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The decades-long recovery of nocturnal bees in logged forests is counteracted by broad resource range and reliance on pioneers

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ACKNOWLEDGMENTS

This work was funded by the Deutsche Forschungsgemeinschaft (DFG), Research Unit REASSEMBLY (FOR 5207; sub-projects LE2750/12-1 and KE1742/13-1). The research and collection permits were granted through Contrato Marco MAE-DNB-CM-2021-0187 by the Ministry of Environment of Ecuador. We thank Martin Schaefer and Citlalli Morelos-Juarez for allowing research in their reserves, Sebastián Escobar for handling export permits, Anika Schopf for processing pollen samples, and the staff of both reserves for support: Katrin Krauth, Julio Carbajal, Jender Vélez, Bryan Tamayo, Lady Condoy, Leonardo de la Cruz, Jefferson Tacuri, Vicente Vélez, Alcides Zambrano, Yadira Giler, Patricio Encarnacion, Adriana Argoti, and many others.

AUTHOR CONTRIBUTIONS

SDL, AK, GB, and UMD conceptualized the research. AK, SDL, and GB acquired and managed the funding. UMD performed fieldwork and data collection, sample processing, and data curation. CR and UMD identified the specimens. UMD performed data analysis and wrote the manuscript draft. All authors contributed critically to the last manuscript draft.

DATA AVAILABILITY

All data and codes used to reproduce the analyses will be made publicly available at a GitHub repository (https://github.com/) upon acceptance. For review, data and code have been uploaded as Supplementary Information.

Main text

ABSTRACT

Nocturnal bees are elusive pollinators for which little and fragmented evidence of their dietary breadth is available. Moreover, despite their assumed relevance as pollinators of tropical plants, there is no information on how nocturnal bees respond to the loss of suitable habitats and forest succession. Here, we investigated the recovery of *Megalopta* bees, a prominent group of nocturnal pollinators, within a forest regeneration chronosequence in northwestern Ecuador. We also assessed the group's resource use and the recovery of interaction networks by employing next-generation sequencing on pollen loads. *Megalopta* bees showed low resistance and delayed recovery, as abundance had not recovered to pre-disturbance forest levels after 38 years of succession. Stratification was the strongest recovery driver, with bees strongly associated with old-growth canopies. In contrast, their diet was broad, encompassing more than 120 plant species. However, the bulk of pollen loads was constituted by pioneer species, while primary forest trees and plants with specialized nocturnal pollination systems were less represented. The use of diverse resources not necessarily tied to old-growth forests thus contributed to network stability across succession. We provide the first molecular assessment of the diet of a dominant group of nocturnal bees, expanding the understanding of their consumption of floral resources. While dietary breadth may buffer the adverse effects of disturbance on the group, their low resilience and dependence on the canopies of old, structurally complex forests, likely for nesting, suggests that nocturnal bees are quite vulnerable to the loss of large portions of primary habitats.

Keywords: Chocó-Darien, Ecuador, forest succession, interaction networks, Halictidae, *Megalopta*, metabarcoding, resilience.

INTRODUCTION

The global collapse of insect diversity threatens to disrupt a range of essential ecosystem processes, from the maintenance of soil function to the pollination of most angiosperms and food web support (van der Sluijs, 2020). The loss of primary habitats and their conversion for land use is the leading driver of insect decline, acting in synergy with climate change and other anthropogenic disturbances such as pesticides, with pollinators being particularly sensitive (Dicks et al., 2021; Sánchez-Bayo & Wyckhuys, 2019). The decline of bees, the leading group of pollinators globally (Brown & Paxton, 2009), leads to the disruption of pollination networks and has adverse effects on the life cycle of plants, ecosystem dynamics, and forest recovery (Ferreira et al., 2013; Kovács-Hostyánszki et al., 2019; Montoya-Pfeiffer et al., 2020; Neuschulz et al., 2016). However, there are still significant knowledge gaps regarding the effects of disturbance on insect pollinators and their interaction networks with plants, especially for nocturnal taxa such as moths (Hahn & Brühl, 2016) and nocturnal bees (Freitas et al., 2009).

The latter encompasses a few selected genera, mainly from the families Colletidae, Halictidae, and Apidae (Wcislo & Tierney, 2009), which are thought to have adopted the nocturnal and crepuscular habit as an evolutionary escape from interference competition with diurnal insects (Smith et al., 2017). Being able to exploit both nocturnal (e.g., bat- and moth-pollinated species) and late-flowering diurnal flowers (Carvalho et al., 2012; de Araujo et al., 2020; Franco & Gimenesb, 2011; Smith et al., 2012), these bees may that may contribute to overall network connectivity and ecosystem stability. While nesting biology and sociality have been investigated for some species (e.g., Janzen, 1968; Santos et al., 2010; Smith et al., 2003), the interaction ecology and knowledge on the vulnerability to disturbance of this elusive group is lagging in the tropics, despite its importance as fundamental ecosystem service provider (Cordeiro et al., 2021). *Megalopta* Smith, 1835 (Halictidae) is the dominant group of Neotropical nocturnal bees. It is constituted of 35 known species of large, facultative social Augochlorini with adaptations to a crepuscular and nocturnal life, mainly in the form of enlarged ocelli that aid in light perception (Moure & Melo, 2022; Smith, 2021). These adaptations have attracted the interest of researchers working, e.g., on circadian rhythms, temperature regulation, and visual acuity of bees (e.g., Greiner et al., 2004; Kelber et al., 2006; Wcislo et al., 2004). However, due to the same nocturnal habits, the group is rarely included in pollinator diversity assessments. Thus, their ecology, habitat requirements, response to disturbances, and plant resource specialization are poorly known (although seasonality has often been explored in the group; see Smith et al., 2012, 2019; Wolda & Roubik, 1986).

Moreover, although scarce and isolated observations at plants suggest that *Megalopta* visit bat- or diurnal bee-pollinated species (Araujo et al., 2020; Hopkins et al., 2000; Lobo, 2021; Oliveira et al., 2016; Siqueira et al., 2018; Smith et al., 2017), diet assessments and resource requirements from the bees' perspective are rare. Smith et al. (2012) performed the only thorough assessment of the pollen use of Megalopta bees on Barro Colorado island via microscopy and described temporal patterns in the consumption of floral resources by the genus. Although pollen loads were diverse, most pollen grains originated from a few large and bat-pollinated trees, suggesting a relatively high fidelity to specific plant species. Such a diet specialized on a few canopy chiropterophilous plant species, a derived and relatively rare syndrome (Fleming et al., 2009), might threaten these bees' survival and provisioning if significant proportions of primary forests are removed or fragmented. Given the assumed ecological importance of this group in the Neotropics, including the pollination of crop species (Cordeiro et al., 2021), the current knowledge of dietary requirements, resource specialization, and pollination by *Megalopta* bees is somewhat fragmented and descriptive. Moreover, there is no information on population trends toward habitat disturbance or along recovery gradients.

We thus aimed to assess the recovery of nocturnal bees in a well-resolved succession chronosequence in the Chocó-Darien Biodiversity Hotspot of western Ecuador. We investigated their dietary breadth and interaction networks through pollen metabarcoding. The Chocó region is a mosaic of intense land and remnants of preserved forests that suffers from fast deforestation rates, offering a suitable and unique setting to examine the patterns of recovery of these bees and their interaction networks. Due to the group's sensitivity to desiccation and heat resulting from their unique nocturnal habits (Gonzalez et al., 2023) and their supposed reliance on slow-growth, canopy trees found in primary forests, we suggest the following hypotheses: (i) *Megalopta* bees will present low resistance to disturbance and low resilience (slow recovery) due to harsher abiotic conditions found in sites with no or early canopy formation (active and early successional plots) and to the lack of specific resources associated with old-growth forests. Moreover, similarly to the results of Smith et al. (2012), we expect to find a wide range of plant genera on the pollen load of *Megalopta* by employing high-throughput pollen sequencing, but (ii) interaction networks should be specialized and dominated by a few bat- or moth-pollinated trees found in old-growth forests, with active and early successional forest showing considerably smaller and generalized networks, most likely containing exogenous interactions from individuals foraging within forests.

MATERIALS AND METHODS

Study site

The study was carried out in the Río Canandé (0°31’33.4 “N, 79°12’46.0” W) and Tesoro Escondido (0°32’30.9 "N, 79°08'41.9"W) reserves in Chocó-Darien ecoregion of northwestern Ecuador. The site is a typical lowland tropical rainforest (Af climate, Köppen scale), with a mean temperature of 23°C and up to 6000 mm of annual precipitation, with a dry season between June and July and a rainy season between October and November (Escobar et al., 2024). The site consists of large extensions of primary forest dotted by human settlements and villages, with frequent and intensive land use for rearing cattle and growing crops, particularly cacao monocultures. Collection was carried out in 62 50x50 m plots belonging to a successional chronosequence consisting of 12 active disturbance plots [six cacao plantations (CA) and six pastures (PA)], 17 regenerating plots, previously cacao plantations (CR, 1–37 years of regeneration), 16 regenerating plots, previously pastures (PR, 1–35 years of regeneration) and 17 old-growth forests (OG), where disturbance has not been registered (more details on the chronosequence in Escobar et al., 2024). Two collection campaigns were carried out between March and May (32 plots) and October and December (30 plots) 2022, each containing half of each plot type.

