et al.*, 2001; Cane & Sipes, 2006; Raw, 2007). The impact that feral *Apis*, habitat alteration, and beekeeping already may have had on such comparative data is unknown.

Solitary bees (i.e. nesting females with no colony or honey) constitute a majority of pollinators, yet no previous work links their flower visitation or 'preference' to population change (Roubik, 1989; Michener, 2007). Bees are the product of previous resource supplies, and flowers are the product of current energy input (Tepedino & Stanton, 1980; Minckley *et al.*, 2003; Wright & Calderón, 2006), thus several years may be required to define particular relationships between pollinators and host flowers. However, theory has never adequately addressed such variation, details on pollen use and pollination are limited, and the lack of competitive impact by an invasive bee at population levels appeared to have no convincing explanation (Roubik, 1996a; Roubik & Wolda, 2001; Goulson, 2003; Paine, 2004; Bascompte & Jordano, 2007). The result obtained in the present study helps to address the last point. Bees may change floral choice to maintain their mutualism within higher plant taxa, which often comprise the flora that share similar flowering peaks. If they successfully replace resources in this manner, then, at the population level, their response to competition may be termed 'silent'. Resource needs are met, but different species are incorporated, thus resembling 'scramble competition' (Andrewartha & Birch, 1954) but at a community-wide level. Because solitary bee abundance increased in some years after feral *Apis* was well established, indirect benefits from the invader, such as greater pollination and abundance of certain native plants, fit the available data. Whether character displacement occurs (Thompson, 2005) may be influenced by how frequently the exotic pollinator augments the host resource base, or preserves it when native bee populations are low (Bascompte & Jordano, 2007). Indeed, reproductive complementarity indicated by the range of pollen species utilized by the solitary bees may help explain why plant communities do not appear to be saturated with competing species (Stohlgren *et al.*, 2008). The resilience that allows pollination mutualisms to persist should be better maintained where

there is a high floral diversity within clades. As a consequence, the impact of invasive honey bees may be inversely related to local floristic diversity.

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