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Do competing honey bees matter? Dynamics and abundance of native bees before and after honey bee invasion

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Abstract To provide replicate samples of local bee populations in a nature preserve, light traps operated continuously on Barro Colorado Island (BCI), Panama, collected bees for 17 years, including 10 years following invasion by African *Apis mellifera*. Honey bees appeared in light traps as the first swarms colonized the Panama Canal area. Their numbers followed seasonal trends shown in independent studies, thus indicating bee abundance and activity in a large area. No measurable population-level impact of competition between this invading honey bee and native bees, despite many demonstrations of resource competition at flower patch and colony levels, changed annual abundances of all 15 native bee species. Native bee abundance did not decrease, nor did native bees show substantial reciprocal yearly change with honey bee abundance. One strong negative correlation of bee catches with an extremely rainy year was found. However, multiple regression using rainfall and honey bee abundance as the independent variables showed that neither was responsible for bee population change over 17 years. Nearly half the native species declined during a year that displayed peak honey bee number. That competition from honey bees on an island the size of BCI was necessarily reduced below impact levels expected on the mainland is discussed using a model of resource and consumer density, foraging range, and island size.

Key words African *Apis* · Impact studies · Neotropical bees

Introduction

Reciprocal population change is a hallmark of significant competition because it demonstrates a pervasive and substantial interaction. Without indication of population-level change, recorded in natural communities, little can validate perceived importance of resource competition, whether its multilevel components build up to a population change or whether other processes largely affect local success and survival of biological species. Two significant competitors, regardless of competitive mechanisms or advantages, should tend to display inverse changes to each other's abundance in the habitat as a whole. On a geographic scale, invasive organisms are among those thought most likely to generate such dynamics (Case and Bolger 1991; Dukes and Mooney 1999; Lawton et al. 1998; Ramakrishnan 1991; Usher 1991; Basset et al. 1998).

We used an extensive insect population data set on a tropical island nature preserve to monitor the influence of an invader (Wolda and Roubik 1986; Wolda 1992). Like forests throughout tropical America, Barro Colorado Island, Panama (BCI) had no honey bees before natural colonization by the African bee *Apis mellifera scutellata* or its hybrids (Roubik 1989). Unlike many such areas, however, the island is a strict forest preserve surrounded by a freshwater lake. Although there is a growing literature on the global ecology of exotic honey bees (Sugden et al. 1996; Roubik 1996a,b; Paton 1997; Butz Huryn 1997; Kato et al. 1999), no long-term data set has verified that *Apis mellifera* becomes abundant regionally while *causing* decline of native bees or other flower-visiting animals in natural habitats. Disturbed habitats, or those lacking predators, competitors, or resources normally present, are unlikely to provide proxy data to show whether exotic honey bees have a significant impact elsewhere. Until the impact issue is resolved, conservation or management implications of such invasive flower visitors, particularly in nature preserves, exist largely without any empirical basis for discussion.

We documented the 1984 arrival of African honey bees on BCI using light traps (Wolda and Roubik 1986; see also Croat 1978; Boreham and Roubik 1987; Leigh et al. 1997), then analyzed African and native bee dynamics and abundance (Roubik and Boreham 1990; Roubik and Wolda, in press). Here we apply the first continuous data series taken on bees to gauge exotic honey bee impact at population

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levels (Roubik 1978, 1996a; Sugden et al. 1996; Schwarz and Hurst 1997; Frankie et al. 1998a,b). Such long-term information in a habitat largely free of manmade perturbation is crucial to understanding the impact by honey bees as exotic organisms. Further biological details, including annual activity and pollen diet, are available for analysis of population change among nocturnal and some diurnal bees arriving at our traps (Roubik 1989; Roulston 1998; Wcislo and Roubik, unpublished data). Here we test the hypothesis that honey bees ultimately reduce the abundance of local bees through a well-documented process of competition, and we extend previous interpretation of light trap data, also placing our observations in population and community perspectives.

Materials and methods

Created by formation of Gatun Lake in the early 1900s, BCI supports a closed-canopy forest of 15.6 km^2, with a dry season of 4 months (January–April) and average yearly rainfall of 2600 mm (Leigh et al. 1997). Half the island's vegetation has not been cut or burned for 500 years, with the remainder in regeneration at least during the past 80 years (Leigh and Wright 1990).

Flying bees were sampled using two ultraviolet fluorescent light traps (Wolda 1992). The trap collections were compared by Pearson product moment correlations among weekly counts from 3 years selected at random to establish whether the trap samples differed significantly. Collections were made from a single large forest tree on a hill overlooking Gatun Lake, where the lake extends approximately 1 km to the east (Wolda 1982). The upper light trap is at 27-m height, where it can be seen at canopy level from several hundred meters. A second trap suspended below, at 3-m height, is visible in the forest within 50 m. The fluorescent ultraviolet lights operated continuously, on a 24-h basis. Our trap data, collected daily and tabulated for weekly intervals, include exactly 17 years ending with the last day of 1993. Male bees, although generally abundant at the same time as their females but much less numerous, are analyzed separately (Roubik and Wolda, in press).

