

Pollen use by *Megalopta* sweat bees in relation to resource availability in a tropical forest

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Abstract. 1. Spatial and temporal availability of pollen helps shape bee foraging behaviour and productivity, which has been studied in great detail at the landscape level, but never in a diverse tropical forest.

2. To study the effect of spatio-temporal variation in resource distribution on pollen use and productivity, we identified pollen from spatially explicit nest collections of two generalist sweat bees, *Megalopta genalis* Meade-Waldo and *M. centralis* Friese, from Barro Colorado Island, Panama, a 50-ha forest dynamics plot during the 2007 dry and early wet seasons. Pollen from nests collected in 1998–1999 without spatial information was also identified.

3. Bees used pollen of at least 64 species; many of these occurred in only one collection. The 2007 collections contained pollen of 35 different species, but were dominated by five species, especially *Hura crepitans* L. and *Pseudobombax septenatum* (Jacq.) Dugand.

4. Temporal availability, but not distance from nest, influenced flower use at a 50-ha scale.

5. Body size was not associated with minimum flight distance as inferred from pollen collections.

6. Nest productivity and pollen diversity decreased from the dry to wet seasons, mirroring community-level availability of floral resources.

7. Results suggest that on a scale of 50 ha, bees are choosing certain host plant species regardless of distance from the nest, but adjusting foraging behaviour opportunistically based on the temporal availability of host flowers.

Key words. Flight distance, foraging range, Halictidae, Hymenoptera, native bees, pollen analysis, resource distribution.

Introduction

Bees' foraging decisions influence plant reproductive success through their role as the primary pollinators in most natural and agricultural ecosystems (reviewed in Bawa (1990) and Klein *et al.* (2007)), or as competitors with other pollinators (Eguiarte *et al.*, 1987; Hargreaves *et al.*, 2009). Because bees are central place foragers, their influence is limited to pollen

sources within their foraging range, which is thus of ecological interest (Roubik, 1989; Wcislo and Cane, 1996). Although many recent studies have used a variety of methods to measure the maximum foraging range of bees, most individuals do not fly as far as the maximum (reviewed in Zurbuchen *et al.* (2010a)). Moreover, maximum ranges alone do not address how bee foraging behaviour is shaped by the spatial and temporal patterns of pollen availability across a landscape, which is critical for understanding bee-plant interactions. For instance, bees in resource-poor or fragmented landscapes fly further to find pollen and have a lower productivity than their counterparts in resource-rich or intact landscapes (Fuchs *et al.* 2003; Westphal *et al.*, 2006; Williams and Kremen, 2007). Specialist bees temporally synchronise their own reproduction with the flowering of their pollen source (Minckley *et al.*, 1994, 2000).

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The effect of spatial heterogeneity on landscape-level pollen availability varies depending on the bee species and its typical foraging range (Beil *et al.*, 2008; Osborne *et al.*, 2008). However, no previous study has jointly analysed spatio-temporal availability of pollen sources and bee foraging behaviour and productivity for a generalist species.

Here we present the first community-level study of the relationship between the spatio-temporal distribution of pollen resources and bee foraging behaviour in a diverse tropical lowland forest using the generalist bees *Megalopta genalis* and *M. centralis* (= *Megalopta ecuadoria*). We tested two hypotheses for how the spatio-temporal distribution of pollen affects floral choice. First, we tested whether bees' foraging choice temporally tracks changes in abundance of their host flower species (O'Neil & Waller, 1984; Minckley *et al.*, 1994; Rasheed & Harder, 1997). Second, bees may preferentially forage for nearby pollen (Williams & Tepedino, 2003; Osborne *et al.*, 2008), and reproductive output may increase as a result (Peterson & Roitberg, 2006; Williams & Kremen, 2007; Zurbuchen *et al.*, 2010b). The effect of spatio-temporal availability on *Megalopta* foraging choice may be especially strong because *Megalopta* are severely time limited because they fly under very dim light conditions, logging approximately 30 min flight time per day (Wcislo *et al.*, 2004; Kelber *et al.*, 2006) (see *Overview of Megalopta natural history*, below, for details). Time-limited foragers should accept resources in the first suitable patch encountered rather than continue to search for more valuable yet difficult-to-find resources (Prinzing, 2003).

