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Floral resources for key pollinators in intact rainforests versus  
oil palm plantations in Costa Rica

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# Abstract

Tropical rainforests experience major threats by deforestation and habitat fragmentation. The loss of tropical forests and rapid land use changes heavily influence many plant species and their pollinators. Reforestation projects and biological corridors help to reconnect isolated forest patches with larger rainforest areas, allowing wildlife movement and exchange. Some agricultural landscapes, such as oil palm plantations, may also contribute to the connectivity of fragmented habitats. The conservation project “COBIGA” (Corredor Biológico La Gamba) aims to create a biological corridor linking the mountain rainforest of the “Fila Cal” with the lowland rainforest of the Golfo Dulce area in southern Costa Rica. In tropical rainforests, plant reproduction mainly depends on animals as pollen and seed vectors. Thus, promoting the movement of animals ensures increased gene flow also among plant populations. However, little is known about pollinator diversity and their host plant species along biological corridors in the tropics. This study investigates the diversity and abundance of floral resources available within the COBIGA biological corridor and the key pollinator groups that visit these flowers, including bees, butterflies, hummingbirds, beetles, wasps, and flies. The diversity of flowers and their floral visitors was compared in three representative corridor habitats: primary forest, old-growth secondary forest (10 to 40 years after reforestation), and oil palm plantations. Specifically, I observed plant species in each habitat type over a period of two months during the progressing rainy season in the forest understory and palm plantations. My results showed that flowers across all three habitat types were visited by a wide variety of floral visitors and potential pollinators. Oil palm plantations supported high floral abundance and floral visitor richness, suggesting that they may play a valuable role in the biological corridor if floral resource density and diversity are maintained. However, the plant and pollinator communities in oil palm plantations were taxonomically and functionally distinct from those in primary and old-growth secondary forests. Forest habitats harbored more specialized communities, underlining the ecological importance of intact tropical forests for the conservation of pollinators and their plants. This study proposes measures to increase the value of oil palm plantations within the biological corridor. This knowledge will support pollinator conservation by improving resource availability and, thus, allowing for easier migration through oil palm plantations within the corridor. Furthermore, the findings provide valuable insight for future restoration efforts by emphasizing the ecological importance of diverse floral resources in different habitats.

**Keywords:** Costa Rica, conservation, biological corridor, tropical lowland rainforest, oil palm plantation, flowers, pollination, plant-pollinator interaction

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# 1. Introduction

Tropical rainforests are known to be the most biodiverse places on earth, but they are under increasing pressure due to human activities. Their biodiversity is mostly threatened by massive deforestation and habitat fragmentation leading to more and more isolated patches. The reduced connectivity of habitats restricts the movement of animals and plants. Fewer opportunities for migration and dispersal of certain species are becoming a major driver for the loss of many wildlife populations, including pollinators (Krishnan, et al. 2020).

Animal pollination is crucial for regulating ecosystem services and ecosystem restoration (IPBES 2016; CBD 2018), which has led to growing concern about pollinator declines (Pots, et al. 2010). It is estimated that up to 94 percent of all flowering plant species in tropical lowland rainforests are pollinated by animals (Bawa 1990; Ollerton, et al. 2011). Thus, understanding plant-pollinator interactions is critical for the conservation of biodiversity (Ebeling, et al. 2008). The most important pollinator group in Neotropical rainforests are bees, notably orchid bees (Euglossini) and stingless bees (Meliponini). However, several other insect groups (mostly beetles, butterflies, wasps, moths and flies), as well as vertebrates (hummingbirds, bats and non-flying mammals) have developed close interactions with plants in the ecosystem. They act as either specialized or generalist pollinators, and many of these interactions have yet to be discovered (Gutiérrez-Chacón, et al. 2020; Bawa 1990; Etl, et al. 2022).

Plant-pollinator interactions can be analyzed by using the concept of pollination syndromes. This concept suggests that specific combinations of floral traits attract different functional pollinator groups (e.g., Faegri & van der Pijl 1966). Floral traits such as floral shape, color, scent, and reward are considered, as they correspond to the preferences of pollinators (Göttinger, et al. 2019; Fenster, et al. 2004). Despite the concept's limitations and ongoing debate within the field of pollination ecology (e.g., Dellinger 2020; Rosas-Guerrero, et al. 2014; Waser, et al. 1996), it continues to receive support. Additionally, pollination syndromes serve as a valuable framework for understanding the mechanisms underlying floral diversification (Willmer 2011). Fenster, et al. (2004) further state that flower color serves as an important predictor across higher taxonomic levels, such as bees, flies, beetles, moths, birds, and bats.

The Pacific lowlands of Costa Rica have been heavily changed by humans over the past decades and now consist of a patchwork of different habitats (Gutierrez, et al. 2019). Primary forests were largely cleared to establish agricultural land such as rice paddies and cattle pastures. This is also the case in the La Gamba valley (Weber 2001), where the current study was conducted. Oil palm plantations were introduced here about 20 to 40 years ago, after the Banana production declined after 50 years (Beggs & Moore 2013; Stephens 2008). Primary and secondary forests surround the valley and are largely protected by the Piedras Blancas National Park (Weissenhofer, et al. 2008).

The possibility for species to move between intact rainforest patches is crucial to maintain species diversity and it allows gene flow between populations to prevent inbreeding and a resulting breakdown of isolated animal and plant populations (Weissenhofer, et al. 2012). A decline in pollinator abundance and diversity caused by landscape fragmentation may result in lowered reproduction efficiency for some plants, especially those that are pollinator-dependent (Rathcke & Jules 1993).

The establishment of biological corridors is a conservation strategy to increase connectivity in fragmented landscapes (Hilty, et al. 2019). The connection supports animals that function as pollen and seed vectors to move between larger forest areas. Kormann, et al. (2016) showed that corridors are effective and increase overall pollination success. Others noted that reforestation efforts take some time to show results, e.g., bee communities respond differently

under different habitat restoration conditions (Gutiérrez-Chacón, et al. 2020). Therefore, it is important to know how and when plant-pollination interactions may be re-established.

The COBIGA (Corredor Biológico La Gamba) is part of the larger Amistad-Osa Biological Corridor (AMISTOSA) corridor (Regenwald der Österreicher 2025). It aims to reconnect remaining tropical rainforest patches between the mountain forest of the “Fila Cal” and the coastal Pacific lowlands. The COBIGA corridor currently includes a variety of habitats. These habitats are primary forests, old secondary forests, multiple different successional stages of replanted forests as well as agroforestry and agricultural sites (Weissenhofer, et al. 2008). Due to the dominance of oil palm plantations in the area, and in tropical ecosystems worldwide, this habitat plays an important role in the connectivity of rainforests. Other than banana plantations, rice fields or pastures etc., the oil palm plantations provide more shade and microhabitats and hosts various plant and animal species that also occur in nearby primary forests (Ramlah, et al. 2021; Friesenbichler 2013).

During preliminary fieldwork, former Master’s students Maria Lindhuber (Lindhuber 2023) and Giulia Micai (Micai 2023) investigated floral resources in young-growth secondary forests, pastures, roadside fences, and oil palm plantations. They observed numerous floral visitors and key pollinators within the COBIGA biological corridor and identified important nectar and pollen plants for the local pollinator community. With this knowledge in hand, the present study incorporates more observations in old, intact forests and intensifies the investigations in oil palm plantations.

### Aims of the study

The purpose of this study is to document and compare available floral resources for key pollinators in three different habitat types: primary forest, old-growth secondary forest (10 to 40 years of age) and oil palm plantations. The study focuses on the composition and abundance of plants and pollinators and the different pollination systems that are present in each habitat type.

Specifically, this study aims to:

- (i) quantify and compare the diversity, availability, and composition of floral resources in primary forest, old-growth secondary forest, and oil palm plantations;
- (ii) characterize pollination systems and flower visitation patterns;
- (iii) evaluate differences in community compositions of both plant species and floral visitors between primary forest, secondary forest, and oil palm plantations;
- (iv) identify key pollinator groups and evaluate their diversity and abundance in each habitat type;
- (v) contribute to applied knowledge to promote pollinator-friendly management in oil palm plantations in biological corridors.

The research will provide insight into the largely unstudied pollinator community of Neotropical lowland rainforests, as well as the dynamics and loss of their interactions when the ecosystem is converted into oil palm plantations or recovers from deforestation. In order to conserve and restore this valuable ecosystem, extensive knowledge in this field is necessary.