Collection of bees and pollen samples

Megalopta bees were collected in each plot with white vane traps (Singh et al., 2022) equipped with a Lepi-LED mini light (Brehm, 2017), set to the mixed (visible and

UV lights). Chloroform fumes were used as a fast-killing agent. The light was placed at the center of the vanes and attached to a power bank and a digital timer. Each plot had one trap placed on the ground (ca. 1.5 m above ground), set to function between 18:00 and 06:00 of the next day. Additionally, because *Megalopta* bees can be associated with the canopy (Janzen et al., 1968), we also installed one trap in the canopy of all plots with a significant canopy cover and at least one tree with 15 m of height or taller (N = 26; all 17 OG plots, 4 CR plots, and 5 PR plots) using a pulley system set with a bow (Diniz et al., 2025). We always installed traps at the highest possible branch on the plot (15 – 37 m above ground). On the day following sampling, bees were identified via specialized literature (Gonzalez et al., 2010; Santos & Melo, 2015). After identification, we checked each specimen under a stereomicroscope for pollen on the leg's scopa or abdomen. Whenever present, we collected a leg or scraped the pollen off the abdominal scopa, depending on placement, pooled samples across individuals of the same species per plot (which ranged from one to three individuals), stored at –20 °C, and sent for molecular analysis.

Environmental variables and plant diversity

The number of years after abandonment is not the only variable tied to forest succession; it can be complemented by a series of environmental variables that affect the colonization of plants and the occurrence of animals. Therefore, we also measured the following five predictive variables for each plot: (i) elevation (m a.s.l.), which affects temperature and humidity and may play a role in the distribution of heat-intolerant nocturnal bees (Gonzalez et al., 2023); (ii) forest connectivity, which is tied to fragmentation and may affect the dispersal ability of pollinators (Didham et al., 1996) and was measured as the amount of forest in a 500 m buffer around each plot's centroid using the latest ESRI database and sourced from Escobar et al. (2024); and (iii) flowering plant diversity, which affects pollinator distribution and diversity via resource availability (Zimmerman & Pleasants, 1982) and was measured as the Shannon diversity of plants flowering on each plot at the time of the sampling. We performed plant surveys by walking the entire 50x50 m area and recording any flowering plant on sight, either directly (flowers on the plant) or indirectly (flowers or traces of flowers from canopy trees on the ground), thereby obtaining a list of floral morphotypes with their respective abundances. Additionally, the (iv) strata from which the samples were collected, either the understory or canopy, were included as an additional predictive variable and a proxy for stratification.

Molecular analysis

Pollen samples underwent multiplexed next-generation sequencing DNA metabarcoding (Bell et al., 2017; Keller et al., 2015) for the ITS2 region. DNA extraction, quality control, library preparation, and sequencing followed the protocol of (Sickel et al., 2015), with hands-on details described in Campos et al. (2021), and were carried out in Germany (Ludwig-Maximilians-Universität München). Bioinformatics followed the pipeline available at https://github.com/chiras/metabarcoding_pipeline (version 8c8536b, Leonhardt et al., 2022). The pipeline uses VSEARCH (Rognes et al., 2016) for quality filtering, merging, dereplication, and definition of amplicon sequence variants (ASVs) through denoising. Taxonomy was assigned with an iterative approach, with first direct global alignments and a threshold of 97% against a localized database. This database was created using BCdatabaser (Keller et al., 2020) and a list of plant species in Ecuador. The remaining unclassified ASVs were compared against a global vascular plant database (Quaresma et al., 2024), and VSEARCH global alignments were used with a threshold of 97%. The remaining unclassified reads were hierarchically classified to the lowest possible taxonomic level using SINTAX (Edgar, 2016) against the same database with a threshold of 0.8. Using the *phyloseq* R package (McMurdie & Holmes, 2013), negative control samples were assessed, and suspicious European taxa ASVs were removed. ASVs were aggregated at the species level and transformed to relative read abundances. Low abundance taxa below 1% of the sample contribution were removed from such samples according to positive control sample results. After filtering, data was used to build an a*ij* adjacency interaction matrix, where a given interaction *a* corresponds to the number of samples of bee species *i* containing pollen from plant species *j*.

Afterward, each plant taxon identified at least to the genus level was classified in terms of their (i) life habit when reproductive adults (herbs, shrubs or creepers; pioneer tree; understory tree or treelet; old-growth tree – including canopy, subcanopy, and emergent trees; epiphyte or liana), (ii) the primary floral resources offered for pollinators (nectar, pollen, resin, oil, or other), and (iii) the pollination system shown by the flowers [diurnal bees, nocturnal bees, moths, bats, birds, diurnal generalists, small diverse insects (SDI), or wind/ambophily). Details on each classification, the categories, the literature, and the databases used can be found in the Supplementary Material (Table S1).

Statistical analysis

Recovery of community parameters and interactions

Analyses were performed in R Studio (v. 4.1.0). To assess the recovery of the *Megalopta* community, we measured four parameters per plot: (i) abundance; (ii) diversity, measured as the rarefied exponential Shannon entropy, for which abundance-based rarefaction was performed to facilitate cross-sample comparisons (Chao et al., 2014); (iii) the ratio of captured bees carrying pollen; and (iv) the total number of interactions determined via metabarcoding.

We employed a generalized linear mixed-effect model (GLMM) for each response parameter above, setting the years after abandonment and disturbance legacy (pastures or cacao plantations) as explanatory variables. We set the collection plot as a random-effect variable for the abundance and diversity models to account for the inclusion of two strata in LR and OG plots (pollen was not found in several samples, leading mostly to one sample per plot for the pollen carryover and number of interactions models). Abundance was fitted with a Poisson error distribution, diversity and ratio of pollen carriers with a Gaussian distribution, and the number of interactions was log-transformed and fitted with a quasipoisson distribution. These error families were chosen to maintain residual normality and homoscedasticity. Old-growth forests have no recovery age and were thus left out of these models. The OG median for each parameter was used as a reference level representing the pre-disturbance state. To account for a possible stratification of bees, the medians of the OG canopy and understory samples were used as independent reference levels.

To examine the role of environmental variables (elevation, forest connectivity, plant diversity, and stratification) on the response parameters, we built a global model with all predictive variables for each parameter, again including the collection plot as a random-effect variable. OG forests were included, and plot age categories [active, early regeneration (1–14 y), late regeneration (15–38 y), and old-growth] were used as proxies of the regeneration gradient and added as a predictive variable. We set an interaction factor between the age category and the collection stratum in all models, as canopy formation is associated with age. Error families for the global models were the same as above, except for abundance, which was fitted with a negative binomial distribution to account for overdispersion, and number of interactions, which was fitted with a Gaussian distribution. Pairwise model selection for each global model was performed by multi-model inference using the *MuMIn* package (Bartoń, 2024) to exclude non-plausible models. The variation of the corrected Akaike Information Criterion compared to the most plausible model (ΔAICc) was employed as the exclusion criteria. Models with ΔAICs ≥ 2.0 were considered equally plausible, and the coefficients of the plausible models were averaged based on model weight (Burnham & Anderson, 2002).

Resource centrality and interaction network structure

To identify the key resource types consumed by *Megalopta*, we estimated each plant taxon's centrality in the pollen transfer network, measured by its weighted closeness centrality. Closeness centrality (ranging from zero to one, with one representing a highly central and generalist species) quantifies the number of shortest paths crossing a given node (species) in a graph and, thus, the proximity to all others in the network, serving as a proxy for importance (Martín González et al., 2010). Centrality was then compared across plant growth habits categories, primary floral resources offered by the host plant, and pollination systems of the host plant through Kruskal-Wallis tests followed by post-hoc Dunn tests.