To measure spatio-temporal availability of pollen sources, we used a forest dynamics plot where resources (flowering trees and shrubs) are spatially mapped, phenologically tracked, and taxonomically identified. To track spatial correlates of bee foraging behaviour, we used spatially explicit collections of bee nests, and subsequently reared bees from these nests and then identified pollen that was cached in the nest brood cells by a bee. To test for year-to-year consistency in pollen preference, we compared data to a previous collection. We then assessed whether bees tracked temporal availability of resources by comparing relative pollen use with relative flower abundance for eight plant species heavily used by the bees (see below for details). To test whether distance to pollen sources affected pollen use, we compared the minimum nest-to-tree distances from nests that contained a particular pollen source with nests that did not; we also tested for similarity of pollen use between neighbouring nests. We then tested whether distance to pollen sources affected productivity, both overall and for the most commonly used species, with the prediction that longer foraging distances would negatively correlate with productivity (Westphal *et al.*, 2006; Williams and Kremen, 2007). Lastly, we tested whether body size correlated with minimum foraging distance, as predicted by Greenleaf *et al.* (2007).

Methods

Overview of Megalopta natural history

All field work was conducted on Barro Colorado Island (BCI), Panama. *Megalopta genalis* and *M. centralis* are

generalist foragers (Roulston, 1997; Wcislo *et al.*, 2004) that nest in dead sticks suspended in the understory. Nest initiation and foraging occur through the dry season (mid-December to late March) until the middle of the wet season (~July) (Wcislo *et al.*, 2004). Nests may be solitary or social, with social nests typically consisting of a non-foraging queen and a forager (Wcislo & Gonzalez, 2006). Pollen in the nest thus represents the effort of individual bees rather than a large social group. These bees are severely time constrained in their foraging behaviour, flying only during two ~70-min periods, one before sunrise and one after sunset; a given forager usually logs < 30 min total flight time per 24 h (Wcislo *et al.*, 2004; Kelber *et al.*, 2006). Their compound eyes are near the functional limits for apposition eyes, suggesting that they cannot extend their foraging time further into the night (reviewed in Warrant, 2008; Wcislo & Tierney, 2009; also Baird *et al.*, 2011).

After all the pollen necessary for offspring development is provisioned in an individual cell, the reproductive female lays an egg on the provision mass and seals the cell. After the larva eats the provisioned nectar and pollen it defecates the pollen exines just prior to pupation and smears them on the rear wall of the cell, from where they can be collected. Egg to adult development time is ~5 weeks (Wcislo & Gonzalez, 2006), so pollen from brood cells of collected nests (either exines from faeces in pupal cells or uneaten pollen from larval cells) represents foraging behaviour extending up to 5 weeks prior to the collection date. The average number of brood cells in nests from four previous collections on BCI ranged from 4.27 to 6.43 (Smith *et al.*, 2007)

Nest collections, pollen analyses, and resource availability

In 1998 and 1999, nests were collected opportunistically on BCI for pollen samples, without data on nest size, contents or location. We collected all faeces or uneaten pollen from each brood cell. Pollen grains or exines from individual brood cells were acetolysed and identified under a light microscope according to Roubik and Moreno (1991, 2009); identifications were confirmed using a pollen reference library maintained by STRI's Center for Tropical Paleocology & Archaeology. Pollen abundance was labelled as dominant if pollen of a single species comprised most of the pollen in the cell by volume; common if it was 30–50% of the pollen in the cell; or scarce if it was 10–30% of the pollen in the cell. Very few pollen types comprised <10% of the pollen in the cell, and these were excluded from all analyses to be conservative and avoid including contaminants. These values are estimates; absolute pollen abundance was not quantified. In the text below, 'sample' refers to a pollen type that comprised >10% estimated volume of the pollen in a cell, so a single cell could contain ≥ 1 pollen sample. Voucher specimens of the bees are in the Invertebrate Museum of the University of Panama, and the Dry Reference Collection of the Smithsonian Tropical Research Institute, which also houses the pollen samples.

In 2007, we collected nests of two species of sweat bee, *M. genalis* and *M. centralis*, from the 50-ha forest dynamics plot on BCI (hereafter, 'the plot'), which contains 20 8400

individuals from 299 plant species, all identified and mapped to a grid with 5 m² cells (Condit, 1998; Hubbell *et al.*, 1999, 2005). Bee nests were collected from the plot for quantitative pollen analyses twice in the dry season (3–8 February and 19–27 March) and twice in the wet season (11–17 May and 1–4 July), which we refer to as early February, late March, mid-May, and early July collections. All but five nests were collected at least 140 m from the edge of the plot. Nest locations were mapped using a marked 5 m² grid on the plot. Nests were opened to mark the brood cells and the nests were stored at an ambient temperature in a clear plastic tube with mesh coverings at each end and checked daily for new adult emergence. Pollen was analysed as described above according to Roubik and Moreno (1991, 2009).