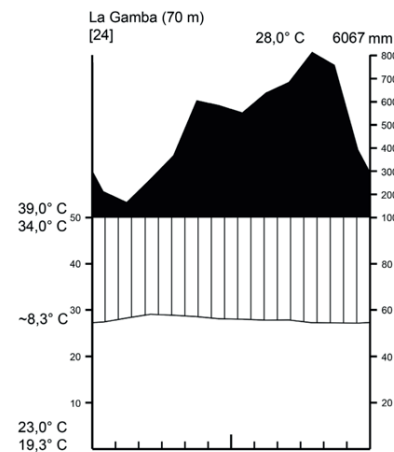


## 2. Material and Methods

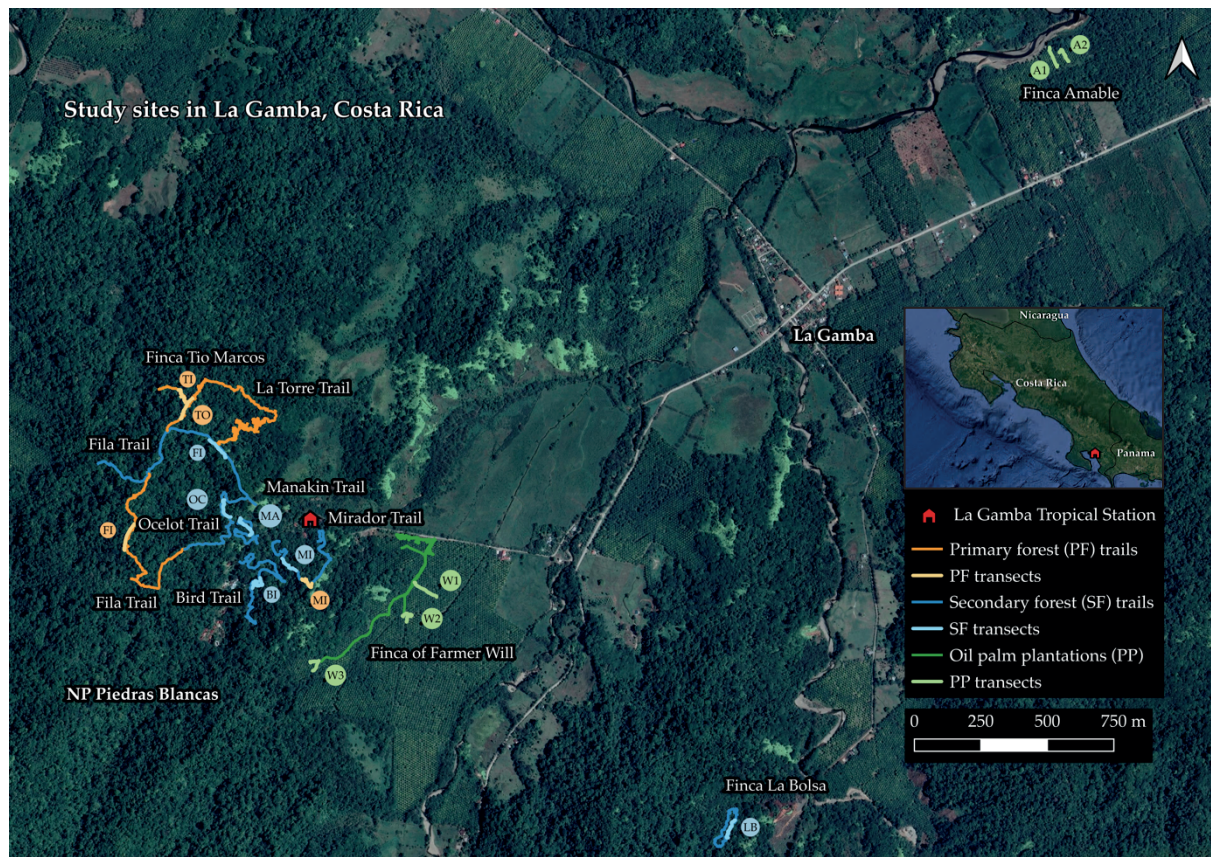
### 2.1. Research area and study sites

The research area is located in the lowlands of the Golfo Dulce region in southwestern Costa Rica close to the village of La Gamba, which is located on the edge of the Piedras Blancas National Park, northwest to the city of Golfito in the Province of Puntarenas (Fig. 2).

The fieldwork was conducted at the Tropical Research Station La Gamba (8°42'03.8"N 83°12'05.6"W, lagamba.at) and neighboring trails of the Piedras Blancas National Park, the Esquinas Rainforest Lodge, as well as oil palm plantations in La Gamba. The study was conducted from August 7, 2022, to October 7, 2022, during Costa Rica's rainy season, which lasts from May to November with the highest precipitation between September and October (Fig. 1). As the study progressed, the intensity of rainfall increased. This posed a major challenge, particularly for observing floral visitors.



**Figure 1** Climate diagram of La Gamba Tropical Station (1998 – 2022)  
© Susanne Pamperl (Huber, et al. 2024)



**Figure 2** Study sites in La Gamba, Costa Rica: 100-meter transects are labeled and highlighted in brighter colors in existing trails in three habitat types: Primary forest (PF, yellow and orange), old-growth secondary forest (SF, light and dark blue), and oil palm plantation (PP, light and dark green). PF sites: Fila Trail (FI), Mirador Trail (MI), Finca Tio Marcos (TI), La Torre Trail (TO). SF sites: Bird Trail (BI), Fila Trail (FI), Finca La Bolsa (LB), Manakin Trail (MA), Mirador Trail (MI), Ocelot Trail (OC). PP sites: Finca Amable (A1, A2), Finca Will (W1, W2, W3) © Melina Maier, based on Google Satellite 2025 with QGIS software.

The map in **Figure 2** shows the location of all study sites selected along the COBIGA biological corridor. In total, 15 study sites were distributed across three different habitat types: primary forest (PF;  $n = 4$ ), old-growth (10 to 40 years old) secondary forest (SF;  $n = 6$ ), and oil palm plantation (PP;  $n = 5$ ). At each site, a transect of approximately 100 meters in length was established along existing trails or within a Finca (see **Tab. 1** for details). These transects were placed in relatively flower-rich sections, compared to the overall floral richness along the corresponding trail. Observations were conducted on both sides of the trail, covering an area of approximately three meters in width and height. GPS tracking was performed using my iPhone 11 (Apple Inc.). A brief description of the sites in each habitat type follows.

**Table 1** Transects, GPS starting and ending point, transect length, and number of transect walks (TW) per transect.

| Habitat type                    | Transect                    | GPS Start (DG)       | GPS End (DG)         | Length | No. of TW |
|---------------------------------|-----------------------------|----------------------|----------------------|--------|-----------|
| <b>Primary forest (PF)</b>      |                             |                      |                      |        |           |
|                                 | Fila ( <i>FI_pf</i> )       | 8.700040, -83.208090 | 8.700940, -83.207780 | 125 m  | 3         |
|                                 | Mirador ( <i>MI_pf</i> )    | 8.699070, -83.202040 | 8.698930, -83.201700 | 137 m  | 5         |
|                                 | Tio Marcos ( <i>TI_pf</i> ) | 8.705040, -83.206030 | 8.705450, -83.206260 | 101 m  | 5         |
|                                 | La Torre ( <i>TO_pf</i> )   | 8.704480, -83.206190 | 8.705160, -83.205760 | 116 m  | 4         |
| <b>Secondary forest (SF)</b>    |                             |                      |                      |        |           |
|                                 | Bird ( <i>BI_sf</i> )       | 8.698760, -83.203740 | 8.699120, -83.203470 | 135 m  | 5         |
|                                 | Fila ( <i>FI_sf</i> )       | 8.703170, -83.204670 | 8.703760, -83.205210 | 117 m  | 3         |
|                                 | La Bolsa ( <i>LB_sf</i> )   | 8.690340, -83.187480 | 8.690930, -83.187240 | 112 m  | 3         |
|                                 | Manakin ( <i>MA_sf</i> )    | 8.701100, -83.204120 | 8.700550, -83.203840 | 124 m  | 3         |
|                                 | Mirador ( <i>MI_sf</i> )    | 8.699770, -83.202720 | 8.699352, -83.202229 | 112 m  | 4         |
|                                 | Ocelot ( <i>OC_sf</i> )     | 8.701730, -83.204710 | 8.701170, -83.204470 | 114 m  | 3         |
| <b>Oil palm plantation (PP)</b> |                             |                      |                      |        |           |
|                                 | Amable 1 ( <i>A1_pp</i> )   | 8.717010, -83.176505 | 8.716360, -83.176240 | 96 m   | 4         |
|                                 | Amable 2 ( <i>A2_pp</i> )   | 8.716550, -83.175840 | 8.716840, -83.176160 | 95 m   | 3         |
|                                 | Will 1 ( <i>W1_pp</i> )     | 8.698480, -83.197440 | 8.698960, -83.198200 | 121 m  | 3         |
|                                 | Will 2 ( <i>W2_pp</i> )     | 8.697810, -83.198580 | 8.697630, -83.198470 | 103 m  | 4         |
|                                 | Will 3 ( <i>W3_pp</i> )     | 8.696250, -83.201740 | 8.695980, -83.201670 | 97 m   | 3         |

### 2.1.1. Primary rainforest (PF)

Four transects were set up in the primary forest. The sites include the Fila Trail, the Mirador Trail, the Finca Tio Marcos, and the La Torre Trail. The sites are characterized by large, old trees with numerous epiphytes on the trunks, many lianas, and low light conditions at the ground level. There are no records of deforestation or reforestation efforts, suggesting that this is primary forest. Some of these trails were made decades ago and are popular destinations for visitors of the Tropical Station. The sites are either protected by the Piedras Blancas National Park or (leased) property managed by the Tropical Station La Gamba.