Moreover, we assessed network structure along the successional gradient. As several plots did not possess pollen samples, we pooled interactions according to the four age categories described in the previous section. We calculated the following metrics for the resulting networks: (i) Interaction Shannon diversity (H’) and (ii) linkage density (LD), i.e., the mean number of links per species weighted by the number of interactions (Dormann et al., 2009), both calculated with the *bipartite* package (Dormann et al., 2008). Higher H’ and LD values indicate rich, evenly distributed interactions and a denser, interconnected network. Finally, we measured (iii) the average similarity of interactions to OG forests (sOG). For the latter, we built an occurrence matrix of each unique interaction at all plots, and interactions underwent a non-metric multidimensional scaling (NMDS) with a Bray-Curtis distance ($k = 2$). The inverse Euclidean distance of each non-OG plot to the OG centroid was taken as a similarity value to old-growth forests, with a value of sOG = 1 meaning that a plot lies exactly on the OG centroid and is thus not distinguishable from OG forests. A PERMANOVA was employed to assess if age types vary significantly.

The visualization of the 25 most abundant plant taxa (higher relative read abundances) in pollen loads was aided with a phylogenetic tree, queried from the Open Tree of Life (OTL) project’s synthetic tree via the *rotl* package (Michonneau et al., 2016).

RESULTS

The recovery of abundance, diversity, and interactions

We captured 493 bees (473 females, 20 males) from four species: *Megalopta genalis* (Meade-Waldo, 1916) (334, 67.7% of captures), a large species belonging to the *genalis* group that could not be keyed out (*Megalopta* sp., potentially *M. sodalis*) (68, 13.8%), *Megalopta amoena* (Spinola, 1853) (90, 18.4%) and (iv) one male individual of nocturnal Augochlorini close to *Megaloptidia* (Supplementary Information, Fig. S1). Since non-*Megalopta* bees were negligible, bees will be henceforth collectively referred to as "*Megalopta"* for simplicity. Thirty-five females from 19 plots had pollen on their bodies, resulting in 28 pooled pollen samples, of which 27 were successfully sequenced.

Bees were rare on plots undergoing active disturbances but increased in abundance and diversity along the chronosequence with no significant difference between legacies (Fig. 1a–b). Bees, however, were considerably more abundant in old-growth forests, specifically in canopies. Their abundance showed low resistance and reached only 41.6% of the OG canopy median by the end of the chronosequence (38 years), which equals 8.3% of the median value observed for OG canopies (Fig. 1a). With a similarly low resistance (31.4% of OG canopy median), diversity recovered considerably faster and reached the observed median of OG canopies in late successional forests (Fig. 1b). Conversely, the ratio of pollen carriers was higher in early regeneration plots and decreased along the chronosequence, but increased again in OG canopies (Fig. 1c). The number of interactions did not vary across the chronosequence (Fig. 1d).

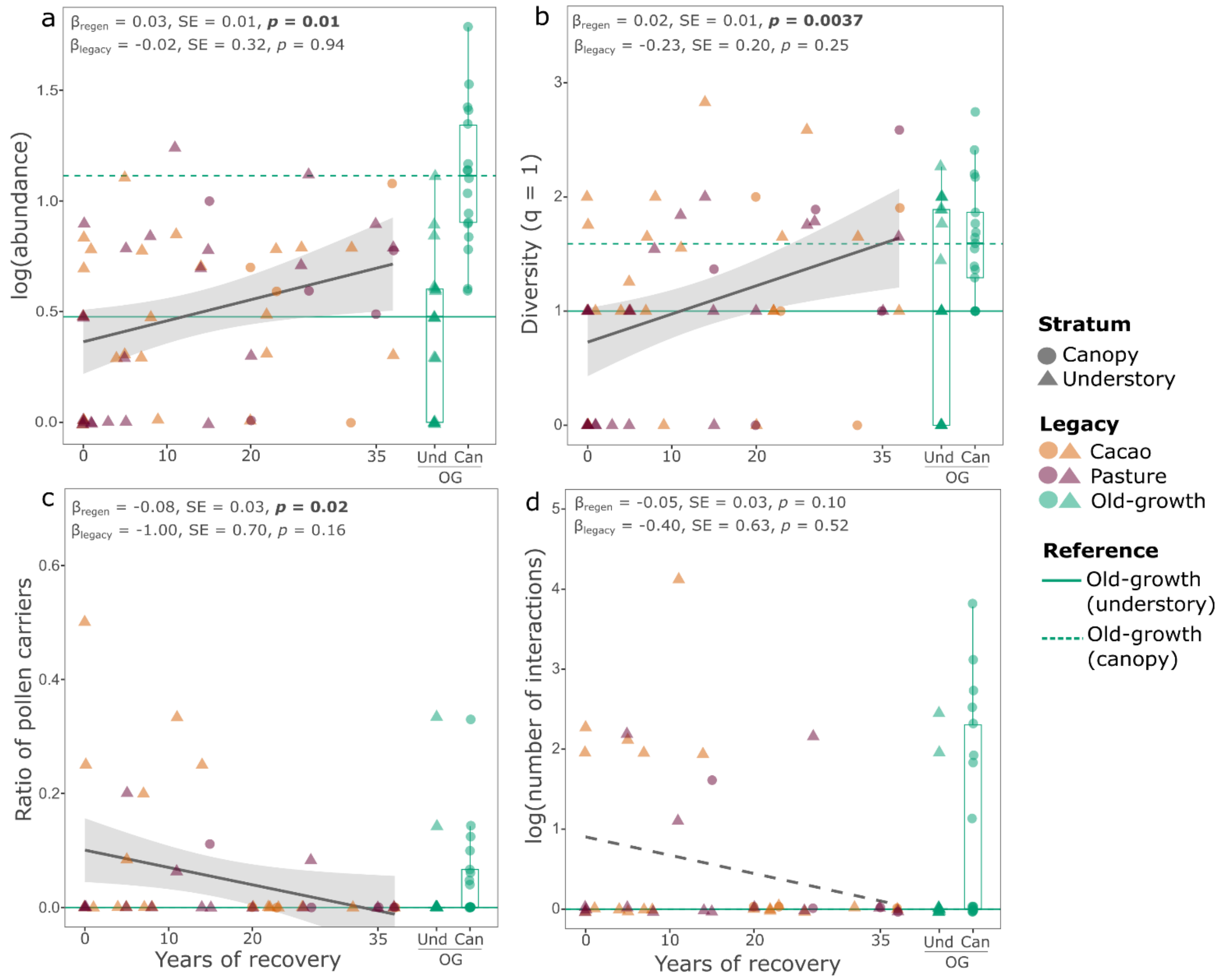

Figure 1. The recovery trajectories of nocturnal *Megalopta* bees along a recovery chronosequence in Ecuador in terms of (**a**) abundance, (**b**) diversity (rarefied exponential Shannon diversity, q = 1), (**c**) the ratio of bees carrying pollen, and (**d**) the total number of interactions assessed via pollen metabarcoding. Black lines and gray zones represent the fitted models and standard errors. Dashed lines indicate non-significant models. The estimates (β), standard error (SE), and significance (*p*) of each model are depicted in the upper left corner of each graph. On the right of each graph, old-growth forests (OG) are shown as a reference state before disturbance, with samples separated into canopy (Can) and understory (Und). Dashed and solid horizontal lines represent the median of the OG canopies and understories, respectively. Samples are colored according to plot legacy, i.e., current or previous use as cacao or pasture, and shaped according to stratum.

The most plausible models (ΔAIC < 2.0) for the recovery of the abundance, diversity, and pollen carryover (including old-growth forests) are shown in Table S2 (Supplementary Information). Considering these models, the abundance of *Megalopta* was significantly affected by the forest stratum, with bees showing a considerably higher abundance in canopies ($\beta = 1.75$, adjusted SE = 0.35, $p < 0.001$). The interaction between stratum and age was also significant, with the understory harboring more bees only at late regenerations ($\beta = 1.70$, adjusted SE = 0.56, $p < 0.005$). Only one model containing the forest stratum was plausible for diversity (Table S2), and bees were also more diverse in canopies ($\beta = 0.47$, aSE = 0.18, Z = 2.65, $p < 0.01$). Conversely, only forest connectivity significantly and negatively affected the ratio of pollen carriers ($\beta = -0.04$, aSE = 0.01, $p = 0.02$). The same negative effect was observed for the number of interactions ($\beta = -0.41$, aSE = 0.15, $p = 0.007$), with interactions also less frequent in the understory ($\beta = -0.66$, aSE = 0.30, $p = 0.03$).

Resource centrality

After filtering, 249 interactions with 124 plant species from 72 genera and 38 families were observed (Supplementary Information, Tab. S3). Eighteen Amplicon Sequence Variants (ASVs) were only identified at the family level. The most common genera were *Clusia* (Clusiaceae) (8 species), *Cecropia* (Cecropiaceae) (6), *Guarea* (Meliaceae) (6), *Piper* (Piperaceae) (5), and *Miconia* (Melastomataceae) (5). Pollen loads were dominated by the pioneer trees *Clusia nemorosa* and *Cecropia insignis* (Fig. 2a). Overall, nectar was the dominant type of primary resource offered, and SDI and diurnal bee-pollinated plants were the most frequent pollination systems (Fig. 2a, for details, see the Supplementary Information, Tables S1 and S3). In terms of species numbers (all interactions considered), plant habits were roughly equally distributed, while nectar and pollen were the dominant resource types. Small Diverse Insects, diurnal bees and moths accounted for ca. 75% of the pollination systems of plants involved in interactions (Fig. 2, b).