To measure flowering phenology and temporal abundance of pollen, we used data from flower traps on the 50-ha plot that were collected weekly (unpublished data for 2007 courtesy of S. J. Wright; see Wright & Calderon, 1995 for details). We used data from the 5 weeks prior to each collection. These traps are located along the trails through the 50-ha plot; coverage for any given species varies depending on the relative abundance of a given species, the numbers of flowers per tree, and the location of individuals relative to the traps. Thus, these data provide a measure of within-species temporal changes in floral abundance but are not quantitatively comparable between species. To statistically test the relationship between flower availability and pollen use, we used a binary logistic regression with pollen presence or absence from each collected nest as the response variable, plant species identity entered as the first predictor variable, and number of flowers in traps as the second. We tested for a relationship between flower availability and pollen use for the eight most common pollen types for which we had trap data, but could not include *Schefflera morototoni* (Aubl.) Maguire, Steyerl. & Frodin in this analysis because none of its flowers were collected in traps.

To obtain data on tree abundance and distribution we used the 2005 census of the BCI 50-ha plot where each individual tree with a stem diameter at breast height (dbh) >10 mm is marked, identified, and mapped (Condit, 1998; Hubbell *et al.*, 1999, 2005). To test whether spatial proximity to floral resources influenced *Megalopta* foraging behaviour, we compared the average minimum nest-to-tree distances of nests containing pollen of a given species to those without pollen of that species for the nine most prevalent species in our 2007 collections; we used individuals >10 cm dbh to exclude saplings except for *Faramaea* sp., *Cordia* sp. and *Eugenia* sp. which can grow as shrubs or small trees. We calculated nest-to-tree distances for the nest collections in which pollen from a particular tree species was common. For example, we did not use the dry season collections in calculating nest-to-tree distances for trees that bloomed in the wet season. The collections we used for each species' calculations were: *Hura crepitans* – mid-May and early July; *Pseudobombax septenatum* – early February and late March; *Faramaea* sp. – mid-May; *Cordia* sp. – mid-May; *Cavanillesia platanifolia* (Bonpl.) Kunth – late March; *S. morototoni* – early February and late March; *Spondias* sp. – late March and mid-May; *Eugenia* sp. – mid-May; and *Trichilia* sp. – mid-May.

To test whether nest-to-pollen source distances were influenced by the overall abundance of source plants, we correlated the average nest-to-tree distance for nests using a given species' pollen with the total number of individuals of that species on the plot. Because the relationship was highly non-linear, we used Spearman's rank correlation.

To assess whether bees differentially used pollen resources based on spatial proximity, we calculated pair-wise distances for each nest in a given monthly collection with every other nest in the collection, and then calculated a Jaccard similarity index for pollen use for each pair using EstimateS v7.5.1 (R. K. Colwell, <http://purl.oclc.org/estimates>) and used a Mantel test to test for a relationship between pair-wise distance between nests and pair-wise pollen similarity. We used PASSAGE 2.0 (Rosenberg & Anderson, 2011) for Mantel tests.

We also tested whether distance to pollen sources affected productivity, measured as the number of active brood cells in collected nests. We tested this for overall pollen use, as well as individually for the two dominant sources of pollen in our study (*H. crepitans* and *P. septenatum*, see Results below).

To test for an effect of body size on flight distance, we compared head width (the distance between the most distal portion of each eye perpendicular to the frontal midline) to both the longest minimum nest-to-pollen source distance among pollen species in a given nest, and to the average minimum distance among all pollen sources present in the nest. In nests with more than one female, we used the body size of the smallest female in the nest because non-reproductive foragers in *Megalopta* nests are generally smaller than the queen or other bees in the nest (Smith *et al.*, 2008, 2009; Kapheim *et al.*, 2012). We performed a general linear model with either the longest or the average minimum nest-to-pollen source distance as the dependent variable, collection date as a random factor, bee species as a fixed factor, and head width as a covariate. We included date because foraging distances correlated negatively with date, and bee species because *M. genalis* is slightly larger than *M. centralis* (Weislo *et al.*, 2004).

To measure the effect of seasonality on productivity, we compared nest productivity across each of the 2007 collections using the non-parametric Kruskal–Wallis test followed by Conover post-hoc comparisons because variance was greater in the dry season. We compared diversity of pollen sources used by the bees with the number of pollen types per nest, divided by the number of cells with identified pollen in the nest, as our measure of diversity.