The Fila Trail is the main trail entering Piedras Blancas National Park from which other trails start or branch off. Shortly after the La Torre Trail branches off, a left turn leads up the slope to a small clearing where the Fila transect (*FI\_pf*) was set up. The Mirador Trail starts at the La Gamba Tropical Station. Primary forest only exists on the ridge of this trail, where I set up the Mirador transect (*MI\_pf*). The Finca La Torre borders the National Park and is owned by the Tropical Station. The La Torre Trail passes through several types of tropical lowland rainforest, including slope, ravine, and ridge forest. The transect (*TO\_pf*) was established on the ridge of the trail near its eastern end. The Finca Tio Marcos is an 80-hectare, leased property adjacent to the Finca La Torre. In the La Torre transect, a path leads north-west in between two trees, just past a signpost. This is where the fourth and final transect (*TI\_pf*) was established.



### 2.1.2. Old-growth secondary rainforest (SF)

The six old-growth secondary forest sites include the Bird Trail, the Fila Trail, the Finca La Bolsa, the Manakin Trail, the Mirador Trail, and the Ocelot Trail. These areas were reforested or replanted at least 10 to 40 years ago (as of the year of data collection, 2022). Some have an agricultural history, such as abandoned cacao plantations, which can sometimes be identified by the presence of cacao trees. Nevertheless, they are now fully covered with forest and therefore considered “intact” in this study. The forests are distinguished by large trees, though they exhibit a lower abundance of epiphytes and lianas compared to primary forests.

The Bird Trail is located at the Esquinas Rainforest Lodge. The trail begins in a disturbed forest with higher light conditions and transitions into overgrown forest, adjacent to a small creek. Abandoned cacao trees indicate that this area has been reforested. The transect (*BI\_sf*) is positioned around the midpoint of the trail. The Fila Trail is the main trail that enters the Piedras Blancas National Park. Beyond the study site, the trail extends through the Valle Bonito to the Rio Bonito. The transect in the secondary forest (*FI\_sf*) was established on the slope close to the entrance of the La Torre Trail. The Finca La Bolsa is located 3 km south of the La Gamba Tropical Station in the valley of the Quebrada La Bolsa. The property features both primary and secondary forest, situated next to the National Park. Part of the area has been used for agricultural purposes. From 2010 to 2012, the Tropical Station's initiative reforested this site. The site is now covered by forest and left undisturbed (lagamba.at 2020). The transect (*LB\_sf*) is positioned near the cabin, crossing a stream twice. The second trail of the Esquinas Lodge is the Manakin (former Riverbed) Trail. This trail is a short walk through secondary forest. The transect (*MA\_sf*) was strategically established where most plant species from other transects have been documented. The Mirador Trail surrounds the Tropical Station and passes through various habitats, including riparian, primary, and secondary forests. The transect (*MI\_sf*) was established at a slope forest in a replanted secondary forest. A popular hiking trail in the Piedras Blancas National Park is the Ocelot Trail, which branches off and is also connected to Fila Trail. At the beginning, the trail leads downhill. The starting point of the transect (*OC\_sf*) is located shortly after the creek-crossing and includes some stairs.

### 2.1.3. Oil palm plantations (PP)

A total of five transects were established within two locally separated oil palm plantations: two transects on the Finca Amable and three transects on the Finca owned by the local Farmer Will Braulio. The agricultural area is characterized by monocultural dominance of palm trees (*Elaeis guineensis*) in a row order on mostly wet soil. Both oil palm plantations were established about 15 to 20 years ago before the time of data collection. Oil palm plantations can provide more shade and microhabitats than other agricultural fields. It is crucial to acknowledge that both oil palm plantations are well-managed (e.g., vegetation on palm trunks, minimal and targeted use of herbicides or no use at all, and extensive mowing or horse grazing), with focus on biodiversity and their function in the corridor. This is a result of an already heightened awareness surrounding these issues in La Gamba.

The first palm plantation (1 ha) is located next to the reforestation area of the Finca Amable, near La Gamba's main street and the river Rio Bonito. The plants that grow between the palm trees are managed and trimmed once a year. Both transects at the Finca Amable (*A1\_pp*, *A2\_pp*) were established in parallel orientation to the oil palms, with some edge areas included. The second plantation (20 ha, owned by Will Braulio) is located next to the Tropical Research Station. Within a 2-meter radius of the palm trees, plants are systematically removed with herbicides. The plantation is also affected by horses that roam freely. These horses have a major impact on the vegetation, affecting its growth through grazing and trampling. The

horses transport palm fruit and materials around the plantation, which has gravel paths to facilitate harvesting and collection of palm fruit. The first transect (*W1\_pp*) is parallel to the palm trees. The second transect (*W2\_pp*) follows the course of a small river that passes through the monoculture. Data collection was conducted on both the left and right banks of the river. The third transect (*W3\_pp*) was located deeper in the plantation, close to the forest boundary.

## 2.2. Data collection

All data collection was conducted during early and late morning hours (6:00 h – 12:00 h). To obtain a comprehensive overview of floral resources and their visitors, I tried to ensure equal numbers of visits to the sites and transects. A variety of digital cameras and video cameras, including a tripod, were used in the field, in addition to binoculars.

### 2.2.1. Floral resource study

A comprehensive inventory of all plants that were flowering (**Tab. 4**) during the study period was conducted during three to five “transect walks” (TW) per transect (for the number of TW, see **Tab. 1**). The number of individuals for each plant species, along with the number of open flowers, was recorded and documented. In the case of Asteraceae, where inflorescences consist of multiple tiny flowers, the number of inflorescences (heads) was counted instead. Plants that were not in bloom during the data collection period were also documented but not included in the data analysis (for data on plants that were not in flower, see **Appendix I**). In addition to photographing the plants, some plant samples were taken to the station and identified in the laboratory. The study included plants from the plantation and forest floors, as well as the forest understory. Since the recorded height was up to three meters, the plants considered were mainly herbs and shrubs, though some epiphytes and lianas were included.

The plant species were mainly identified using two field guides (Gargiullo & Magnuson 2008; Weber 2001), with additional assistance from the iNaturalist ([www.inaturalist.org](http://www.inaturalist.org)) platform or Florian Etl, an expert on local plants. Most of the plant species could thus be identified to species level, some are classified at the genus level, a few at family level, and one forest floor plant in the primary forest is yet to be identified. The “Plants of the World Online” ([www.powo.science.kew.org](http://www.powo.science.kew.org)) website was used to check for plant names and native distribution. The studied plants were classified into pollination syndromes based on floral traits, such as floral shape, color, and rewards, following the criteria described by Faegri & van der Pijl (1966) and Weber (2008), along with other relevant literature.