Several statistical tests were used to evaluate different aspects of population changes among the samples of local bees. Repeated-measures and model I ANOVA, and multivariate regression, were applied to study the 15 most abundant native species and honey bees. For ANOVA, the presence of honey bees was used as the fixed treatment effect. A finer resolution of cause and effect of honey bee presence and rainfall were evaluated by using log-transformed and raw data as independent variables in multiple regression models of annual bee abundance. In the multiple regression models, a t-value >2.5 for a two-tailed test was applied to determine which independent variable had a significant correlation with the abundance of each native bee species. Effects of rainfall were further assessed by contingency table analysis for trends of bee abundance in the 7 years before honey bees arrived. Certain deviations from normality and homogeneity in variance between the two periods compared by statistical tests (when honey bees were "present" or "absent") prompted analyses of log-transformed data. We therefore applied $\ln x + 1$ transformation. For a model I ANOVA, both raw abundance and a "differenced" data series were inspected. Differencing, which transforms raw data series into arithmetic differences between adjacent data points, largely removes time-series trends or autocorrelations and gives the magnitude and direction of change between sequential observations (Roubik 1983).

To explore the short-term impact of potential competition, tests were designed to show whether reciprocity existed in abundance trends of honey bees and native bees. As already stated, reciprocity is viewed here as the single variable available to test cause and effect in population change that may be caused by competition. Coupled with a documentation for general change in the abundance of native species in replicate time-series samples, after arrival of a competing invader, the two results can be used to refute the hypothesis that an invader has caused a population-level impact. Reciprocity in annual population changes of bees was assessed both by setting a null expectation at equal numbers of concordant or discordant changes and by comparing native bee changes relative to honey bees with the mean change relative to other native bee species (see Table 1). The array of 15 native species was compared in a paired t-test (one-tailed) to both null expectations.

Results

Designs that can randomize environmental factors including the presence or absence of the experimental variable, such as an invasive insect species (see Roubik 1983; Stewart-Oaten et al. 1986; Carpenter 1990; Reckhow 1990), could not be applied to our data because too few annual population measures were available. Equal trappability over sampling intervals forms a critical assumption of repeated surveys aimed at detecting possible disturbances (Shaffer et al. 1998). Because many individual daily, weekly, or monthly catches had no individuals of common species, and because local events such as flowering near traps caused large fluctuations in short-term trapping results (Wolda and Roubik 1986), we chose to make each data point the sum of catches in an entire year. As such, the desirable preintervention data series of 20–40 points could not be modeled for ARIMA, Fourier, or similar time-series applications to test for significant perturbation.

The use of a calendar year was advantageous because it did not divide major peaks and troughs of annual bee abundance. All common species encountered in traps reached peak abundance within the dry to early wet season, during March through July (Roubik and Wolda, in press), and the annual low was at the end of the wet season (October and November). Bee seasonality in light traps, including *Apis*, generally showed no large variation; maximum catches of each species, calculated by week, occurred within a 0.5- to

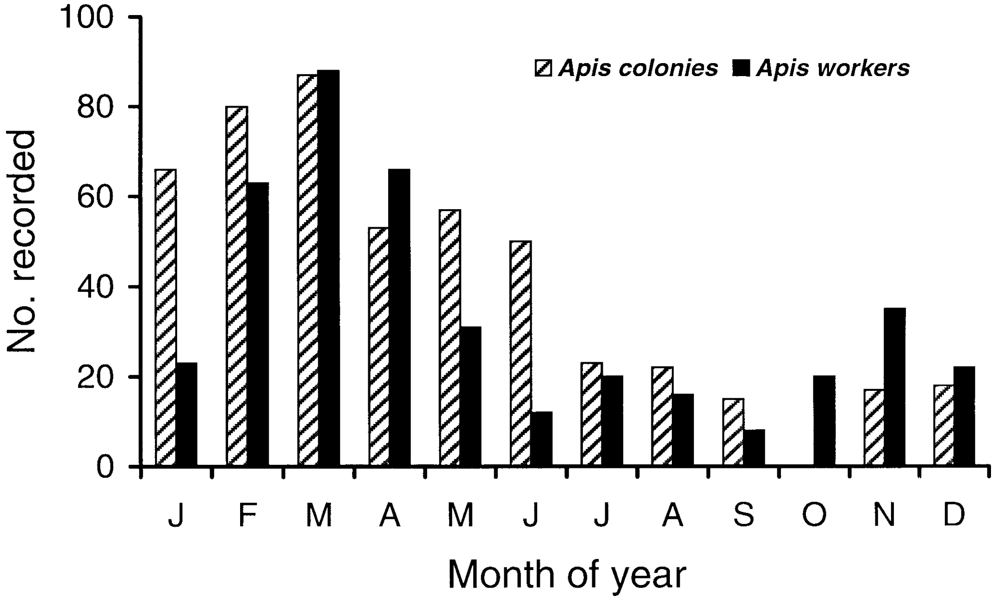

Fig. 1. Two measures of African honey bee dynamics in the Panama Canal area. Bees sampled per week at two light traps on Barro Colorado Island (summed over a 10-year period) are plotted against swarms and nests destroyed monthly in the Panama Canal area (data for the central canal area, summed over 1984–1990; see Boreham and Roubik 1987; Roubik and Boreham 1990)

2.0-month standard deviation (Roubik and Wolda, unpublished data).