Results

Pollen identification

From the 1998 to 1999 collections we identified pollen from 92 brood cells, including pollen from ≥51 plant species (Figure S1). From the 2007 collections, we collected 95 nests containing 379 brood cells (75 *M. genalis*, 20 *M. centralis*; 15 nests from early February, 16 from late March, 45 from mid-May, 19 from early July) (Fig. 1) We analysed pollen from 274 of these cells, 51.3% of which contained only one species of pollen. The maximum number of species in one

cell was seven, the mean \pm SD was 1.73 ± 0.92 . Individual nests contained pollen from between 1 and 11 plant species (mean = 2.77 ± 1.96). In total, our 2007 collections contained pollen from at least 37 plant species. We could identify some pollen only to family, and 36 samples remained unidentified, but none of these unidentified samples were a dominant or common pollen type in their cells.

Overall, only 14 of the pollen types identified at least to genus were found in both collections, whereas 31 were found only in the 1998–1999 collection, and 11 in only the 2007 collection. *Parathesis microcalyx* Donn. Sm., *Pachira quinata* (Jacq.) W.S. Alverson and *Dolioscarpus major* J.F. Gmel. together accounted for 20% of pollen identifications from the 1998 to 1999 collection (Figure S1) but were absent from the 2007 collection (Fig. 1). There is only one individual of *P. quinata* on the plot, and none of *P. microcalyx*; the flowers of neither species were found in traps during our study in 2007. However, *D. major* flowers were found in 98 traps on the plot during May and June of 2007, so it was available but unused by *Megalopta* foragers. Two significant sources of pollen in the 2007 collection, *S. morototoni* and *Faramea* sp., which together accounted for 13.8% of pollen identifications (Fig. 1), were absent from the 1998 to 1999 collection (Figure S1).

All further results refer to the 2007 collections. *Hura crepitans*, *P. septenatum* (Malvaceae), and *Faramea* sp. (Rubiaceae) accounted for 33%, 15.9%, and 10.5% of total pollen identifications, respectively. These species were not only common, but were also the dominant, and often sole, pollen source in the cells from which they were collected. *Hura crepitans*,

P. septenatum, and *Faramea* sp. were the single dominant pollen source in 87%, 92%, and 65% of cells, respectively, in which they were identified, indicating that once the resources were discovered, the bees typically continued exploiting those pollen sources in provisioning a given cell. *Cavanillesia platanifolia* was the dominant source of pollen in 69% of the cells from which it was identified; *Cordia* sp. (two cells), *Mangifera indica* L., *Spondias mombin* L., and *Quararibea asterolepis* Pittier (one cell each) were the only other species recorded as a dominant source of pollen within a cell. Only five species exceeded 10% of pollen identifications for any given collection: *H. crepitans* in all but the late March collection, *P. septenatum* in the early February and late March collections, *Faramea* sp. in the mid-May collection, *C. platanifolia* in the late March collection, and *S. morototoni* in the early February collection (Fig. 1).

Pollen use and temporal distribution

Variation in pollen use generally corresponds to relative pollen availability as measured by the numbers of flowers in traps for the eight most commonly used species for which we have trap data (*S. morototoni* was not collected in any flower traps; Fig. 2). After accounting for the variation between species (LR $\chi^2 = 171.43$, d.f. = 7, $P < 0.001$), the number of trapped flowers significantly predicted pollen presence/absence (LR $\chi^2 = 21.80$, d.f. = 1, $P < 0.001$). Many common species on the plot were not used by the bees, but since timing of