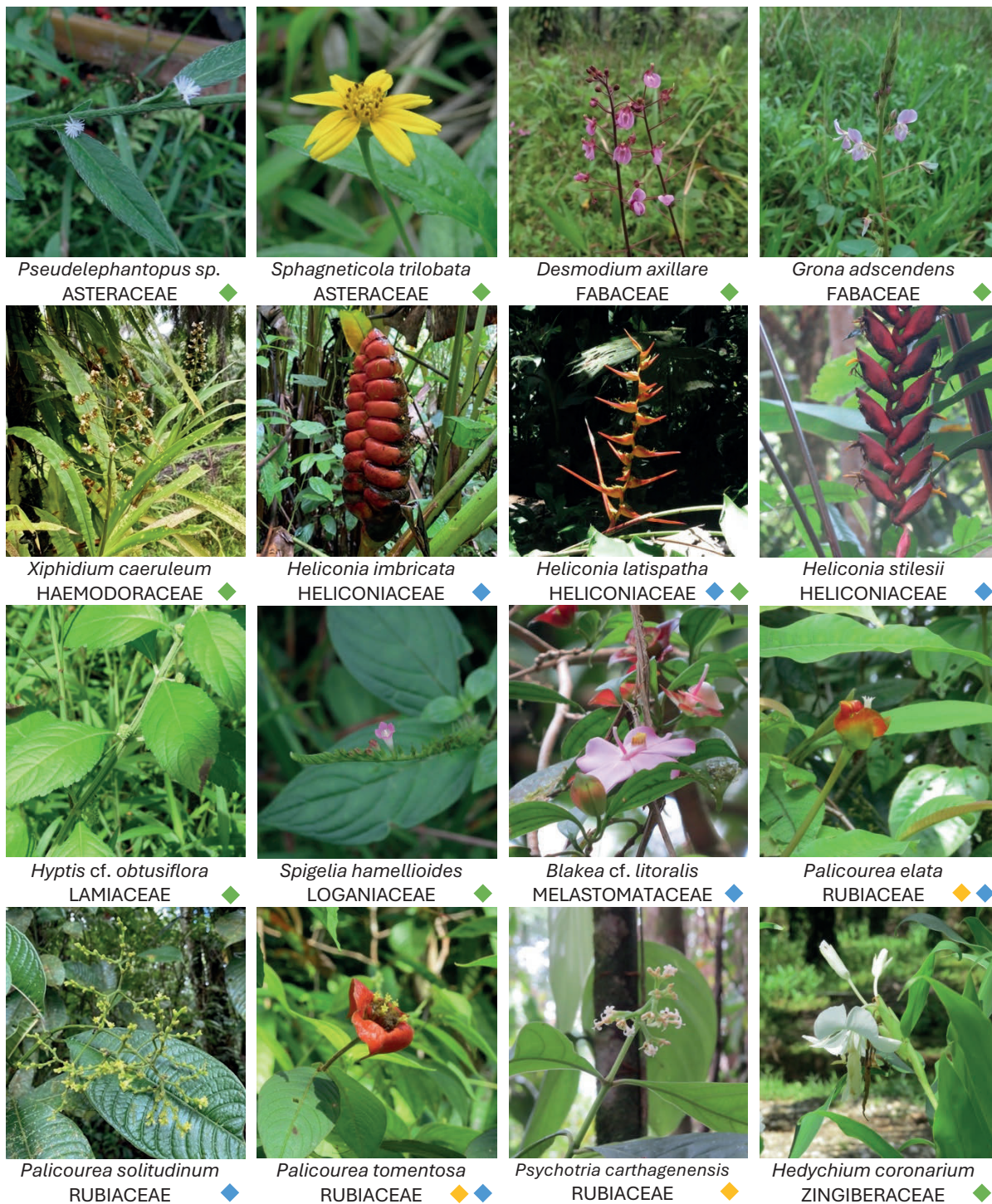
### 2.2.2. Floral visitor study

Two methods were employed to study floral visitors within the transects: (i) observations focused on selected plant species, and (ii) observations on all plants flowering along the transects, during transect walks (TW). Observations that were conducted outside the transects (e.g., on other sections of the existing trails) are marked with \* and listed in the **Appendices II & III** and not included in the data analysis.

#### Focused observations of floral visitors on selected plant species

The selection of suitable plant species for the focused observations was based on their abundance, presumed significance to pollinators, and distribution across the fifteen transects. Ideally, the chosen plant species were present in more than one transect within a habitat type and in more than one of the studied habitat types. However, this proved challenging in oil palm plantations because the plant species composition differed much from the other habitats. Thus, the plants in oil palm plantations were chosen by their abundance and distribution across the oil palm plantation transects. In total, 16 plant species were selected (**Fig. 3**).





**Figure 3** Plants selected for focused observations (15-min and long-term). A total of 16 plant species in nine plant families. The color of the square indicates the habitat type where a given species was present (PF, yellow; SF, blue; PP, green).

In the primary forest, three species were selected to conduct focused observations: *Palicourea elata*, *Palicourea tomentosa*, and *Psychotria cathagenensis*. In the secondary forest, focused observations were made on *Heliconia imbricata*, *H. latispatha*, *H. stilesii*, *Blakea* cf. *litoralis*, *Palicourea elata*, *P. tomentosa*, and *P. solitudinum*, counting six different plant species. In oil palm plantations, nine plant species were selected as observation plants. These include: *Pseudelephantopus* sp., *Sphagneticola trilobata*, *Desmodium axillare*, *Grona adscendens*, *Xiphidium caeruleum*, *Heliconia latispatha*, *Hyptis* cf. *obtusiflora*, *Spigelia hamellioides*, and *Hedychium coronarium*.



Standard observations were conducted by standing next to the plant for 15 minutes in the early and late morning between 06:00 h and 12:00 h. Additionally, long-term observations were made by placing a video camera up to approximately five meters away from a flower (**Fig. 4a**). Extended observation periods of up to six hours with video recording were sometimes necessary due to low visitation rates in certain plant species. Long-term observation increased the chance of documenting a pollinator. The number of open flowers was noted for each plant. The total observation time for each plant species and transect during 15-minute observations and long-term observations are presented in **Table 2**. The total number of observations obtained from 15-minute observations and long-term observations were summed up (**Tab. 6**).

**Table 2** Overview of selected observation plants and the minutes observed in transects in habitat types primary forest (yellow), old-growth secondary forest (blue), and oil palm plantation (green).

| Plant family    | Plant species                    | Observation time (min) |           |            |            |            | Observation time (min) |            |            |            |           |            |           | Observation time (min) |            |            |            |           |            |
|-----------------|----------------------------------|------------------------|-----------|------------|------------|------------|------------------------|------------|------------|------------|-----------|------------|-----------|------------------------|------------|------------|------------|-----------|------------|
|                 |                                  | TOTAL                  | Fl pf     | MI pf      | TI pf      | TO pf      | TOTAL                  | BI sf      | Fl sf      | LB sf      | MA sf     | MI sf      | OC sf     | TOTAL                  | A1_pp      | A2_pp      | W1_pp      | W2_pp     | W3_pp      |
| Asteraceae      | <i>Pseudelephantopus sp.</i>     |                        |           |            |            |            |                        |            |            |            |           |            |           | 15                     |            | 15         |            |           |            |
| Asteraceae      | <i>Sphagneticola trilobata</i>   |                        |           |            |            |            |                        |            |            |            |           |            |           | 165                    | 75         | 45         |            | 45        |            |
| Fabaceae        | <i>Desmodium axillare</i>        |                        |           |            |            |            |                        |            |            |            |           |            |           | 15                     |            |            |            | 15        |            |
| Fabaceae        | <i>Grona adscendens</i>          |                        |           |            |            |            |                        |            |            |            |           |            |           | 122                    | 28         |            | 15         |           | 79         |
| Haemodoraceae   | <i>Xiphidium caeruleum</i>       |                        |           |            |            |            |                        |            |            |            |           |            |           | 692                    |            |            | 367        |           | 325        |
| Heliconiaceae   | <i>Heliconia imbricata</i>       |                        |           |            |            |            | 73                     |            |            | 73         |           |            |           |                        |            |            |            |           |            |
| Heliconiaceae   | <i>Heliconia latispatha</i>      |                        |           |            |            |            | 30                     |            |            | 30         |           |            |           | 185                    | 185        |            |            |           |            |
| Heliconiaceae   | <i>Heliconia stilesii</i>        |                        |           |            |            |            | 15                     | 15         |            |            |           |            |           |                        |            |            |            |           |            |
| Lamiaceae       | <i>Hyptis cf. obtusiflora</i>    |                        |           |            |            |            |                        |            |            |            |           |            |           | 100                    | 15         | 40         | 15         | 15        | 15         |
| Loganiaceae     | <i>Spigelia hamelliioides</i>    |                        |           |            |            |            |                        |            |            |            |           |            |           | 15                     |            |            | 15         |           |            |
| Melastomataceae | <i>Blakea cf. litoralis</i>      |                        |           |            |            |            | 45                     | 45         |            |            |           |            |           |                        |            |            |            |           |            |
| Rubiaceae       | <i>Palicourea elata</i>          | 265                    |           | 220        | 30         | 15         | 107                    | 77         | 15         |            |           |            | 15        |                        |            |            |            |           |            |
| Rubiaceae       | <i>Palicourea solitudinum</i>    |                        |           |            |            |            | 130                    |            |            |            | 15        | 115        |           |                        |            |            |            |           |            |
| Rubiaceae       | <i>Palicourea tomentosa</i>      | 346                    | 93        | 72         |            | 181        | 127                    |            | 97         |            | 15        | 15         |           |                        |            |            |            |           |            |
| Rubiaceae       | <i>Psychotria carthagenensis</i> | 89                     |           | 15         | 74         |            |                        |            |            |            |           |            |           |                        |            |            |            |           |            |
| Zingiberaceae   | <i>Hedychium coronarium</i>      |                        |           |            |            |            |                        |            |            |            |           |            |           | 95                     |            | 95         |            |           |            |
|                 | <b>TOTAL</b>                     | <b>700</b>             | <b>93</b> | <b>307</b> | <b>104</b> | <b>196</b> | <b>527</b>             | <b>137</b> | <b>112</b> | <b>103</b> | <b>30</b> | <b>130</b> | <b>15</b> | <b>1404</b>            | <b>303</b> | <b>195</b> | <b>412</b> | <b>75</b> | <b>419</b> |

During the observations, all floral visitors and their behavior were carefully recorded. The recorded behavior included the duration of each visit, the number of flowers visited, and whether the visitor contacted the reproductive organs (anthers and stigmas) of the flower. Floral visitors that touched the reproductive organs were classified as potential pollinators for the respective plant species.