General trappability

Abundance ranks remained constant for the three most commonly trapped species, but less frequently sampled bees varied widely in rank (Table 1). Two nocturnal *Megalopta* (Halictidae) and the stingless bee (Meliponini) *Partamona peckolti* were highest in annual abundance (Table 1). *Megalopta* arrived almost every week in light traps, totaling about 34 000 individuals during the 17 years. The most common species, *Megalopta genalis*, was on an annual basis consistently three times more abundant than *Megalopta ecuadoria*. Other bees appeared in traps on average every 2 to 20 weeks, even perennially active Meliponini and *Apis*. Mode averages show low weekly numbers for *Apis* (3), Meliponini (1 or 2), *Centris* (1), *Megalopta* (10 and 28), and *Partamona* (6). Maxima trapped in a single week included as many as 528 *M. genalis*, 248 *Partamona*, 112 *M. ecuadoria*, and 5 to 23 of the other species. (These data include 906 consecutive weeks, 5 months more than the 17-year period we analyzed for honey bee impact.)

Did the high and low traps function independently? A random sample of 3 years for the two most common bees showed that the weekly cross-correlations between traps in a given year, both between species and within bee species, although generally positive were not appreciable (Table 2). Product-moment correlations were mostly nonsignificant (for $df = 50$, coefficients between -0.3 and 0.3 are the same as 0.0, at the 0.05 level; Rohlf and Sokal 1969, p. 224).

Concurrent with our study on BCI, the Panama Canal Commission gathered monthly data on colonies of Africanized honey bees found within the entire Panama Canal area (Roubik and Boreham 1990). For the period 1984–1990, cumulative honey bee abundance in the central canal area flanking BCI was matched by the trends of honey bee catches at light traps on BCI (Fig. 1).

Rainfall and bee abundance

Absence of the normal dry season in 1981 evidently had a profound effect on bees in general (Wolda and Roubik 1986) (Fig. 2). The catches of *Megalopta* decreased by 71% and 79% during 1981 (Table 3). As previously shown (Wolda and Roubik 1986), the pattern of seasonality for *Megalopta* in light traps was that of relatively low abundance during dry season, while annual peaks during wet season varied in timing.

Differences between adjacent years show that *Megalopta* catches often varied as the inverse of annual rainfall (Fig. 3). This variation occurred in 69% of 16 yearly intervals for *M. genalis* and 63% for *M. ecuadoria*. In only 6% of yearly intervals did these species change in opposite directions. The results of multiple regression analysis, however, failed to substantiate a general correlation between rainfall and the abundance of any bee, with one exception (Table 3). *Plebeia franki* (Meliponini) showed a significant positive association with annual rainfall. The Meliponini taken as a group did not show such correlation to rainfall, with reciprocal change in only 25% of years. Abundance shifts of the honey bee were without particular relation to rainfall, displaying opposite shifts in five of nine intervals. A test of association of species abundance and annual rainfall failed to show any significance during the period before honey bees arrived ($P = 0.09$; Table 4).

Impact of honey bees

Native bee populations did not decline during the 10 years after arrival of honey bees (see Table 1 and Fig. 2). In fact,

Table 1. Summary of annual bee abundance data from two light traps operated continuously on Barro Colorado Island, Panama, for 17 years (1977–1993)