In terms of importance in the network, pioneer trees showed the highest centrality, significantly differing from all other plant habit types except old-growth canopy trees ($\chi^2 = 10.41$, df = 4, $p = 0.03$) (Fig. 2c). Centrality did not significantly differ between resource types ($\chi^2 = 4.76$, df = 3, p = 0.19), even though post-hoc pairwise comparisons indicated a significantly higher importance of resin-rewarding plants when compared to pollen- and nectar-rewarding plants (Fig. 2c, see SI Tables S1 and S3 for details). Centrality did not vary among pollination systems ($\chi^2 = 5.17$, df = 6, p = 0.52).

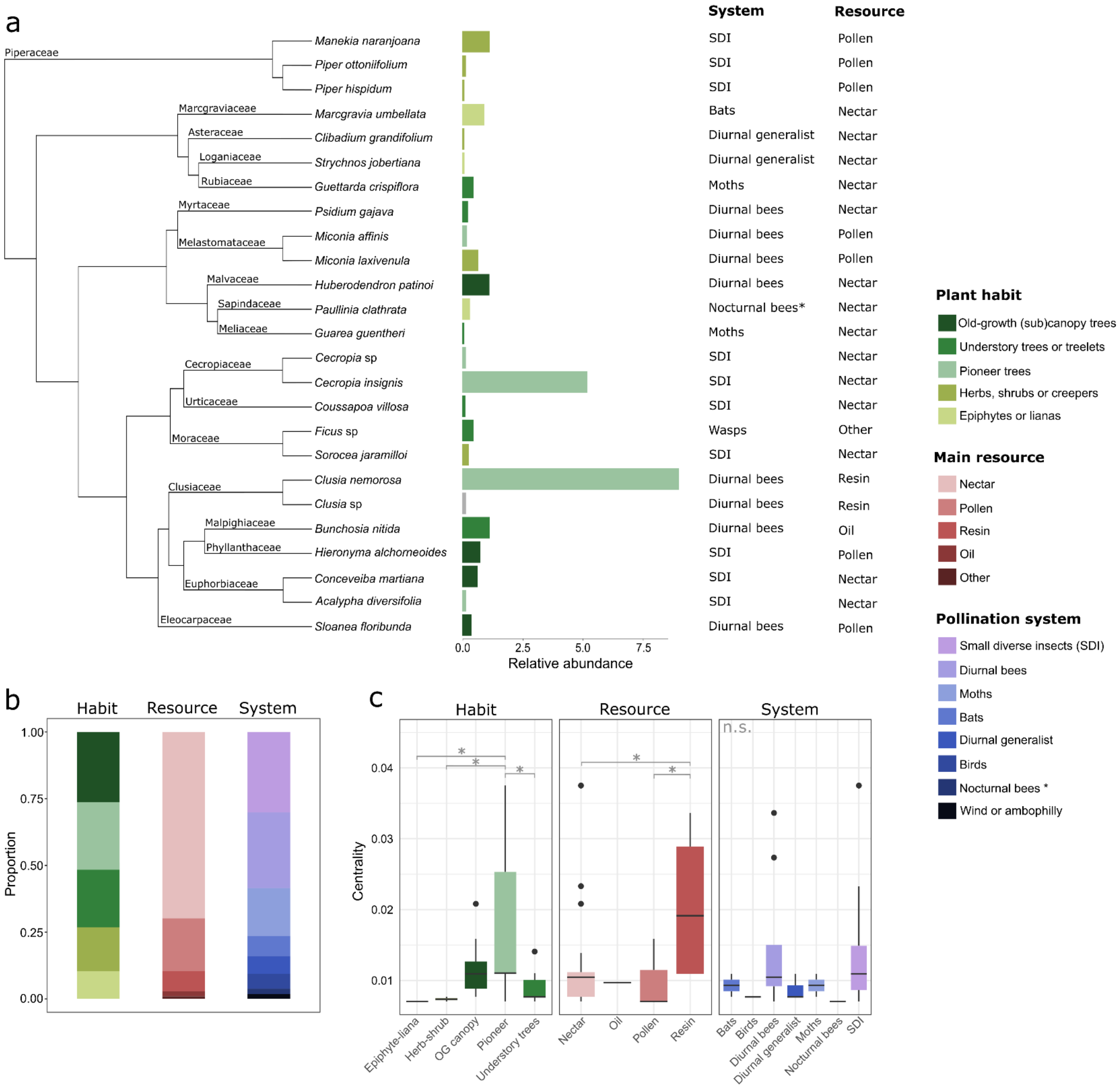

Figure 2. Summary of the resources consumed by *Megalopta* bees inferred via the metabarcoding of pollen loads. (**a**) The 25 main resource plants are represented by the relative abundance of reads in pollen pooled across all samples. Plants are colored according to their habit categories, pollination system, and main floral resource offered. (**b**) The relative proportions of plant habits, primary resources offered, and pollination systems across all observed interactions. (**c**) The distribution of plant network centrality values

across habits, main resources, and pollination systems, considering all non-singleton species (more than one interaction). A bar and asterisk between two groups indicate a significant difference. n.s. = non-significant. *The visitation by *Megalopta* occurs in the genus (Supplementary Information, Tables S1 and S3). SDI: Small diverse insects.

Interaction networks and interaction composition

Network structure changed considerably across the successional gradient. Interactions were rarely observed in active disturbances, in which important species (e.g., *Clusia, Guarea*) and primary resource types offered by plants (resin) were not present (Fig. 3). Interaction diversity, linkage density, and the range of plant habits, resource types, and pollination systems were higher in early successional plots and comparable to those of old-growth forests. Late successional forests had remarkably few interactions, and network structure was similar to that of active disturbance (Fig. 3).

The successional stages highly overlapped regarding interaction composition, including the reference OG forests (PERMANOVA, stress = 0.096, F = 1.01, R^2 = 0.18, df = 3, p = 0.41). Additionally, OG forests were highly variable, as indicated by the moderate similarity of OG plots to their centroid (sOG = 0.62 ± 0.15). Nonetheless, active plots had the lowest similarity to OG, followed progressively by early and late successions, the latter comparable to OG forests despite the small network size (Fig. 3).