The visitors were identified either directly in the field, if they were easily recognizable, or captured and examined under a binocular in the laboratory. The insects were collected using glass cups and nets, euthanized with ethyl acetate, and prepared for identification in the lab (**Fig. 4b & c**). The bees collected were identified with the help of Mauricio Fernández Otárola (UCR), a taxonomic specialist working in San José, Costa Rica, at the end of the study. Butterflies and birds were primarily identified using the photographs and videos taken during observations. Specimens that could not be identified to species or genus level were categorized in different morphospecies based on their distinctive characteristics.

To facilitate a more precise discussion on pollination syndromes and key pollinators, and to ensure the data remained manageable, the observed animals were grouped into the following functional groups: *beetle*, *butterfly*, *hummingbird*, *fly*, *large bee*, *small bee*, *true bug*, *wasp*, and an *other* category for insects (e.g., ants, grasshoppers) and spiders that do not fit into the specified groups. Bees of the tribe Euglossini (orchid bees) are referred to *large bee*. Other “large” bees such as bumble bees were not observed during the study period, otherwise they would have been assigned to this functional group. Solitary bees, stingless bees (tribe Meliponini) and all other bees in the clade Anthophila were referred to *small bee*. The categorization of species and morphospecies within these functional groups is provided in **Appendix III**. The functional groups are based on Bawa (1990), and Kress & Beach (1994).



**Figure 4** Documentation, collection, and preparation of floral visitors: (a) Video camera placed next to *Hyptis* cf. *obtusiflora* for long-term observation. (b) Solitary sweat bee (cf. *Augochlora* sp. 1) collected on *Sphagneticola trilobata*. (c) Solitary bee (*Ceratina* sp. 1) collected on *S. trilobata*.

### Floral visitor observations during transect walks (TW)

During the standardized transect walks, floral visitors were observed on all plant individuals flowering within the transect, while slowly walking back and forth along it. During these walk-throughs, the number of floral visitors on each plant was noted, as well as their behavior (see the section above). Each transect was visited three to five times, as in the floral resource study (see **Tab. 1** for the number of TW).

## 2.3. Data analysis

The analysis of floral resources and their visitors in three different habitat types was conducted using a variety of statistical methods. The Microsoft® Excel “Analyze Data” tool was used to calculate, summarize, and analyze data by creating PivotTables and visualizing PivotCharts. Kruskal-Wallis test followed by Dunn’s post-hoc test with Bonferroni correction was used to analyze differences in plant species richness and open flower abundance between habitats. These statistical analyses were performed using the PAST (PAleontological STatistics) software (version 4.17). All species accumulation curves were generated using the Rstudio software (version 4.3.3). The essential R package to calculate and visualize rarefaction and extrapolation of species diversity was “iNext” (Hsieh, Ma, & Chao 2016). The calculation of Shannon-Wiener-Indices ( $H'$ ), Simpson’s Diversity Indices ( $1 - D$ ), and Pielou’s Evenness Index ( $J$ ) was performed using RStudio. The Shannon index is a widely applied metric for quantifying alpha diversity, considering both species richness and species evenness. Higher values in the Shannon Index (0 to 6) indicate greater species diversity. Pielou’s evenness ( $J$ ) is defined as the ratio of the observed Shannon index ( $H'$ ) to the maximum possible richness ( $H'_{\max} = \ln(S)$ ), providing a quantitative measure of species distribution in a sample. The value ranges from 0 (uneven distribution) to 1 (perfectly even distribution).

The map showing the research area and study sites (**Fig. 2**) was created using the open-source geographic information system (GIS) software QGIS (version 3.34), with the GPS data exported and converted to fit the program’s requirements.

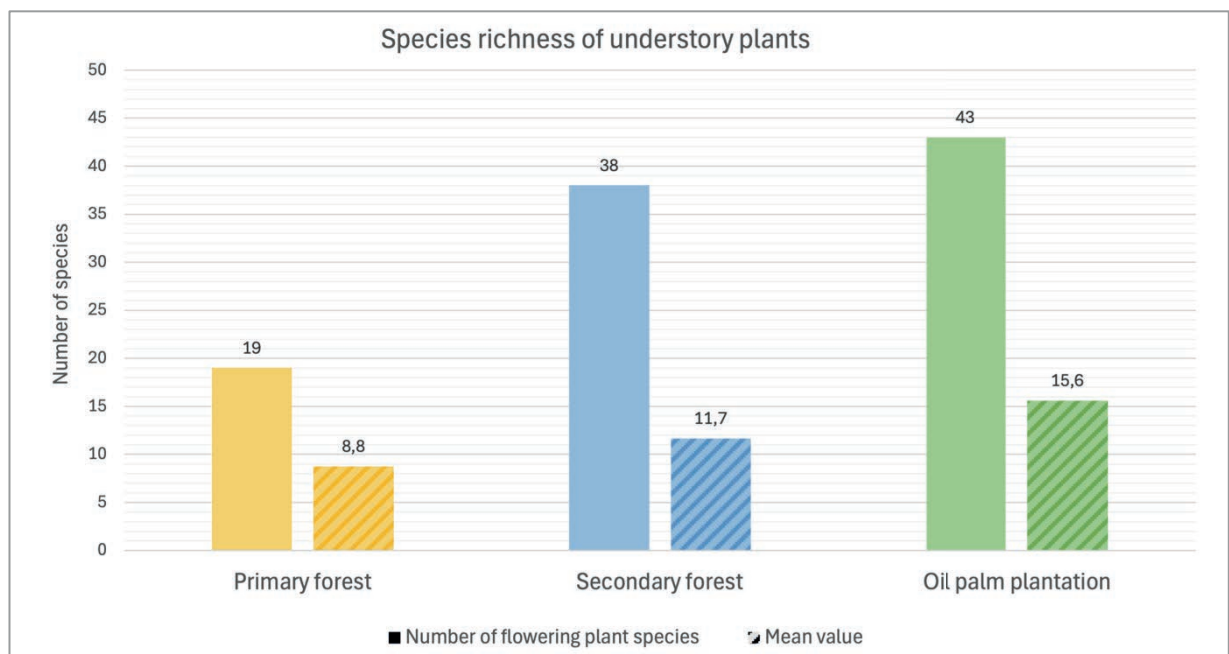
## 3. Results

### 3.1. Floral resources

#### 3.1.1. Species richness

During this study, a total of 84 plant species in 29 plant families were identified at the study sites. In the four transects within the primary forest, 19 different plant species were counted (mean = 9; min-max = 6 – 10). In the six old-growth secondary forest transects, 38 species were counted (mean = 12; min-max = 8 – 14), and in the five transects within the oil palm plantations, 43 different plant species were recorded (mean = 16; min-max = 13 – 26) (**Fig. 5**). The oil palm plantations showed the highest species richness, followed by the old-growth secondary forest, and lastly, the primary forest. The resulting data set revealed a statistically significant difference in the mean number of plant species across primary forest and oil palm plantations (Kruskal-Wallis test:  $H_c = 7,41$ ,  $p = 0,02816$ ).

In terms of native distribution, all documented plant species in the primary forest are native to Costa Rica. In old-growth secondary forest sites and oil palm plantations, two non-native plant species each account for 5% of the total plant species documented in these habitat types.



**Figure 5** Number of flowering plant species and mean value per habitat type. Difference in species richness among habitat types were significant (Kruskal-Wallis test:  $H_c = 7,41$ ,  $p = 0,02816$ ). Dunn's post-hoc test with Bonferroni correction revealed significant difference between primary forest and oil palm plantation ( $p = 0,0228$ ).

#### 3.1.2. Plant species composition

The communities of flowering plant species in each habitat type belonged to several plant families (see **Tab. 4**). The plant families with the highest species richness in all three habitat types were the families Rubiaceae (PF: 7 spp., SF: 6 spp., PP: 4 spp.) and Melastomataceae (PF: 3 spp., SF: 8 spp., PP: 4 spp.). In the primary forest, the 19 flowering plant species belonged to (at least) nine plant families (one species awaits identification). The most species-rich family, with seven out of 19 species, was the family of Rubiaceae, followed by Melastomataceae with three species. In the old-growth secondary forest, 38 plant species belonged to 15 different



plant families. The family Melastomataceae, with eight species, was the most species-rich family followed by Rubiaceae (6 spp.), Marantaceae (5 spp.), and Heliconiaceae (4 spp.). In the oil palm plantations, a total of 43 flowering plant species across 24 different families were documented (excluding the cultivated oil palm *Elaeis guineensis*). The families with the highest richness of species were Rubiaceae and Melastomataceae, each with four species.

An analysis of the overlap in plant species flowering at the time of study in the three habitat types revealed notable differences in species composition and shared taxa. The calculation of the differences and similarities in the composition of plant species in flower indicates that 42% of species in the primary forest (= 8 out of 19) also occurred in old-growth secondary forest. *Episcia lilacina* (Gesneriaceae) was the only species in the oil palm plantations that was also documented in the primary forest. This number accounts for 5% (= 1 out of 19). This species was also the only one found in all three habitat types. Eight species recorded in oil palm plantations have also been identified in the secondary forest. The species overlap therefore is 21%.