Native bee (family)	*n* (Mean)	Mean reciprocity[a]		Raw data				Differenced data			Multiple regression ln*x* + 1[d]	
		Native	*Apis*	Trend[b]	Means[c]	*F*	*P*	Means[c]	*F*	*P*	*F*	*P*[d]
Megalopta genalis (H)	1544	4.2	5	+	1106, 1851	2.7	0.12	−92, 83	0.07	0.80	0.2	0.82
Megalopta ecuadoria (H)	533	4.2	7	+	360, 688	7.3	0.02	−1, 15	0.01	0.94	0.2	0.79
Partamona peckolti (A)	181	4.6	6	+	101, 237	4.1	0.06	−33, −4	0.08	0.78	0.0	0.99
Oxytrigona mellicolor (A)	24	4.4	5	+	8, 35	13.7	0.002	1, 3	0.07	0.80	1.4	0.30
Scaptotrigona barrocoloradensis (A)	18	4.4	4	+	9, 25	2.8	0.11	3, 1	0.02	0.90	4.7	0.05 (0.03)
Trigona fulviventris (A)	15	4.1	5	+	8, 21	3.3	0.09	−5, 2	0.5	0.48	3.7	0.08
Plebeia franki (A)	10	4.4	4	−	11, 7	0.5	0.51	0.2, 0.5	0.0	0.97	1.7	0.24
Centris flavilabris (A)	10	5.1	5	+	4, 13	2.4	0.14	1, −0.25	0.02	0.90	1.2	0.37
Plebeia jatiformis (A)	9	5.1	3	−	10, 9	0.2	0.65	3, −1	0.70	0.42	2.4	0.15
Trigona corvina (A)	8	4.1	6	+	6, 10	0.8	0.40	−1, 2	0.25	0.62	3.8	0.08
Rhinetula dentricus (H)	8	4.4	3	+	4, 10	1.2	0.30	2, −1.3	0.21	0.66	3.8	0.08 (0.03)
Scaptotrigona luteipennis (A)	8	3.9	1	−	10, 6	2.5	0.14	−0.5, 0.0	0.30	0.87	2.4	0.16
Plebeia frontalis (A)	6	3.3	3		4, 4	1.6	0.23	0.5, 0.5	0.0	1.0	0.1	0.95
Trigona nigerrima (A)	5	4.1	4		5, 5	0.2	0.75	0.3, −0.3	0.15	0.70	0.7	0.52
Ptiloglossa sp. (C)	2	3.8	4	−	3, 2	0.4	0.56	0.0, −0.5	0.15	0.70	2.7	0.14

Bee family: H, Halictidae; A, Apidae; C, Colletidae

Records given are for the 15 most abundant native bee species

[a] Years when abundance trends were opposite with either the 14 other native bees (mean) or with *Apis*

[b] + or − signifies changes observed during honey bee presence

[c] Single-factor ANOVA comparing bee species abundance in light trap catches during 7 years before honey bee presence and during 10 years after honey bee colonization of Barro Colorado Island, Panama. Mean yearly captures are given for the two periods. Results are for the raw data and differenced data series (see Methods)

[d] Second *P* value for honey bee abundance component of model

Table 2. A random 3-year sample of weekly abundance correlations between two light traps considering the two most common bees (*Megalopta*) in trap catches on Barro Colorado Island (1977–1993)

Year	Correlation of high and low traps		Correlation between species	
	M. genalis	*M. ecuadoria*	High trap	Low trap
1983	0.32	0.47	0.71	0.55
1984	0.20	0.28	0.49	0.03
1992	0.21	−0.15	0.07	0.32

the 15 species jointly showed a slight increase during the entire 17-year period (*df* = 16, 226, *P* = 0.02, and df = 15, 210, *P* = 0.02, repeated-measures ANOVA for raw data and differenced series, respectively). Analysis of variance for a single factor, the presence or absence of honey bees, revealed no decrease in native bee numbers either in totals trapped during a year or in direction and magnitude of yearly change in abundance indicated by transformed raw abundance data (Table 1). ANOVA of log-transformed data (not shown) confirmed the changes of individual

Table 3. Seasonal rainfall and the abundance of two *Megalopta* on Barro Colorado Island in 17 years of continuous light trap samples (1977–1993)

Rainfall and season (mm wk^{-1})		Year	Bee species and mean seasonal weekly abundance:			
Dry	Wet		*M. genalis*		*M. ecuadoria*	
			Dry	Wet	Dry	Wet
10.16	77.69	1977	18.30	28.03	7.58	6.85
9.00	53.94	1978	11.80	92.05	6.80	12.70
4.00	72.48	1979	5.90	15.20	3.80	10.02
11.78	60.00	1980	6.00	15.90	5.60	10.26
38.14	116.05	1981	4.85	5.18	2.07	2.29
19.90	49.74	1982	4.18	12.53	0.59	5.93
1.75	72.94	1983	20.81	12.58	12.31	5.06
13.11	73.23	1984	14.72	16.03	5.27	4.35
5.53	61.37	1985	14.47	79.46	7.52	29.53
16.75	56.44	1986	30.52	70.72	9.42	15.84
10.63	77.36	1987	30.63	52.33	13.68	17.92
4.61	74.11	1988	14.67	22.06	8.00	13.97
8.77	60.89	1989	25.95	54.33	13.39	29.42
7.52	73.58	1990	49.25	40.03	15.25	8.17
14.03	68.69	1991	13.52	26.76	3.12	13.56
2.98	83.36	1992	20.13	31.49	10.63	10.14
14.51	66.24	1993	22.86	34.16	12.29	9.26