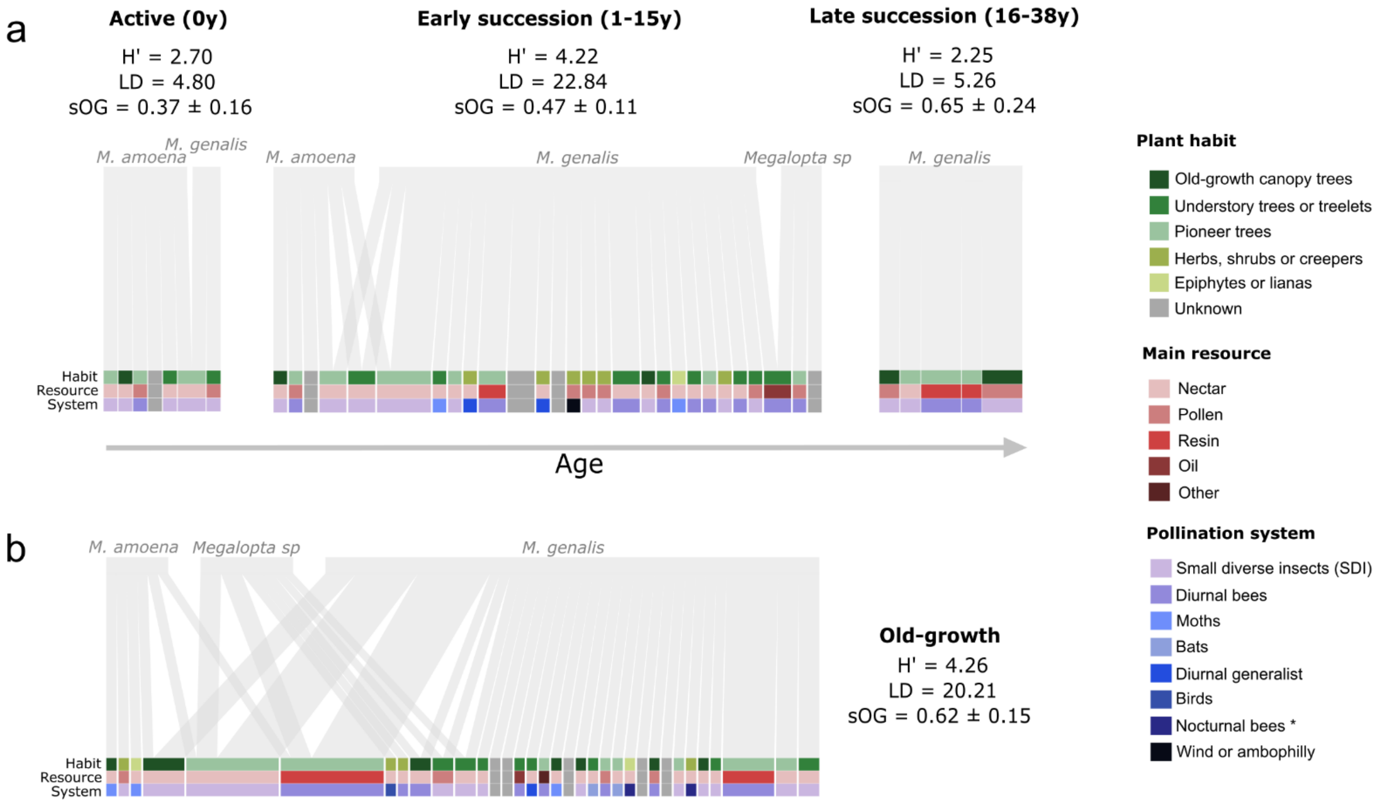

Figure 3. The structure of pollination networks and interaction diversity (**a**) across the successional gradient, divided into active disturbances (0 years of regeneration), early successional plots (1-15 years), and late successional plots (>15 years). The reference old-growth forest is shown below (**b**). Bee species are on top and plant species are on the bottom, identified by their habits, main floral resources, and pollination systems. Networks were built only with interactions that had a relative abundance above 0.01 to improve visualization, but metrics were calculated using all interactions. H': interaction Shannon diversity, LD: linkage density, sOG: similarity to the old-growth forest (see methods).

4. DISCUSSION

This study sheds light on the habitat usage and vulnerability to disturbance of *Megalopta* bees, as well as their recovery trends and their visitation to flowering plants. Bees showed a strong stratification and association with old-growth canopies in their abundance and diversity, presenting low resistance at active disturbances. While diversity recovered to reference levels within the four decades presented by the chronosequence, abundance did not fully recover. Diversity, however, was in general, low, with a maximum of three species per plot, which hinders a concrete interpretation of this trend due to the small space for variation across plots. In contrast to abundance and diversity, pollen carryover was more frequent on active sites or in early regenerating forests. These opposite trends of occurrence and plant visitation, allied with the prominence of pioneer plants in pollen loads, suggest that the high abundance of *Megalopta* in pristine forests is not mainly driven by resource availability and that they frequently forage in nearby open areas.

Therefore, the bees' apparent dependence on OG canopies might be only partly associated with the concentration of floral resources in tropical canopies (Nadkarni, 1994), but may, to a greater extent, be related to the availability of nesting substrates. In fact, *Megalopta* bees excavate nests in dead branches and lianas that are usually suspended above ground (Santos et al., 2010; Smith et al., 2008). Janzen (1968) suggested that *Megalopta* are more prone to forage and nest in the canopy canopy. Canopies are rich in natural cavities and are frequently populated by cavity-nesting insects (Sobek et al., 2009). Furthermore, although much more light-sensitive than diurnal insects with standard apposition eyes, nocturnal bees do not have superposition compound eyes as found in many moths Greiner et al. (2004). Thus, both their foraging and general orientation are regulated by light intensity (Liporoni et al., 2020), which may be hindered in the dark understory and lead to bees seeking the canopy or open patches for nesting and foraging, respectively. Additionally, *Megalopta* is facultatively social, with up to 10 females per colony (Smith et al., 2003), likely increasing the density of bees near nesting sites and hence trapping rates.

Forest occupancy may also be driven by abiotic stress. Nocturnal bees are susceptible to high temperatures and low humidity (Gonzalez et al., 2023), which may restrict their foraging in the open (as seen by the high proportion of pioneers and light-demanding species in OG samples) to short bouts. Commuting to foraging areas outside the forest is likely enabled by their medium to large size and consequent wider foraging range (Greenleaf et al., 2007; Smith, 2021), in contrast to many eusocial small bee colonies (Grüter & Hayes, 2022). This foraging behavior is further supported by the observed negative effect of forest connectivity on pollen carryover, as foraging bouts would be favored by the proportion and proximity of the matrix surrounding the forest. This dichotomous usage of canopies for nesting and the matrix for foraging potentially also explains the low abundance of bees and interactions in late regeneration plots, where canopy closure is at initial stages, but light-demanding pioneers (e.g., *Cecropia*) have already been out-competed

The evident reliance of *Megalopta* bees on primary and stratified forests in lowland rainforests suggests that the loss of large portions of old-growth forest cover, which significantly increases the harshness of abiotic conditions (McAlpine et al., 2018) and likely leads to the removal of nesting resources, will most likely reduce local *Megalopta* populations. This reliance also possibly applies to other nocturnal or crepuscular bee groups (e.g., *Ptiloglossa*, *Xylocopa*, *Megommation*), other forest-associated nocturnal insects (e.g., moths and beetles, Kirmse & Chaboo, 2020; Ober & Hayes, 2008), and even social diurnal bees that also show a strong reliance on canopies

(Diniz et al., 2025; Ramalho, 2004). Despite their sensitivity to forest loss, *Megalopta* showed a broad resource use, including a myriad of low-abundance plants in their pollen loads, which aligns with our expectations and confirms generalism in the group (Smith et al. 2012). In the event of chronic or moderate habitat loss, *Megalopta* bees may still be able to sustain populations via diet plasticity. Even ambophilous species (e.g., *Paspalum*, Poaceae), which generally possess small generalist flowers and offer small resource quantities (Abrahamczyk et al., 2023), were recorded in pollen loads, indicating that the bees are not selective and can forage even in open grassland habitats.

However, unlike in previous observations (Smith et al., 2012; Wcislo et al., 2004) on the visitation to large-flowered and night-blooming trees [in our site represented mainly by *Inga* (Fabaceae), *Ochroma*, and *Quararibea* (Malvaceae) that were flowering during bee collection], these were not strongly representative in pollen loads in our study. Moreover, pioneer chiropterophilous species that were common on the site (e.g., *Chelonanthus*, Gentianaceae) were peripheral in the network, further indicating that the reliance on the pioneers *Clusia nemorosa* and *Cecropia insignis* is not incidental and may happen in detriment of nectar-rich nocturnal flowers. While *Clusia* primarily rewards resin (Gustafsson & Bittrich, 2002), and while the potential pharmacological or sanitary usage of resin in nests should not be excluded (Erler & Moritz, 2016; Fowler et al., 2019), there is no evidence of resin collection in *Megalopta,* suggesting that bees are foraging on the genus for pollen. The same likely applies to the oil-rewarding Malpighiaceae found in pollen loads. The usage of only a few plant species for pollen provisioning by individual bees was also reported by Smith et al. (2012) and indicates that *Megalopta* does not mix pollen in provisions as observed in other solitary polylectic bees (Eckhardt et al., 2014). Plant selection may thus be driven primarily by pollen density and exposure coupled with plant availability within the landscape (e.g., abundant and open-flowered *Cecropia*), by specific volatile bouquets (Carvalho et al., 2012), or by species-specific nutritional characteristics of pollen (Leonhardt et al., 2024). However, disparities with previous assessments of pollen use (Smith et al., 2012) point out that resource preferences may further depend on the ecosystem, biome, and plant community considered. Stochastic factors, such as the distance of plants from nesting sites or the concentration of certain species in dense and attractive patches, may also play a role in resource selection, as seen in other bees (Jha & Kremen, 2013). The latter is likely the case of *Clusia nemorosa*, which was not recorded in our plots.

In addition to the unexpectedly low pollen carryover from nocturnal flowers, *Paullinia clathrata* (Sapindaceae) - the only genus in the network confirmed to be specialized in nocturnal bees (Cordeiro et al., 2021) - was not dominant in pollen pools. Such an interaction suggests an asymmetry between a specialized pollination system and a generalist pollinator, as is frequently observed in pollination networks (Vázquez & Aizen, 2004). Another curious outcome is the observed interaction with *Souroubea guianensis* (Marcgraviaceae), which has floral traits not associated with any particular syndrome and whose pollinators are still unknown (but nocturnal bees may play a role: Machado & Lopes, 2000). The species is a canopy-occurring liana; therefore direct observations of visitors are difficult (Isabel Machado, pers. comm.). The presence of its pollen on *Megalopta* and the bees' association with forest canopies might hint on a nocturnal bee pollination system. These findings highlight the advantage of animal-centered pollen analysis when placing interactions and pollinator diets in a community context (Vizentin-Bugoni et al., 2018), particularly with the aid of high throughput molecular analysis that may detect rare interactions (Arstingstall et al., 2021).