As illustrated in **Table 4**, the composition and distribution of plant species and families differed not only between the habitat types but also among transects within the same habitat type. In the primary forest, *Palicourea elata* (Rubiaceae), *P. tomentosa*, and *Becquerelia cymosa* (Cyperaceae) were documented in all four transects, *Heliconia irrasa* (Heliconiaceae) and *Psychotria carthagenensis* (Rubiaceae) were identified in three primary forest transects. In the old-growth secondary forest, no flowering plant species was documented in all six transects, but six plant species were documented in at least four transects. These species include *Palicourea elata*, *P. tomentosa*, and *P. solitudinum* (all Rubiaceae), *Aciotis* cf. *rubricaulis* (Melastomataceae), *Calathea crotalifera* (Marantaceae), and *Heliconia irrasa* (Heliconiaceae). In the oil palm plantations, three species were identified in all five transects: *Hyptis* cf. *obtusiflora* (Lamiaceae), *Grona adscendens* (Fabaceae), and *Cyperus luzulae* (Cyperaceae).

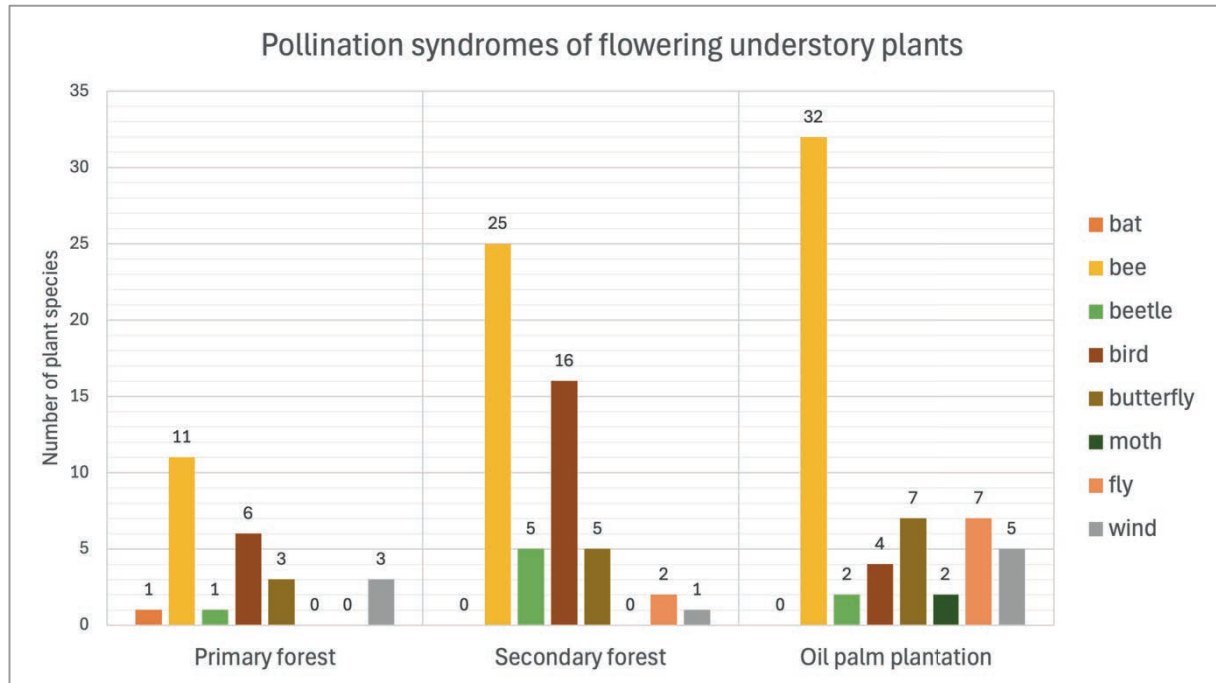
### Pollination syndromes across the three habitat types

Regarding the pollination syndromes determined for each plant species based on their floral traits, including floral shape, perianth (and modified bract) color, and reward, the bee syndrome was the most represented pollination syndrome in all three habitat types (**Fig. 6**). In detail, 56 out of all 84 plant species (67%) had traits that were specialized for bees (melittophily). Another 22% (19 spp.) of the studied plant species were specialized for bird pollination (ornithophily). The remaining species were classified as belonging to other pollination syndromes (e.g., fly-/butterfly-/beetle-/wind-/moth- or bat pollination syndrome). Regarding the floral reward, 83% (70 spp.) of species rewarded pollen, and 64% (54 spp.) rewarded nectar (see **Tab. 4**).

In the primary forest, 58% of the flowers were most likely bee-pollinated and 32% were most likely bird-pollinated. Examples for ornithophilous plants included *Guzmania lingulata* (Bromeliaceae), *Heliconia irrasa* (Heliconiaceae), and some Rubiaceae (see **Tab. 4**). Notably, *Mabea* sp. from the Euphorbiaceae family represented an example of likely bat-pollination (chiropterophily). Additionally, *Philodendron fragrantissimum* (Araceae) was specialized for beetle-pollination (cantharophily). Both these plants were documented in the primary forest. In the secondary forest, 65% of flowers were likely pollinated by bees and 42% were likely pollinated by birds. Noteworthy examples for bird-adapted study plants included four *Heliconia* species (Heliconiaceae) and two *Costus* species (Costaceae). Five plant species in the secondary forest were specialized for beetle pollination. These included *Carludovica drudei* (Cyclanthaceae) and two Arecaceae species, which also had myophilous traits (pollination by flies). In the oil palm plantations, 74% of the plant species were specialized for bee pollination,



while only 9% were specialized for bird pollination. *Lantana camara* (Verbenaceae) was the only plant species adapted to butterflies (psychophily). Both *Piper* species present in oil palm plantations were likely pollinated by beetles and flies. Pollination by moths (sphingophily) was found in two species in the oil palm plantations: in the native *Pentagonia cf. tinajita* (Rubiaceae) and in the naturalized, white-flowered *Hedychium coronarium* (Zingiberaceae). For some plant species, the selected floral traits were insufficient or contradictory to assign a pollination syndrome, so they were assigned as unknown (see **Tab. 4**).



**Figure 6** Number of plant species exhibiting different pollination syndromes per habitat type.

**Table 3** shows the values for diversity indices and evenness. The primary forest had the highest diversity with a balanced distribution of syndromes, while the old-growth secondary forest had a lower diversity and a more uneven distribution, followed by oil palm plantations. The oil palm plantations had the highest number of pollination syndromes, but the bee syndrome dominated strongly, reducing both evenness and overall diversity of pollination syndromes.

**Table 3** Shannon Index, Simpson's Diversity Index, Pielou's Evenness, species richness, and total number of pollination syndromes for flowering plant species in three different habitat types.

| Habitat type                    | Primary forest | Secondary forest | Oil palm plantation |
|---------------------------------|----------------|------------------|---------------------|
| Shannon Index (H')              | 1,47           | 1,35             | 1,46                |
| Simpson Diversity (1 - D)       | 0,717          | 0,679            | 0,664               |
| Pielou's evenness (J)           | 0,82           | 0,76             | 0,75                |
| Species richness                | 19             | 38               | 43                  |
| Number of pollination syndromes | 6              | 6                | 7                   |

↓ **Table 4** Flowering plant species identified in the transects, their floral reward (fr; n = nectar, p = pollen, unk. = unknown), and their assigned pollination syndrome (ps; ba = bat, be = bee, beet = beetle, bi = bird, bu = butterfly, mo = moth, fl = fly, wi = wind, unknown). Plants present in the transect and/or habitat type are marked with "x". Study habitat types: Primary forest (PF), old-growth secondary forest (SF), and oil palm plantation (PP). PF sites: Fila (*FL\_pf*), Mirador (*MI\_pf*), Tio Marcos (*TI\_pf*), La Torre (*TO\_pf*). SF sites: Bird (*BL\_sf*), Fila (*FL\_sf*), La Bolsa (*LB\_sf*), Manakin (*MA\_sf*), Mirador (*MI\_sf*), Ocelot (*OC\_sf*). PP sites: Amable 1 & 2 (*A1\_pp*, *A2\_pp*), Will 1, 2 & 3 (*W1\_pp*, *W2\_pp*, *W3\_pp*).