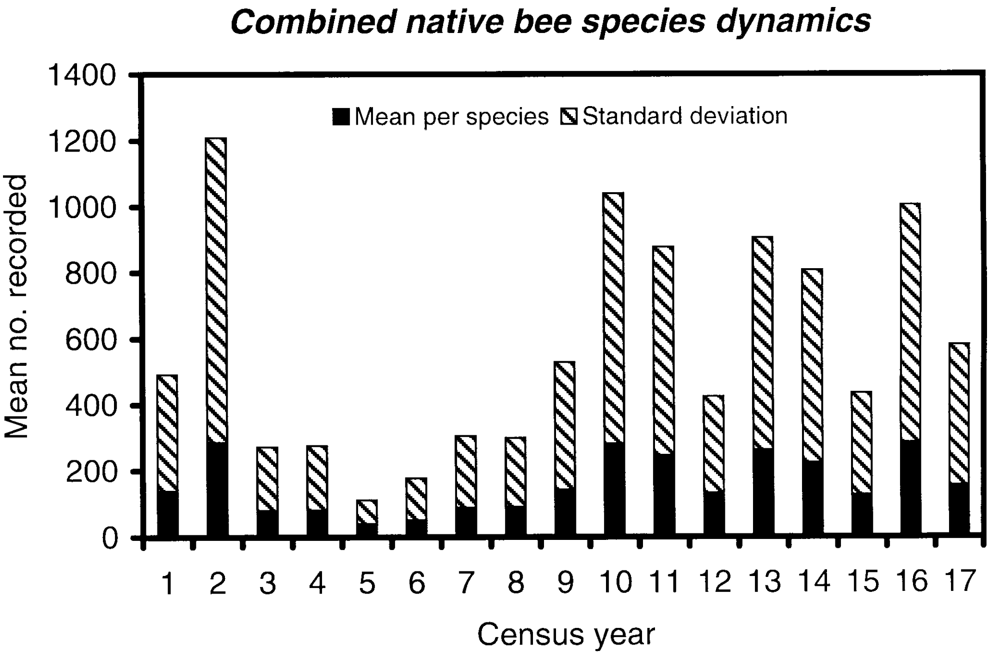

Fig. 2. Abundance trends during 17 years of the 15 native bee species sampled on Barro Colorado Island, Panama, using two light traps under continuous operation. In 1984, African honey bees colonized the island (see Fig. 3)

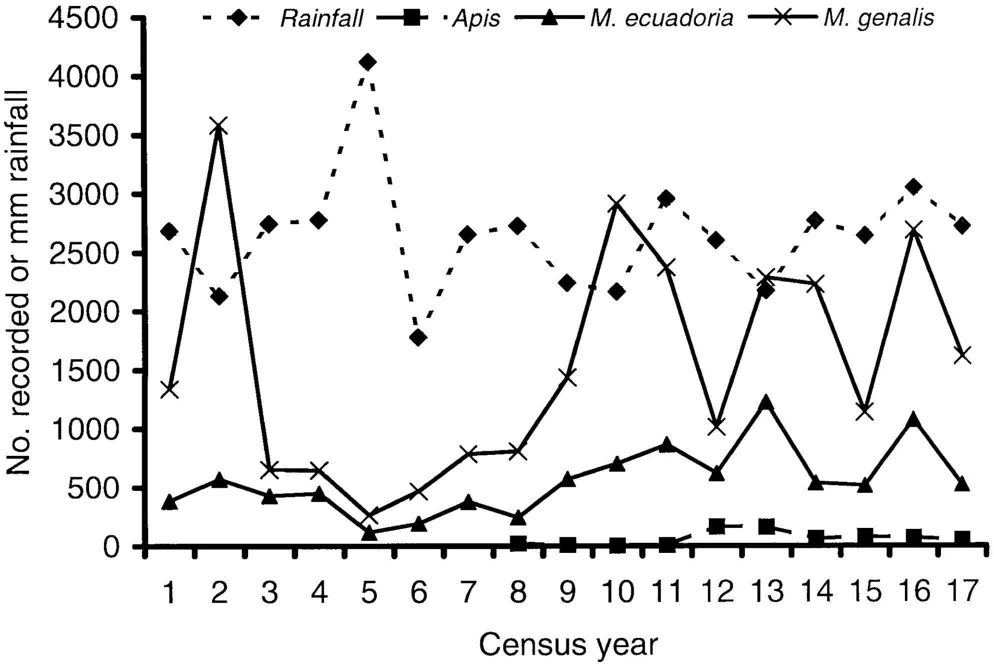

Fig. 3. Yearly abundance trends of native bees and African honey bees on Barro Colorado Island, Panama, compared to annual rainfall during 10 years (1984–1993)

Table 4. Contingency table test of association between annual change in native bee catches (15 species) at two light traps and changes in rainfall when no honey bees were present (1977–1983) (chi-square = 2.84, $P = 0.09$)

Rainfall changes	Changes in bee abundance	
	Positive	Negative
Positive	26	26
Negative	22	10

species demonstrated with raw data and also revealed significance ($P < 0.05$) in abundance change of five additional species. The nine species with substantial change (all positive) while *Apis* was present were *Megalopta, Centris, Rhinetula, Scaptotrigona, Trigona fulviventris*, and *Oxytrigona*.