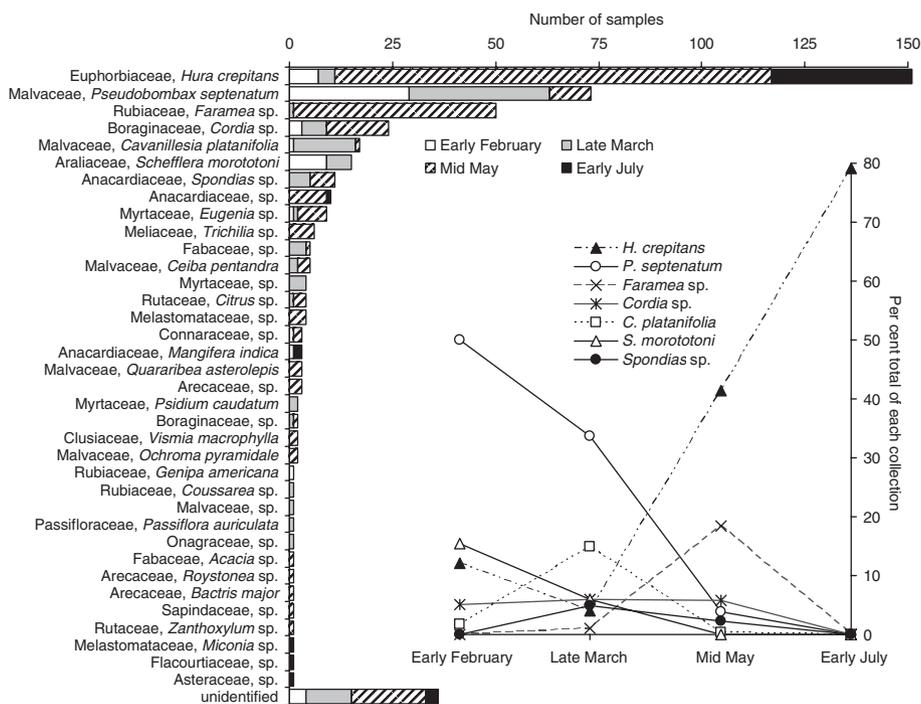


Fig. 1. The bar graph on the left shows pollen abundance by species (or lowest identified taxonomic group) from brood cells of *Megalopta genalis* and *M. centralis* from four collections in 2007 on BCI. Different patterns represent which collection yielded each sample. The line graph at the right shows the relative abundance of the seven most common pollen types plotted as the per cent total of identified samples for each collection.

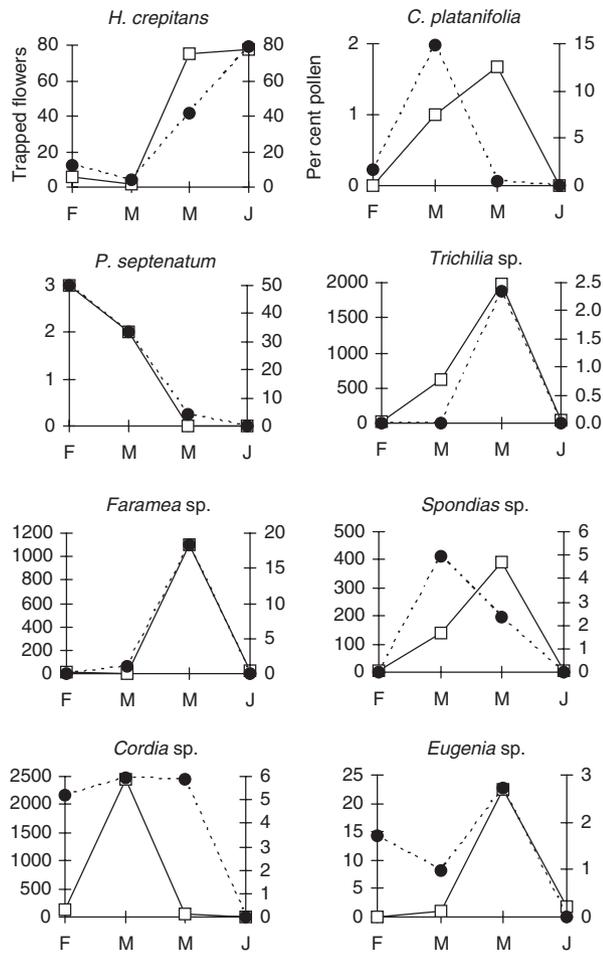


Fig. 2. Pollen use by *Megalopta genalis* and *M. centralis* relative to floral availability for eight common pollen types. Each collection (early February, late-March, mid-May, and July) is listed on the X-axis as F, M, M, and J, respectively. The number of trapped flowers from the 5 weeks preceding collection is on the left Y-axis, represented by open squares, and the per cent of identified pollen samples from brood cells in each collection is on the right Y-axis, represented by closed circles.

anthesis is not known for most tropical diurnal-flowering plants, it is uncertain which species were available to the nocturnally foraging bees. One exception to this is *D. major*. Because *D. major* was common in the 1998–1999 collections and present in traps in 2007, we know that the flowers were available to the bees, but not used.