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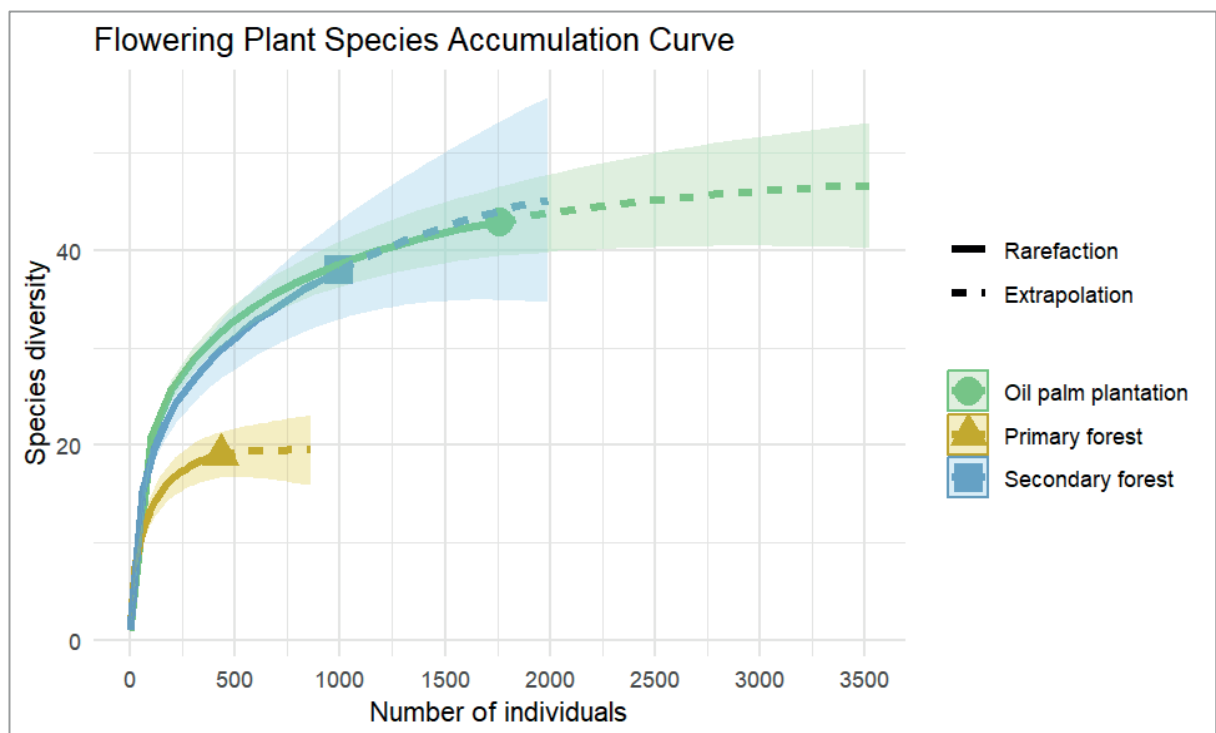
### 3.1.3. Plant species diversity

The sites in old-growth secondary rainforest demonstrated the highest alpha diversity (2,61) and the most even species distribution (0,72). The oil palm plantations had the highest species richness (43 spp.) and total number of individuals (1761). The alpha diversity (2,59) was comparable to that of secondary forest, while the evenness value was lower (0,69) in oil palm plantations. In contrast, the primary forest sites showed the lowest alpha diversity (2,0) and a less even distribution among species (0,68). The Shannon diversity indices ( $H'$ ) and Pielou's evenness ( $J$ ) for the plant communities are shown in **Table 5**.

**Table 5** Shannon Index, species evenness, species richness, and total number of individuals of plant species flowering at the time of study in three different habitat types.

| Habitat type                | Primary forest | Secondary forest | Oil palm plantation |
|-----------------------------|----------------|------------------|---------------------|
| Shannon Index ( $H'$ )      | 2,008298       | 2,614523         | 2,589154            |
| Pielou's evenness ( $J$ )   | 0,682064738    | 0,718752185      | 0,688385069         |
| Species richness            | 19             | 38               | 43                  |
| Total number of individuals | 430            | 994              | 1761                |

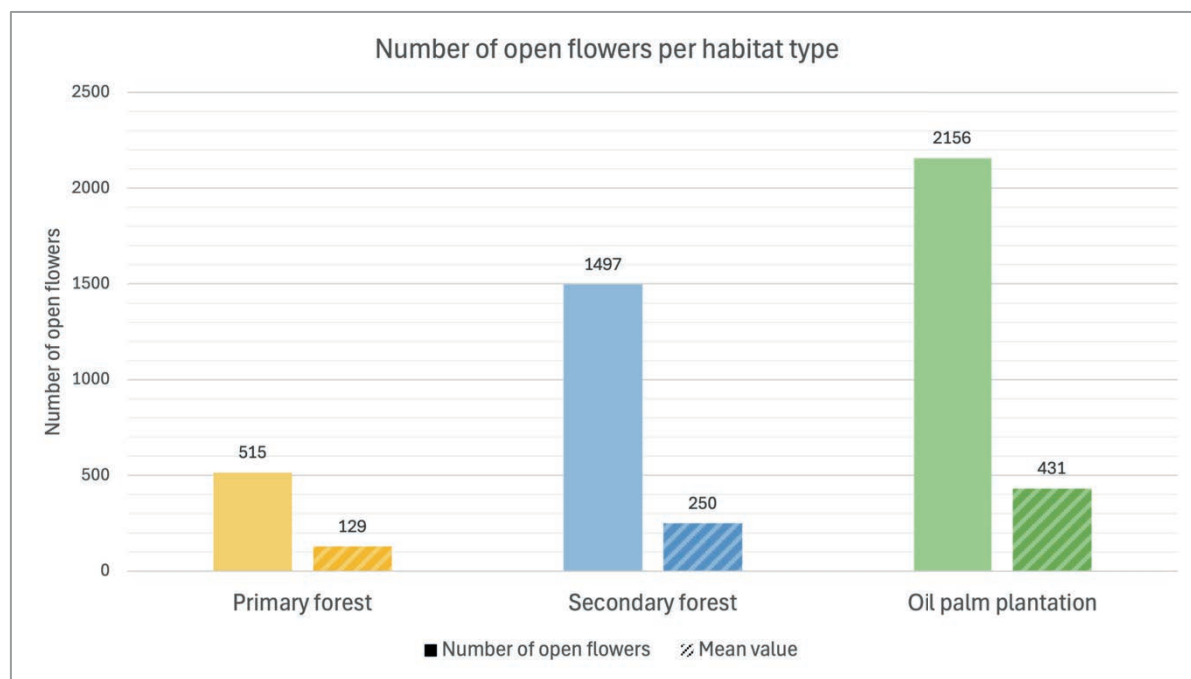
The species accumulation curve (**Fig. 7**) shows that both the old-growth secondary forest and the oil palm plantations had a higher diversity of plants in flower than the primary forest. The curve for the secondary forest continues to rise, suggesting that even more species might be found with additional sampling. In contrast, the curve for the primary forest increases more slowly, indicating fewer plant species overall. Although the curve for oil palm plantations also rises, the wider confidence interval shows that there is more uncertainty in this estimate.



**Figure 7** Plant species accumulation curve ( $q = 0$ ,  $CI = 95\%$ ). Habitat types: Primary forest (yellow), old-growth secondary forest (blue), and oil palm plantation (green).

### 3.1.4. Open flower abundance

During transect walks, the number of open flowers (flower heads in Asteraceae) was recorded to quantify flower abundances in each habitat type. In total, 4168 open flowers were counted. The highest number of flowers was recorded in the oil palm plantations (2156; mean = 129; min-max = 85 – 179), followed by the old-growth secondary forest (1497; mean = 250; min-max = 56 – 569), and finally the primary forest (515; mean = 431; min-max = 249 – 678) (**Fig. 8**). The Kruskal-Wallis test indicated a statistically significant difference in flower abundance among habitat types. ( $H_c = 6.885$ ,  $p = 0.03198$ ). Dunn's post hoc test showed that oil palm plantation sites had significantly more open flowers than primary forest sites.



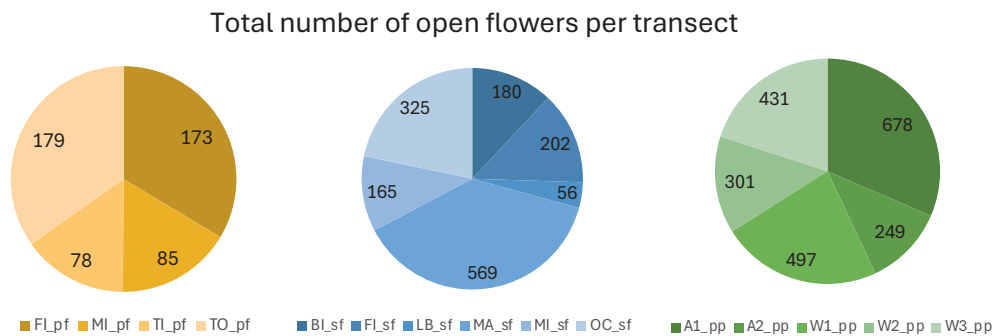
**Figure 8** Number of open flowers and mean value per habitat type. Difference in flower abundance among habitat types were significant (Kruskal-Wallis test:  $H_c = 6,885$ ,  $p = 0,03198$ ). Dunn's post-hoc test with Bonferroni correction revealed significant difference between primary forest and oil palm plantation ( $p = 0,02797$ ).