Yearly trends in abundance at light traps revealed some reciprocal changes for native bees and honey bees (Table 1 and Fig. 2). A paired *t*-test in which the number of reciprocal years with *Apis* was compared to the expected number (4.5, taking the average of the 9 intervals, or 4.2 taking the mean reciprocity among native bees, see Table 1), showed no evidence of population-level competition for the 15 native bee species ($df = 14$, $P > 0.6$). During four yearly intervals, honey bee number and rainfall rose or fell together, but during two intervals honey bee number increased when rainfall decreased. In 1988 and 1991 the numbers of honey bees increased and rainfall did not, which allowed negative effects from honey bee competition to be separated from any negative association with yearly rainfall. Both *Megalopta* and *Partamona* decreased in both these years (see Fig. 3), as did *Plebeia frontalis*, *Trigona nigerrima*, *T. corvina*, *Ptiloglossa*, and *Rhinetula*. The other native bees showed different trends. This particular analysis is critical to the hypothesis of competition because honey bees were most abundant in light traps on BCI during these years (Fig. 3) and would, all other factors remaining equal, be expected to have the greatest impact. Removing the possibility of negative impact from rainfall coinciding with a negative impact from honey bees is the purpose of this individual analysis. The seven bee species, including three perennial colonies, showed population changes consistent with significant competition with honey bees. Nonetheless, the multiple regression of honey bee abundance and native bee abundance in traps indicated that such annual changes were similar among honey bees *Plebeia jatiformis* and *Oxytrigona mellicolor*, whereas no other species responded the same way and none was influenced considerably by annual rainfall.

Discussion

Analysis of bee community samples from traps

Fixed-position traps that do not attract insects but intercept their flight paths are thought to provide accurate long-term abundance data (Southwood 1988). The possibility exists that, as central-place foragers, female bees with nests are not trapable in the same way as insects lacking a home base. However, changing positions of bee resources should, certainly in a year, assure the spread of bees through the habitat. Light traps would then function as do other fixed-position traps that are not attracting insects over large distances (in contrast to pheromone lures, for example).

Catches at two ultraviolet lights coincided with the first swarms and nests of Africanized bees in the Panama canal area (Boreham and Roubik 1987; Roubik and Boreham 1990). Thus, one central criterion for animal population studies with light traps was met: corroborating data were provided by an independent method (see Ackerman 1983; Woiwood and Dancy 1986; Muirhead-Thomson 1991). As part of the long-term monitoring program of insects on BCI (Wolda 1992), our analysis considered bee abundance changes over a continuous 17-year period. However, the two periods of principal interest, 7 years with no honey bees and 10 years during their presence, are considerably shorter. Certain correlations are therefore likely to either be absent or undetectable in different subsets of the data series. We thus attempt to identify some of the short- and long-term contributors to fluctuations in bee abundance measured by light traps.

One may also ask why 15 species of bees were repeatedly sampled and others not. Two reasons the traps collect this subset of the roughly 250 bee species on BCI are general abundance and nondiurnal habits. The highly social bees (Apinae: Meliponini and Apini) are the most abundant and constantly active of all bees, the former having an estimated 20000 foraging adults per hectare on BCI (Roubik 1993b). For inadequately explained reasons, most flying nocturnal insects arrive in light traps, except during moonlit nights (Muirhead-Thompson 1991). Moonlight evidently did not diminish the effectiveness of light traps on bees, however, because catches had no correlation with moonlight (H. Wolda, unpublished data). Although ultraviolet is well known to cause positive taxis in bees, traps themselves probably did not function as long-distance attractants or beacons (Collett and Zeil 1998), and where studies have been made, insects trapped at lights can generally be repulsed by light from as far away as 200m (Muirhead-Thomson 1991).

We believe the light traps recorded aerial bee density in the habitat, functioning primarily as intercept traps over a short distance. This conclusion is supported by the meager correlation between weekly catches of the same species at two traps (see also Roubik 1993a), the few bees of a given species arriving on a given day or week, the gaps of several weeks between arrival of the same species, even the perennial colonies, and the abrupt increase in catches when a flowering tree canopy was within a few meters of traps (Wolda and Roubik 1986). On the other hand, positive changes in abundance of most native bees occurred after the arrival of honey bees, even though a net annual correlation with honey bees was substantiated in only two species (Table 1). We therefore reject the alternative hypothesis that trap samples were extremely local in nature, driven primarily by flowering intensity and foraging activity in the immediate area of the traps that produced correlated increases in bees sampled there. Such varied methods of data analysis seem essential in determining causes of abundance change in flying insects like bees (Roubik, in press).