Pollen use and spatial distribution

Mapping the locations of nests and individuals of plant species used for pollen shows that the minimum foraging distances were large for source species such as *S. morototoni* (mean \pm SD = 240 \pm 112 m), *C. platanifolia* (206 \pm 92.8 m), and *P. septenatum* (110 \pm 61.8 m). *Hura crepitans* was intermediate (48.1 \pm 33.4 m), and the smallest was *Faramaea* sp. (3.83 \pm 1.75 m) (Fig. S2). There was no

correlation between distance from nest to plot edge and minimum foraging distance ($r = -0.12$, $P = 0.26$; for nests with pollen from multiple species, the largest minimum distance was used). In none of the nine most common pollen sources were there significant differences between average nest-tree distances of nests that did and did not use that pollen (Figure S2 and Table S1). The number of individuals of pollen source species varied over almost five orders of magnitude from one (*S. morototoni*) to 9089 (*Faramaea* sp.; Table S1). In general the minimum distance from a nest to a pollen source negatively correlates with the relative abundance of different plant species on the plot, such that average minimum distances are large for less-common species, whereas no nest is particularly far from an individual of the most abundant species (Spearman's $\rho = -0.97$, $N = 9$, $P < 0.001$). Because the more abundant tree species used by *Megalopta* flowered in the wet season, nest-to-tree distances were shorter then (see below for statistics).

Similarity analyses showed little effect of distance between nests on similarity of pollen use. There were no correlations between pair-wise values for Jaccard similarity indices (J) and pair-wise distance in the collections in early February (Mantel test: $r = 0.24$, $P = 0.05$), and May (Mantel test: $r = -0.06$, $P = 0.3$); there was a weak yet significant correlation in the predicted direction in the March collection (Mantel test: $r = -0.24$, $P = 0.02$). This analysis was not performed for nest collections in July because nest contents were dominated by pollen from *H. crepitans* (34 of 38 cells).

There was a correlation between nest productivity and the longest of the nest-pollen source minimum distances, but in the opposite direction predicted (partial correlation controlling for collection date $r = 0.30$, d.f. = 90, $P = 0.003$); bees from more productive nests tended to forage farther. The correlation between productivity and average nest-pollen source distance was not significant ($r = 0.16$, d.f. = 90, $P = 0.12$). For nests that contained *P. septenatum* pollen in the dry season, there was no correlation between bee productivity (brood cells produced per nest) and distance to the nearest *P. septenatum* tree (Pearson's $r = -0.22$, $N = 31$, $P = 0.24$), nor was there any such correlation for *H. crepitans* in the wet season (Pearson's $r = 0.13$, $N = 59$, $P = 0.34$).

Body size and minimum flight distance

Neither body size nor bee species influenced foraging distance, although the effect of collection date was significant (GLM on largest minimum distance, species $F_{1,68} = 0.15$, $P = 0.70$; date $F_{3,68} = 17.00$, $P < 0.001$; size $F_{1,68} = 0.06$, $P = 0.81$. GLM on average minimum distance, species $F_{1,68} = 0.02$, $P = 0.90$; date $F_{3,68} = 15.79$, $P < 0.001$; size $F_{1,68} = 1.22$, $P = 0.27$).

Seasonality, productivity, and diversity of pollen use

Bee productivity (brood cells per nest; overall range: 1–13, mean = 3.99 \pm 2.17) was high in the dry season (February and March collections) and then declined in the wet season

(May and July collections) (Fig. 3a; Kruskal–Wallis $X_3^2 = 24.02$, $P < 0.001$). Conover post-hoc comparisons showed that the May collection was significantly lower than the two dry season collections, and the July collection lower still (Fig. 3a). Diversity of pollen used per nest showed a similar pattern, declining from the dry to the wet season (Fig. 3b; Kruskal–Wallis $X_3^2 = 14.60$, $P = 0.002$). Conover post-hoc comparisons show that both wet season collections were significantly lower than the March collection, but only the July collection was lower than the February collection (Fig. 3b). The proportion of social and solitary nests did not differ between collections ($\chi^2 = 0.04$, d.f. = 1, $P = 0.84$).

Discussion

Megalopta bees used ≥ 64 plant species for pollen on BCI, but their diet was dominated by relatively few species. The large number of species present in only the 1998–1999 or 2007