Our results underline the power of animal-centered molecular methods in assessing resource use by pollinators, especially as stratification may lead to difficulties in their detection in forested ecosystems and due to the logistic limitations in directly assessing interactions at night, particularly in the canopy. These approaches may substantially increase our knowledge on the resource requirements of pollinators and inform us on their foraging strategies and landscape usage. Indeed, the observed ecological generalism of *Megalopta* and the consumption of plants of diverse habits and pollination systems may serve as a lifeline against the loss of primary forests. However, the incomplete recovery of *Megalopta* bees after four decades suggests their vulnerability to large-scale loss of primary forests or the targeted logging of veteran hard-wood canopy species (Asner et al., 2006), which significantly reduces forest structural complexity. These detrimental effects will likely also apply to other nocturnal genera that may undergo abiotic stress, as well as to a myriad of canopy-specialist or cavity-nesting animals, and thus highlight the pressing need to protect primary rainforest habitats. Our results also warrant more detailed examinations of drivers of vertical stratification, differences in foraging patterns in non-forested ecosystems, and the co-dependence between *Megalopta* bees and resin-rewarding and diurnal generalist flowers.

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SUPPLEMENTARY INFORMATION

Figure S1. Specimens from the four (morpho)species of nocturnal bees captured in the research site. a: *Megalopta genalis* (m), the most common species. b: *M. amoena* (m). c: *Megalopta* sp. (f), a species belonging to the "genalis" group that could not be keyed out with the available literature. The species is robust and larger than *M. genalis*, potentially being *M. sodalis*. d: A Nocturnal Augochlorini (m) close to *Megaloptidia*, for which generic identification could not be reached.

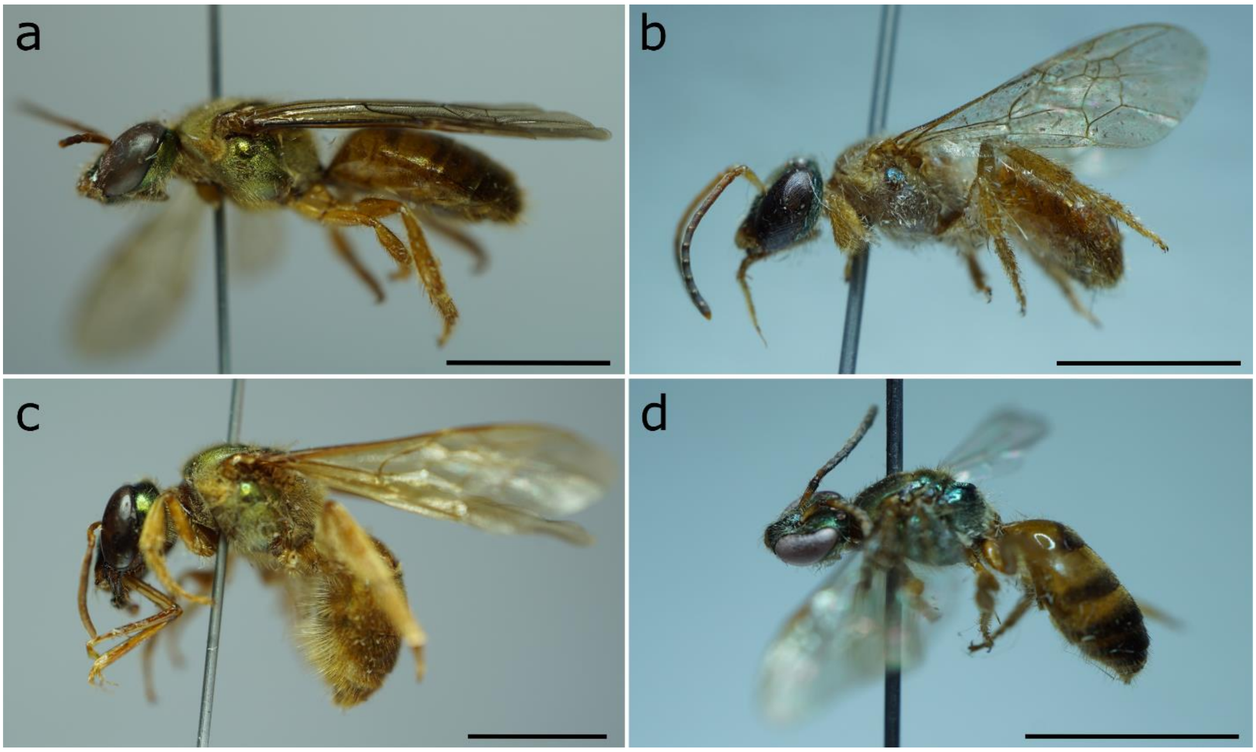

Table S1. Description and details of the categories assigned to plant ASVs found in the pollen loads of *Megalopta* for plant habit, main floral reward, and pollination system (see methods for more information).

Category	Description	Observation
Life habit	A plant’s growth habit at the reproductive stage (flowering).	Inferred from Gentry & Vasquez (1996), Jørgensen & León-Yánez (1999) and Lozano et al. (2024), as well as databases such as the Plants of the World Online (https://powo.science.kew.org/) and the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/).
Herbs, shrubs or creepers	Short-statured plants (< 1.5 m at adult stages) associated with the forest understory or with open areas, clearings, and forest edges.	
Pioneer tree	Plants with a fast growth rate associated with disturbed areas, acting as colonizers and contributing to succession. They are differentiated from other tree types by their aversion to shade and occurrence in open areas/clearings.	The status of pioneer was determined via species-specific literature, and applied to the species of *Cecropia* (Cecropiaceae) (Sposito & Santos, 2001), *Croton* (Euphorbiaceae) (Dalling & Brown, 2009), *Inga* and *Parkia* (Fabaceae) (Hands, 1998; Maekawa & Coelho, 2021), *Ficus* (Moraceae) (REF), *Triplaris* (Polygonaceae) (Brandbyge, 1986), *Isertia* (Rubiaceae) (Boom, 1984), *Matayba* (Sapindaceae) (Ruggiero et al., 2021) and the identified species of *Miconia* (Brokaw, 1985; Pearson et al., 2003). While there is literature on the pioneer status of *Clusia nemorosa* only (Rodríguez-Páez et al., 2024), all species from the genus were assumed pioneers based on their CAM metabolism (Luján et al., 2023).
Understory tree or treelet	Trees associated with the under- and midstories of forests and with a plastic growth habit, varying from ca. 2 m to a dozen meters of height, usually not reaching canopy height in its flowering stage.	
Old-growth (sub)canopy trees	Slow-growing and late-flowering trees associated with old-growth forests, presenting a large diameter at breast height (> 100 cm). Usually presenting dense crown that composes either the forest subcanopy, canopy, or emergent layer	
Epiphytes or lianas	Plants with its growth associated with other plants, either completely separated from the ground (epiphytes) or depending on other plants’ structures for support (lianas).	

Main floral resource	The main resource produced by floral structures for attracting and rewarding pollinators.	Inferred from Gentry & Vasquez (1996), Jørgensen & León-Yánez (1999) and Lozano et al. (2024) as well as databases such as the Plants of the World Online (https://powo.science.kew.org/) and the Global Biodiversity Information Facility (GBIF) (https://www.gbif.org/).
Nectar	The most common floral resource for pollinators, consisting of a sugary solution (e.g., sucrose, hexose) and produced by floral glands (nectaries). Nectar is considered as the main floral reward unless one of the other specialized floral rewards is present and surpasses nectar production and/or when nectar production is absent, e.g., incomplete flowers without a perianth.	Extrafloral nectaries are not considered in this study. In the case of small incomplete flowers with no nectar production but where there is no other form of specialized floral resource, such as in Piperaceae (De Figueiredo & Sazima, 2000), pollen was assumed as the main reward.
Pollen	Reward aimed at female bees, which require pollen for raising progeny. Pollen is often rewarded via feeding anthers, which differ from pollination anthers. Most pollen-rewarding flowers either lack nectar or produce very small quantities of it (Proctor & Yeo, 2009)	Assumed for flowers with specialized pollen-rewarding systems (e.g., buzz-pollination in Melastomataceae and Solanaceae), or when nectar and other resources are lacking (e.g., Piperaceae).
Oil	Production of fatty acids by floral glands, characteristic of the family Malpighiaceae and targeted at female bees (Torretta et al., 2022).	
Resin	Rare floral resource produced by at least two plant families (Clusiaceae, genus *Clusia;* Euphorbiaceae genus *Delachampia*). (Armbruster, 1984).	In our study, this category is exclusive to the genus *Clusia* (Clusiaceae). Extrafloral resin production in other species is not considered.
Other	In this study, it includes only the specialized wasp-pollination in *Ficus* (Moraceae), which offers oviposition sites (Jousselin et al., 2003).	
Pollination system	The main functional group of animals expected to be the plant's most effective pollinators, inferred via the set of floral traits and rewards offered by the plant.	Estimated via the set of floral traits presented by the plant, using the criteria of (Faegri & Pijl, 2016; Proctor & Yeo, 2009)
Diurnal bees	Flowers adapted to attracting and being pollinated by bees by offering pollen, resin or oil as main rewards, by showing morphologies adapted to the bodies of bees (e.g., quill-shaped flowers in Papilionoideae), or by presenting a set of floral structures related to bee pollination (i.e, melittophily). These traits include diurnal anthesis, usually blue, pink, or white flowers with nectar guides and/or high anther-corolla color contrast (Faegri & Pijl, 2016).	