In general, although foraging success cannot show net interaction, change in absolute abundance can (Cane and Payne 1993; Roubik 1996a; Shaffer et al. 1998). Our methods and data, however, cannot show net impact of honey bees on most bees on BCI, which are strictly diurnal and were rarely sampled using only two light–intercept traps. We recognize the limitations of light trap methods discussed elsewhere (Southwood 1988; Muirhead-Thomson 1991; Roubik and Wolda, in press), but validity of our study rests upon its replication over time, wherein bees regularly flew into the two traps through the 17-year period. Visibility of the light traps and their interception of flying bees are taken to be constant. We also avoided stochastic bias by pooling data from 730 trap-days to derive each yearly data point. The assumption of constant trappability would be difficult to defend for shorter time periods or for supraannual periods that combine more than one major annual flowering or dearth period (see Wright et al. 1999)

Stochastic variation in insect samples was expected as the result of shifting locations of bee nests, the weather, positions of flowers that bees visit, and variation in absolute abundance caused by mortality and natality (see Wolda and Roubik 1986; Roubik 1993b). Behavioral differences certainly might produce different trappabilities. Roulston (1998) obtained almost no captures of *Megalopta* carrying pollen, which may imply that its navigation or susceptibility to light traps varies as a function of foraging activity. Wcislo and Roubik (unpublished data) found in samples of 285 nest cells of *Megalopta* that more than 85% of its pollen comes from bombacaceous trees flowering during January to April, suggesting trappability declines at this time.

Diurnal bees seem to come to lights only during a brief interval near dawn or dusk, even though honey bees and *Megalopta* each arrive at ultraviolet lights en masse approximately 30min before dawn (D.W. Roubik, personal observations). Although one is diurnal and the other nocturnal, these bees overlap in flower visitation and foraging activity. We suggest, however, the short overlap in time is not directly interpretable as extent of interaction between *Apis* and *Megalopta*. *Megalopta* clearly must preempt *Apis* by foraging on flowers blooming at night.

Bee abundance and causal factors over time

Three indices of honey bee abundance in the environment were obtained that showed similar seasonal trends (Fig. 1): (1) the regional abundance of established nests, (2) the regional abundance of swarms, and (3) the abundance of honey bees in flight within forest. That these coincide is evidence the light trap data show population trends, not merely relative abundance in an area much smaller than the potential flight and activity ranges of bees, ordinarily reflected in data such as the number of bees at a patch of flowers or nesting site (Ginsberg 1983; reviews by Roubik 1989, 1996a,b).

An increase in honey bee abundance was noteworthy during 1988 to 1993 on BCI, but in the Panama Canal area outside forested areas recorded abundance trends differed; they indicated relatively stable or occasionally decreasing populations over the same interval (Roubik and Boreham 1990). Seasonal reproductive patterns and absolute abundance trends may be shown by both data sets, but multiyear trends on BCI had little counterpart in the swarms and nests reported near the Panama Canal, where much of the vegetation is early secondary growth or more open.

Multiple regression showed that rainfall was a poor explanatory variable considering the yearly abundance of bees in light traps, despite an enormous drop in *Megalopta* during a very rainy year. Annual rainfall on BCI varied by more than 100% during 17 years of our study, with a maximum of 4121 mm in 1981 compared to 1780 mm in 1982. When honey bee dynamics matched that of rainfall, the effect of these two variables on native bees was potentially confounded. Multiple regression analysis showed that there neither was a significant decrease in any native bee due to the presence of honey bees nor a significant change due to the recorded levels of rainfall.

Honey bee impact

If the abundance of native bees had shifted to lower levels after honey bee arrival and if the yearly honey bee–native bee dynamics were overwhelmingly reciprocal, we would have concluded that the type of competition between honey bees and native bees shown experimentally (Roubik 1978, 1983, 1989; Roubik et al. 1986) had likely culminated in altering population levels of native bees. This alteration was clearly not the case on BCI. However, in Fig. 3, only two of nine intervals provided the opportunity to observe an impact of increasing honey bee density without the intrusion of increased rainfall. One of these two periods, 1988, coincided with the largest annual increase in honey bee abundance; 7 of 15 local bee species decreased in this year. During the following year, the trend of decreasing rainfall continued but honey bee abundance remained relatively stable. At this time both *Megalopta* species increased to levels recorded before the preceding rise in honey bee abundance. Such interwoven trends may illustrate compensatory effects of potentially limiting factors on populations in nature and underscore the need for extended analytical population surveys.

Competition between populations considered here involved trophic linkage in the early stages of colonization, before niche partitioning could be realized. In the case of nocturnal foragers (*Megalopta*) some niche partitioning was obligatory, causing them to preempt the honey bee at certain resources. However, 13 of the native bee species were diurnal foragers, 3 of them solitary bees, and the remainder perennial social bee colonies that likely compete with *Apis* for both food and nest sites (Roubik 1991; Ramalho et al. 1990). Further, at least Meliponini, *Megalopta*, and *Apis* were known to have similar pollen diets, with *Pseudobombax* foremost in biomass of pollen harvest by several bees (Roubik 1988, 1989; Roubik et al. 1986; Roulston 1998; W. Wcislo and D.W. Roubik, unpublished data).