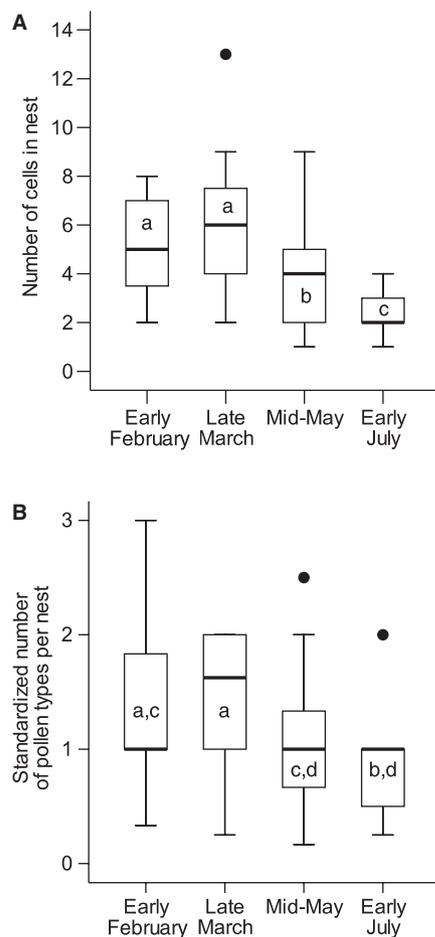


Fig. 3. Seasonal variation in productivity and diversity of pollen sources of *Megalopta genalis* and *M. centralis*. Bars with different letters significantly differed from each other. (a) Productivity (brood cells per nest) by collection date. (b) Standardised number of pollen types per nest (the number of pollen types per nest divided by the number of cells with identified pollen samples in that nest) by season.

collections, the many rarely-used species present in the bees' diet, and the shunning of *D. major* in 2007, suggest that many more species are available to *Megalopta* than are commonly used. Many cells contained pollen of only one species (especially *H. crepitans* and *P. septenatum*), so *Megalopta* are apparently not seeking out less common or more distant species in order to produce mixed provisions, as seen in some other bee species (e.g. Williams & Tepedino, 2003).

Of the species most used for pollen by *M. genalis* on BCI, both *H. crepitans* (Steiner, 1982) and *P. septenatum* (Lobo *et al.*, 2003) are primarily bat pollinated. *Faramea occidentalis* (L.) A. Rich. is visited by sphingid moths at night, and by various Lepidoptera and euglossine bees during the day (Travers, 1999); *S. morototoni* is visited by diurnal bees (Roubik & Moreno, 2009); and *C. platanifolia* is visited by moths and night monkeys at night (Murawski *et al.*, 1990). *Ceiba pentandra* (L.) Gaertn., Fruct. & Sem. and *P. quinata* are also primarily visited by bats (Lobo *et al.*, 2003), and *Cordia bicolor* A. DC., *Spondias mombin*, *D. major*, *Eugenia oerstediana* O. Berg (Croat, 1978) and *Trichilia pallida* Sw. (Chazdon *et al.*, 2003) are visited by insects. The pollination biology of *H. crepitans*, *P. septenatum*, and *C. pentandra* has been studied through intensive observations (Steiner, 1982; Lobo *et al.*, 2003). But none of the other species listed above have well-studied pollination biology, and none at all have been subject to experimental exclusions to test pollinator efficacy, so it remains an open question whether or not *Megalopta* are pollinators. Hopkins *et al.* (2000) hypothesise that nocturnal bees such as *Megalopta* sp., which is one of the most common floral visitors to a species of *Parkia* in Brazil, may have played a key role in the evolutionary transition from insect to derived bat pollination in that genus (Baker & Harris, 1957; Luckow & Hopkins, 1995, reviewed in Fleming *et al.*, 2009).

In general *Megalopta* bees temporally track pollen availability at the population level and opportunistically use preferred sources when available, as evidenced by the relative abundance of the three most frequently used plants, *H. crepitans*, *P. septenatum*, and *Faramea* sp. An association between relative use and availability is weaker for less frequently used species, which may result from our inability to distinguish pollen to the species level for the genera *Spondias*, *Trichilla*, *Eugenia*, and *Cordia*. Additionally, individual trees distant from the flower traps may have flowered at different times from those recorded in the traps.

Our spatial data do not support the prediction that *Megalopta* select pollen resources opportunistically on the basis of proximity. Pollen use differed between nests, but distance to pollen source did not predict pollen use. Nest-to-nearest-tree distances establish only minimum, not actual, foraging distances flown by the bees. These were not informative for the wet season collections when *Megalopta* were using very common species, and were limited in the dry-season analyses because the nearest tree may not have been in flower. Finally, in some cases it was not possible to identify all pollen to species. In spite of the limitations of nearest-tree analyses, if distance to pollen source strongly influenced pollen use we would still expect to see neighbouring nests using

similar species of pollen, which we did not. Moreover, specific analyses of the two most important pollen sources in this study, *P. septenatum* and *H. crepitans*, showed no effect of distance on productivity. The correlation between productivity and longest nest-tree distance is probably a result of the fact that nests with more cells (the measure of productivity) are more likely to include pollen from a distant source. Bee size also had no effect on foraging distance, suggesting that flight energetics are not important at the spatial scale of 50 ha. Distance to pollen source at this scale is apparently not important to *Megalopta* bees in spite of their severely restricted foraging time. This observation is consistent with flight range studies of similarly sized diurnal bees from the temperate zone (Greenleaf *et al.*, 2007, Beil *et al.*, 2008), but contrary to other studies demonstrating a negative effect on productivity with distance at a scale of hundreds of metres (Williams & Kremen, 2007; Zurbuchen *et al.*, 2010b).