Nocturnal bees	Night-blooming plants where the pollination by nocturnal bees has been either assumed or proven. The only representants of this system in our study are *Paullinia clathrata* (Sapindaceae), where the pollination by *Megalopta* has been observed (REF) and Souroubea guianensis (Marcgraviaceae), whose syndrome and pollination system are unknown (Machado & Lopes, 2000). Pollination by *Megalopta* is possible and likely as suggested by the author (I.C. Machado, personal communication).
Diurnal generalists	Species with accessible nectar-producing flowers not tied to a specific insect group, usually pollinated by several species of bees, wasps, butterflies, beetles, etc. Inflorescence often form landing platforms (e.g., Asteraceae, Lamiaceae).
Small diverse insects (SDI)	An agglutinative syndrome, defined by small, inconspicuous, and accessible flowers that usually produce small quantities of nectar and that do not show a specific pollination syndrome (Bawa et al., 1985; Moreira & Freitas, 2020). Species are thus assumed to be pollinated by a variety of small bees, flies, ants, thrips, beetles, etc.
Moths	Here comprising the pollination by both Sphingidae (sphingophily) and other moth groups (phalenophily). Night-blooming flowers with long and narrow tubes or organized in congested inflorescences that serve as a landing platform (phalenophily). May produce a sweet and strong scent (Faegri & Pijl, 2016)
Bats	Flowers characterized by nocturnal anthesis, large brush-, cup-, or campanula-shaped flowers of drab colors that produce a large amount of diluted nectar and usually emit musky odors (Faegri & Pijl, 2016)
Birds	Flowers characterized by long floral tubes, diurnal anthesis, large quantities of diluted nectar, and usually bright red or yellow corollas or bracts (Faegri & Pijl, 2016)
Wind or ambophily	The dispersal of pollen by wind (anemophily) or complemented by the attraction of insects through nectar of pollen offering (ambophily). Common to the families Poaceae and Cyperaceae (Abrahamczyk et al., 2023)

Table 1. Most plausible models (ΔAIC < 2.0) for the effect of plot variables (recovery stage, stratum, elevation, forest connectivity, and plant diversity) on the abundance, diversity (q = 1), the ratio of pollen carriers, and number of interactions of nocturnal *Megalopta* bees. The probability distribution of each model is specified, alongside the corrected Akaike Information Criterion (AICc), the ΔAICc in comparison to the most parsimonious model, the degrees of freedom (df), and weight. NULL: null model. Predictors: plot connectivity (connect), elevation (elev), flowering plant diversity (plantdiv), stratum (strat), and age category (age). The collection plot was added as a random variable for abundance and diversity (1 | plot) (see Methods in the main manuscript for details).

Model	**Probability distribution**	**AICc**	**ΔAICc**	**df**	**R^2**	**Weight**
Abundance	Negative binomial					
~ strat + age + strat*age + (1|plot)		469.2	0.00	8	0.41*	0.310
~ strat + age + strat*age + elev + (1|plot)		472.9	1.32	9	0.40*	0.146
~ NULL		503.6	34.31	3	-	0.000
Diversity (q = 1)	Gaussian					
~ strat + (1|plot)		213.0	0.00	4	0.05	0.514
~ NULL		216.2	3.13	3	-	0.112
Ratio of pollen carriers	Gaussian					
~ connect + plantdiv		-126.2	0.00	4	0.24	0.213
~ connect		-125.5	0.66	3	0.20	0.151
~ connect + strat + plantdiv		-124.9	1.29	5	0.23	0.110
~ connect + strat		-124.7	1.43	4	0.22	0.103
~ NULL		-114.7	11.43	2	-	0.001
Log (Number of interactions)	Gaussian					
~ connect + strat		207.9	0.00	4	0.14	0.223
~ connect + strat + age		209.6	1.67	7	0.07	0.097
~ connect + strat + elev		209.8	1.88	5	0.16	0.087
~ NULL		212.8	4.9	2	-	0.019

* Lognormal R^2

Table S2. List of all the Amplicon Sequence Variants (ASVs) sequenced from the pollen loads from *Megalopta* considered as interactions (>0.01 relative read abundance), and the lowest identifications reached. Each ASV is followed by its plant habit category, main resource type, pollination system, and centrality values (normalized to vary between zero and one) (see Methods of the main manuscript for details on each of these variables). OTUs identified to the family level only, or to a large and variable genus, could not have a habit, pollination system or main resource defined (NA). SDI = small diverse insects.

ASV	Habit category	Pollination system	Main resource	Centrality	OBS
Actinidaceae					
Saurauia herthae	Pioner tree	Diurnal bees	Pollen	0,00	
Anacardicaceae					
Anacardiaceae spc	NA	NA	NA	0,11	
Tapirira guianensis	Old-growth canopy	SDI	Nectar	0,21	
Araliaceae					
Schefflera spc	NA	NA	NA	0,00	1
Sciodaphyllum pedicellatum	Understory trees or treelets	SDI	Nectar	0,09	
Arecaceae					
Bactris spc	Understory trees or treelets	SDI	Pollen	0,00	2
Asteraceae					
Adenostemma spc	Herb, shrub or creeper	SDI	Nectar	0,00	
Asteraceae spc	NA	NA	NA	0,39	
Baltimora recta	Herb, shrub or creeper	Diurnal generalist	Nectar	0,00	
Clibadium grandifolium	Herb, shrub or creeper	Diurnal generalist	Nectar	0,11	
Helianthus annuus	Herb, shrub or creeper	Diurnal generalist	Nectar	0,00	
Vernonanthura patens	Herb, shrub or creeper	SDI	Nectar	0,00	
Cannabaceae					
Trema integerrima	Pioneer tree	SDI	Nectar	0,17	
Trema micrantha	Pioner tree	SDI	Nectar	0,00	
Caricaceae					
Jacaratia spinosa	Old-growth canopy	Moths	Nectar	0,00	
Cecropiaceae					
Cecropia garciae	Pioneer tree	SDI	Nectar	0,24	
Cecropia insignis	Pioneer tree	SDI	Nectar	1,00	
Cecropia pachystachya	Pioneer tree	SDI	Nectar	0,00	
Cecropia reticulata	Pioneer tree	SDI	Nectar	0,24	
Cecropia sp. WuZY-2013K	Pioneer tree	SDI	Nectar	0,21	