In a biogeographic analysis, dynamics caused by large bee colonies may finally result in diminished species richness (Roubik 1980, 1989, 1996a). Where honey bees are native, bee species diversity is lessened. Further, where any Apini or Meliponini are abundant within local assemblages there are relatively fewer solitary bee species (Michener 1979; Zanella et al. 1998). However, studies that have monitored populations for 17 years in two sites, Panama and French Guiana (Roubik 1996b), each suggested no substantial impact during the first few decades of honey bee presence in *mature, biologically diverse, lowland tropical forest.* Although several reviews of data for Australia suggest honey bees cause community changes (Sugden et al. 1996; Paton 1997; Schwarz and Hurst 1997; Manning 1997), Australia is a special case because no significant predators of honey bee colonies exist there, unlike other continental areas that have the full complement of both invertebrate and vertebrate bee colony predators (Roubik 1989, and personal observation).

Beyond competition at resource patches, we now need studies following results of medium-term community experiments lasting decades (Simberloff 1986; Wiens 1989). In the ecosystem of BCI, 10 years may not have been long enough to expose a population-competitive impact of exotic honey bees. In less complex habitats, there may be rapid response to perturbation, even at the population level (Porter and Savignano 1990; Strong 1992; Aizen and Feinsinger 1994; Roubik 1996b; Gross and Mackay 1998; Hingston and McQuillan 1998).

Invasive species and competition on islands

The BCI data suggest that island communities are perhaps less vulnerable to disturbance from invasive species. A topographic model can be used to explore this subject (Fig. 4). Our general hypothesis is that if the foraging range of an invasive species is greater than that of the island it occupies, its ecological impact is reduced. The model includes resource and consumer density, island size, and foraging range.

There are two central issues in viewing the ecology of this situation. First, reduced foraging range, for example, on

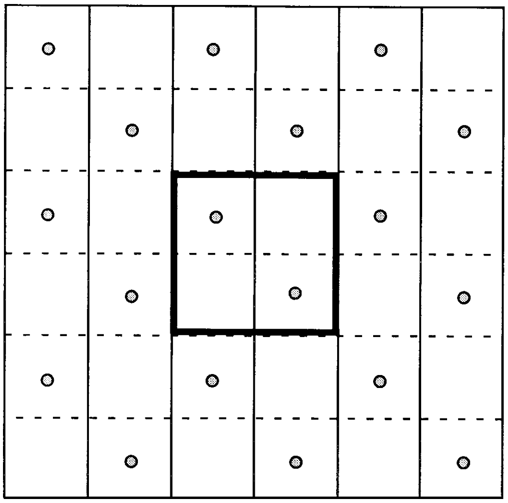

Fig. 4. Graphic representation of foraging intensity and overlap in resource exploitation on an island (2 × 2 central grid) and the mainland. When allowed to forage freely, each honey bee colony (represented by *shaded dots*) would use 25 squares of resource space; those within one square of the *central square* representing the bee nest are exploited at twice the rate as the *outer squares* (see text)

an island, may lead to concentrated foraging efforts in an area smaller than normal. And second, whether or not the first condition is met, consumer density may ultimately be reduced to match the lower availability of resources. Because the foraging range of an African honey bee colony is 7–8 km (Roubik 1989), native bees on BCI were less exposed to this exotic competitor than they would be on the mainland. In extensive mainland forest, any point is within range of honey bee colonies nesting within 200 km^2. BCI is 16 km^2 and the "colony equivalents" of honey bees that impinge on the native bees are far less. For example, if each honey bee colony depicted in Fig. 4 uses a 5×5 grid for its normal foraging, then 18 colonies would use the resources of the 2×2 grid depicted in the middle of the diagram. Let the middle 2×2 square represent BCI; then, only 2 colonies of honey bees interact with the native bees, rather than the 18 colonies that would arrive to this foraging area at any point on the mainland. This comparison is misleading, because bees would not use each of the 25 squares representing foraging range evenly. Those closest to the nest, within one square, could be assigned twice the foraging intensity of those located two squares from the honey bee nest (Roubik 1989). Calculating the total squares of overlap, and their intensity of use by foragers from uniform distribution of honey bee colonies shown in Fig. 4, resource use from the combined 18 colonies is 32 units (foraging exploitation) compared to only 8 units that would result from 2 resident colonies on an island using all the resource that normally would be taken from the four squares within one square of their nests.

If, however, the two resident colonies were able to take all the resource that they normally would find in a larger foraging territory, they would exploit a total of 34 units, producing nearly the same effect as the more diffuse competition from more colonies. A reduced resource availability probably leads to more intense exploitation, but in the case of the African honey bee on an island, the reduced food availability would likely result in colony emigration (see Roubik 1989), followed by a relative lowering of honey bee density on the island. For the native bees resident on BCI, which presumably were exploiting the island's resources as fully as possible before the honey bee arrived, we infer that the intensity of competition from the invading honey bee is lower than in the mainland forest.

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