Even though many flowers in the lowland tropics live only 1 day (Endress, 1994; Travers, 1999), an individual tree may bloom over an extended period of time, and have many flowers on a given night, such as *P. septenatum* (ARS, pers. obs.) and *H. crepitans* (Steiner, 1982). Thus, predictability of pollen may be more important than absolute pollen abundance or quality as factors shaping the evolution of foraging behaviour in bees (Augsburger, 1985; Wcislo & Cane, 1996).

Bee productivity and diversity of pollen found in cells was highest in the dry season, which is when community-level pollen availability and diversity is also highest (Wright & Calderon, 1995). The dry season was also when flowers from the family Malvaceae, which are generally associated with nocturnal pollen consumers (Fleming *et al.*, 2009), were most common in the bees' diet. Our quantitative sampling (2007) may have underestimated the importance of Malvaceae flowers in the bees' diet because our collections occurred after the flowering peaks of the malvaceous trees *C. pentandra* (December) and *Ochroma pyramidale* (Cav. ex Lam.) Urb. (November–December), and in an area with few individuals of *P. quinata*, all of which were present in our 1998–1999 collections and previous collections of *Megalopta* pollen (Roulston, 1997; Wcislo *et al.*, 2004). Even though the bees heavily used *P. septenatum* and other Malvaceae trees in the dry season, the overall diversity of pollen in brood cells was also most diverse during this season. Thus it is unclear if the decrease in productivity (number of brood cells) as the wet season progressed was driven by the decline of Malvaceae, especially *P. septenatum*, pollen availability, or pollen availability in general.

As with nocturnality in general (Park, 1940), dim-light foraging behaviour in bees represents a resource specialisation (Linsley & Cazier, 1970; Wcislo & Cane, 1996; Wcislo & Tierney, 2009). Access to nocturnal flowers without competition from diurnal bees may compensate for the extremely short foraging time available to *Megalopta*, especially because many tropical-forest bee communities are dominated by social stingless bees. These stingless bees monopolise significant amounts of floral resources (Roubik, 1989), and can competitively exclude other bees from a given resource (Nagamitsu & Inoue, 1997; Nieh *et al.*, 2003, Lichtenberg *et al.*, 2010).

Thus, while *Megalopta* bees are severely time limited, their short foraging windows may help them avoid other limiting factors.

Conclusions

The floral landscape in a neotropical forest is spatially and temporally heterogeneous for foraging bees. *Megalopta* bees foraging on the 50-ha plot of BCI used more than 64 species of pollen, but relied heavily on just a few species. Strong correlations between the relative abundance of a species' pollen in brood cells and flowers in flower traps indicate that *Megalopta* are tracking the temporal availability of pollen. In contrast, we found no evidence that bees chose pollen sources based on distance from their nest. Taken together, these data suggest a paradox: *Megalopta* bees prefer some pollen types over others and can routinely fly hundreds of metres to get them. Yet, while certain species dominate their diet, many others are used. Why do all bees not fly to the preferred pollen source? Or, if all sources are relatively equal, why do so few species dominate their diet? The pollination biology of many tropical species is not well understood, and we lack detailed behavioural studies of most tropical bees, which are needed to better understand the population-level phenomena that we document here in trying to understand the relationships between the reproductive biology of flowering plants and bees.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: [10.1111/j.1365-2311.2012.01367.x](https://doi.org/10.1111/j.1365-2311.2012.01367.x)

Figure S1. Pollen abundance by species (or lowest identified taxonomic group) from the 1998 to 1999 collection of *Megalopta genalis* and *M. centralis* brood cells on BCI. Different patterns represent the relative abundance of each sample in the brood cell from which it was collected.

Figure S2. Mean minimum distances between nests of *Megalopta* bees and pollen source plants. Grey bars represent nests with brood cells that contained pollen from each plant species and white bars nests that did not contain pollen from that plant species.

Table S1. Statistical comparisons of mean minimum distances between nests of *Megalopta* bees and pollen source plants. 'w/pollen' refers to nests containing pollen of the given species; 'w/o pollen' refers to nests not containing pollen of the given species. N refers to the number of nests in each group. Test statistics for independent sample *t*-tests without equal variance assumed are presented for each species. 'Number of individuals' refers to the number of individuals of each plant species on the plot included in the analysis (see Methods for description of which individuals were included and which collections were used for each species).

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