Cecropia spc	Pioneer tree	SDI	Nectar	0,58	
Clusiaceae					
Clusia magnoliiflora	Pioneer tree	Diurnal bees	Resin	0,21	
Clusia multiflora	Pioneer tree	Diurnal bees	Resin	0,00	
Clusia nemorosa	Pioneer tree	Diurnal bees	Resin	0,88	
Clusia sp. JA 3635	Pioneer tree	Diurnal bees	Resin	0,00	
Clusia sp. JA 3833	Pioneer tree	Diurnal bees	Resin	0,21	
Clusia sp. JA 3854	Pioneer tree	Diurnal bees	Resin	0,00	
Clusia spc	Pioneer tree	Diurnal bees	Resin	0,70	
Clusia tocuchensis	Pioneer tree	Diurnal bees	Resin	0,00	
Curcubitaceae					
Citrullus lanatus	Herb, shrub or creeper	Diurnal bees	Nectar	0,00	
Eleocarpaceae					
Elaeocarpaceae spc	NA	NA	NA	0,00	
Sloanea laevigata	Old-growth canopy	Diurnal bees	Pollen	0,00	
Sloanea spc	Old-growth canopy	Diurnal bees	Pollen	0,00	
Ericaceae					
Anthopterus revolutus	Herb, shrub or creeper	Birds	Nectar	0,00	
Sphyrospermum microphyllum	Epiphyte or liana	Moths	Nectar	0,00	
Euphorbiaceae					
Acalypha diversifolia	Pioneer	SDI	Nectar	0,21	
Conceveiba martiana	Old-growth canopy tree	Diurnal generalist	Nectar	0,00	
Croton lechleri	Pioneer tree	Diurnal generalist	Nectar	0,00	
Euphorbiaceae spc	NA	NA	NA	0,00	
Mabea occidentalis	Understory trees or treelets	Bats	Nectar	0,11	
Sapium glandulosum	Old-growth canopy	SDI	Nectar	0,11	
Fabaceae					
Brownea multijuga	Old-growth canopy	Birds	Nectar	0,00	
Dussia lehmannii	Old-growth canopy	Diurnal bees	Nectar	0,00	
Fabaceae spc	NA	NA	NA	0,30	
Inga manabiensis	Old-growth fast-growing tree	Moths	Nectar	0,00	
Inga sp.1	Old-growth fast-growing tree	Moths	Nectar	0,00	
Parkia multijuga	Old-growth fast-growing tree	Bats	Nectar	0,21	3
Gentianaceae					
Chelonanthus acutangulus	Herb, shrub or creeper	Bats	Nectar	0,00	
Gesneriaceae					
Besleria filipes	Herb, shrub or creeper	Diurnal bees	Nectar	0,00	
Besleria sp. MLS-2017	Herb, shrub or creeper	Diurnal bees	Nectar	0,00	
Heliotropiaceae					
Heliotropiaceae spc	NA	NA	NA	0,11	
Hypericaceae					
Hypericaceae spc	NA	NA	NA	0,00	
Vismia cayennensis	Understory trees or treelets	Diurnal bees	Nectar	0,00	
Lamiaceae					

Aegiphila alba	Pioneer tree	Moths	Nectar	0,11	
Loganiaceae					
Strychnos cogens	Epiphyte or liana	Moths	Nectar	0,00	
Strychnos jobertiana	Epiphyte or liana	Moths	Nectar	0,00	
Symphonia globulifera	Old-growth canopy	Birds	Nectar	0,11	
Loranthaceae					
Oryctanthus occidentalis	Epiphyte or liana	SDI	Nectar	0,00	
Malpighiaceae					
Bunchosia cornifolia	Understory trees or treelets	Diurnal bees	Oil	0,17	
Byrsonima ligustrifolia	Understory trees or treelets	Diurnal bees	Oil	0,00	
Malvaceae					
Apeiba membranacea	Old-growth canopy	Diurnal bees	Pollen	0,00	
Huberodendron patinoi	Old-growth canopy	Diurnal bees	Nectar	0,18	
Huberodendron spc	Old-growth canopy	Diurnal bees	Nectar	0,00	
Malvaceae spc	NA	NA	NA	0,00	
Pachira trinitensis	Old-growth subcanopy tree	Bats	Nectar	0,00	
Quararibea spc	Old-growth subcanopy	Bats	Nectar	0,00	
Marcgraviaceae					
Marcgravia umbellata	Epiphyte or liana	Bats	Nectar	0,00	
Marcgraviaceae spc	NA	NA	NA	0,00	
Norantea guianensis	Epiphyte or liana	Birds	Nectar	0,00	
Souroubea guianensis	Herb, shrub or creeper	Nocturnal bees	Nectar	0,00	4
Melastomataceae					
Melastomataceae spc	NA	NA	NA	0,09	
Miconia affinis	Pioneer tree	Diurnal bees	Pollen	0,00	
Miconia laxivenula	Pioneer tree	Diurnal bees	Pollen	0,09	
Miconia multiplicata	Pioneer tree	Diurnal bees	Pollen	0,00	
Miconia sp.1	NA	NA	NA	0,00	
Miconia sp.3	NA	NA	NA	0,09	
Rhexia nashii	Herb, shrub or creeper	Diurnal bees	Pollen	0,00	
Rhexia spc	Herb, shrub or creeper	Diurnal bees	Pollen	0,00	
Meliaceae					
Guarea cartaguenya	Old-growth canopy	Moths	Nectar	0,00	
Guarea gentryi	Old-growth canopy	Moths	Nectar	0,00	
Guarea guentheri	Old-growth canopy	Moths	Nectar	0,00	
Guarea kunthiana	Old-growth canopy	Moths	Nectar	0,00	
Guarea macrophylla	Old-growth canopy	Moths	Nectar	0,21	
Guarea spc	Old-growth canopy	Moths	Nectar	0,00	
Ruagea glabra	Old-growth canopy	Moths	Nectar	0,00	
Trichilia pallida	Understory trees or treelets	SDI	Nectar	0,00	
Monimiaceae					
Mollinedia latifolia	Understory trees or treelets	Diurnal bees	Nectar	0,00	
Moraceae					
Brosimum spc	Old-growth canopy	SDI	Pollen	0,00	
Ficus sp. Clement 184	Pioneer tree	Diurnal bees	Other	0,00	5
Maclura tinctoria	Old-growth canopy	Wind or ambophily	Pollen	0,00	

Maquira guianensis	Old-growth canopy tree	Bats	Nectar	0,00	
Perebea xanthochyma	Old-growth canopy	SDI	Nectar	0,00	
Sorocea jaramilloi	Understory trees or treelets	SDI	Nectar	0,30	
Sorocea muriculata	Understory trees or treelets	SDI	Nectar	0,00	
Sorocea spc	Understory trees or treelets	SDI	Nectar	0,11	
Musaceae					
Musa acuminata	Herb, shrub or creeper	Bats	Nectar	0,00	
Myrtaceae					
Psidium guajava	Understory trees or treelets	Diurnal bees	Nectar	0,11	
Phyllanthaceae					
Hieronyma alchorneoides	Old-growth canopy	SDI	Pollen	0,36	
Piperaceae					
Manekia naranjoana	Herb, shrub or creeper	SDI	Pollen	0,09	6
Peperomia spc	Epiphyte or liana	SDI	Pollen	0,00	6
Piper brachypodon	Herb, shrub or creeper	SDI	Pollen	0,00	6
Piper flagellicuspe	Herb, shrub or creeper	SDI	Pollen	0,00	6
Piper hispidum	Herb, shrub or creeper	SDI	Pollen	0,00	6
Piper ottoniifolium	Herb, shrub or creeper	SDI	Pollen	0,00	6
Piper pequeina	Herb, shrub or creeper	SDI	Pollen	0,00	6
Poaceae					
Paspalum conjugatum	Herb, shrub or creeper	Wind or ambophily	Pollen	0,00	
Polygonaceae					
Triplaris cf. *cumingiana*	Pioneer tree	Diurnal bees	Nectar	0,00	
Rubiaceae					
Cosmibuena grandiflora	Understory trees or treelets	Moths	Nectar	0,00	
Guettarda crispiflora	Understory trees or treelets	Moths	Nectar	0,00	
Isertia laevis	Pioneer tree	Moths	Nectar	0,00	
Palicourea allenii	Understory trees or treelets	Moths	Nectar	0,00	
Palicourea chignul	Understory trees or treelets	Birds	Nectar	0,00	
Rubiaceae PR21-2 spc	NA	NA	NA	0,00	
Rubiaceae spc	NA	NA	NA	0,00	
Sapindaceae					
Matayba sp.1	Understory trees or treelets	SDI	Nectar	0,00	
Paullinia clathrata	Epiphyte or liana	Nocturnal bees	Nectar	0,09	
Sapotaceae					
Pouteria caimito	Understory trees or treelets	Diurnal generalist	Nectar	0,11	
Pouteria torta	Understory trees or treelets	Diurnal generalist	Nectar	0,21	
Sapotaceae sp JSA315 spc	NA	NA	NA	0,11	
Sapotaceae spc	NA	NA	NA	0,00	
Solanaceae					
Juanulloa spc	Epiphyte or liana	Birds	Nectar	0,00	
Schultesianthus coriaceus	Epiphyte or liana	Moths	Nectar	0,00	
Solanaceae spc	NA	NA	NA	0,09	
Urticaceae					
Coussapoa villosa	Old-growth canopy	SDI	Nectar	0,50	

1. The genus is too large and variable for the habit, system or resource to be assumed.
2. Palm probably pollinated by Coleoptera, but grouped with understory trees or treeless and with SDI as it’s the only palm and beetle-pollinated plant in the list
3. Potentially also pollinated by *Megalopta*, as seen in *Parkia velutina* (Hopkins et al., 2000).
4. Syndrome and pollination system unknown (Machado & Lopes, 2000). Pollination by *Megalopta* possible and likely as suggested by the author (I.C. Machado, personal communication).
5. Wasp-specialized pollination, typical of the genus. Classified as “other”.
6. No suggestions in the literature of relevant amounts of nectar in the flowers. Produces very small, incomplete flowers in spikes. Therefore, pollen as main reward is assumed.

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