Within the primary forest, the species with the highest abundance of open flowers was *Palicourea tomentosa* (214 open flowers), *Psychotria carthagenensis* (93), and *Palicourea elata* (81), all members of the Rubiaceae family. They accounted for 75% of all open flowers in the habitat type. In the six secondary forest sites, the most abundant flower was *Palicourea solitudinum* with 291 open flowers. Other species with high flower abundances were *Aciotis* cf. *rubricaulis* (Melastomataceae) with 253 open flowers, *Palicourea tomentosa* (100), and *Calathea crotalifera* (Marantaceae, 81). In the oil palm plantations, 2156 open flowers were counted, with an average of 431 open flowers per transect. The plant species with the highest abundance of flowers was *Sphagneticola trilobata* (Asteraceae), where 579 flowers represent 27% of the flowers counted in all oil palm plantation sites. Other examples with high abundances were *Grona adscendens* (Fabaceae) with 349 flowers, *Xiphidium caeruleum* (Haemodoraceae, 193), *Desmodium axillare* (Fabaceae, 149) and *Hyptis* cf. *obtusiflora* (Lamiaceae) with 140 flowers.

The distribution of open flowers varied between transects within each habitat type as shown in **Figure 9**. In the primary forest, the transects with the most open flowers were La Torre (*TO\_pf*) and Tio Marcos (*TI\_pf*), each with more than twice as many flowers as the other two primary forest sites. In the secondary forest, the lowest number of open flowers (56) was recorded in the La Bolsa transect (*LB\_sf*), while the highest (569) was recorded in the Manakin



transect (*MA\_sf*), where “Arecaceae sp. 2” produced about 200 simultaneously open flowers during a brief flowering period of only a few hours. In oil palm plantations, the highest flower abundance was documented at the Finca Amable (*A1\_pp*, 678). This single transect recorded more open flowers than the total number observed across all primary forest sites combined.



**Figure 9** Number of open flowers that was counted in each transect within three different habitat types: Primary forest (PF, yellow), old-growth secondary forest (SF, blue), and oil palm plantation (PP, green). PF sites: Fila (*FL\_pf*), Mirador (*MI\_pf*), Tio Marcos (*TL\_pf*), La Torre (*TO\_pf*). SF sites: Bird (*BL\_sf*), Fila (*FL\_sf*), La Bolsa (*LB\_sf*), Manakin (*MA\_sf*), Mirador (*MI\_sf*), Ocelot (*OC\_sf*). PP sites: Amable 1 & 2 (*A1\_pp*, *A2\_pp*), Will 1, 2 & 3 (*W1\_pp*, *W2\_pp*, *W3\_pp*).

## 3.2. Floral visitors and potential pollinators

### 3.2.1. Floral visitors on selected plant species

In the primary forest, a total of 162 observations (obs. time = 700 min; **Tab. 6**) were made on open flowers of *Palicourea elata*, *Palicourea tomentosa*, and *Psychotria cathagenensis*. A total of 23 (morpho-) species of floral visitors were documented. These visitors belonged to three insect orders (Coleoptera, Hymenoptera, and Lepidoptera), one bird order (Apodiformes), and one class of Arachnida. The most abundant visitors belonged to Lepidoptera with 73 visits (45%), Hymenoptera with 72 visits (44%), and Apodiformes with 13 visits (8%). The mean number of visits per transects in primary forest was 41 (min–max = 16 – 68; **Fig. 10**).

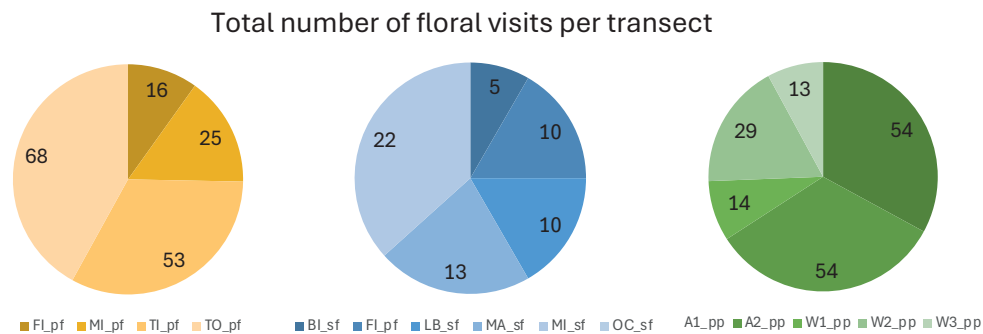
In the secondary forest, a total of 60 observations (obs. time = 527 min; **Tab. 6**) were conducted on *Heliconia imbricata*, *H. latispatha*, *H. stilesii*, *Blakea cf. litoralis*, *Palicourea elata*, *P. tomentosa*, and *P. solitudinum*. Eighteen different (morpho-) species of floral visitors were recorded. These visitors belonged to two different insect orders (Hymenoptera, Lepidoptera), and one bird order (Apodiformes). The most frequent visitors were Hymenoptera with 28 visits (47%), Lepidoptera with 20 visits (33%), and Apodiformes with 7 visits (12%). The mean number of visitations per transects in secondary forest was 10 (min–max = 5 – 22; **Fig. 10**).

In the oil palm plantations, a total of 164 observations (obs. time = 1404 min; **Tab. 6**) were recorded on open flowers of *Pseudelephantopus sp.* (Asteraceae), *Sphagneticola trilobata*, *Desmodium axillare*, *Grona adscendens*, *Xiphidium caeruleum*, *Heliconia latispatha*, *Hyptis cf. obtusiflora*, *Spigelia hamellioides* (Loganiaceae), and *Hedychium coronarium* (Zingiberaceae). The floral visitors belonged to 45 different (morpho-) species across five insect orders (Coleoptera, Diptera, Hymenoptera, Lepidoptera, and Orthoptera), and one bird order (Apodiformes). The most frequent visitors were Hymenoptera with 104 visits (85%), followed by Lepidoptera with 45 visits (27%), and Orthoptera with 8 visits (5%). The mean number of visitations per transects in oil palm plantations was 33 (min–max = 13 – 54; **Fig. 10**).

The number of visitor observations (V), visitor species (VS), potential pollinator observations (P), and potential pollinator species (PS) per plant species are presented in **Table 6**. The potential pollinators are listed separately and are not included in the visitor counts. The number of documented floral visits (including all) per transect are shown in **Figure 10**.

**Table 6** Observation time (minutes) and number of potential pollinator observations (P), potential pollinator species (PS), visitor observations (V), and visitor species (VS) per plant species and habitat type. The potential pollinators counts are not included in the visitor counts. The observation numbers recorded during 15-minute observations and long-term observations are summed up.

| Plant family    | Plant species                        | Primary forest |            |           |           |           | Secondary forest |           |           |           |          | Oil palm plantation |            |           |           |           |
|-----------------|--------------------------------------|----------------|------------|-----------|-----------|-----------|------------------|-----------|-----------|-----------|----------|---------------------|------------|-----------|-----------|-----------|
|                 |                                      | obs time       | P          | PS        | V         | VS        | obs time         | P         | PS        | V         | VS       | obs time            | P          | PS        | V         | VS        |
| Asteraceae      | <i>Pseudelephantopus</i> sp.         |                |            |           |           |           |                  |           |           |           |          | 15                  | 1          | 1         |           |           |
| Asteraceae      | <i>Sphagneticola trilobata</i>       |                |            |           |           |           |                  |           |           |           |          | 165                 | 93         | 29        | 6         | 3         |
| Fabaceae        | <i>Desmodium axillare</i>            |                |            |           |           |           |                  |           |           |           |          | 15                  | 1          | 1         |           |           |
| Fabaceae        | <i>Grona adscendens</i>              |                |            |           |           |           |                  |           |           |           |          | 122                 |            |           | 5         | 2         |
| Haemodoraceae   | <i>Xiphidium caeruleum</i>           |                |            |           |           |           |                  |           |           |           |          | 692                 | 9          | 3         | 5         | 4         |
| Heliconiaceae   | <i>Heliconia imbricata</i>           |                |            |           |           |           | 73               | 3         | 1         | 1         | 1        |                     |            |           |           |           |
| Heliconiaceae   | <i>Heliconia latispatha</i>          |                |            |           |           |           | 30               |           |           | 6         | 2        | 185                 |            |           | 6         | 2         |
| Heliconiaceae   | <i>Heliconia stilesii</i>            |                |            |           |           |           | 15               | 1         | 1         |           |          |                     |            |           |           |           |
| Lamiaceae       | <i>Hyptis</i> cf. <i>obtusiflora</i> |                |            |           |           |           |                  |           |           |           |          | 100                 | 14         | 7         | 8         | 3         |
| Loganiaceae     | <i>Spigelia hamellioides</i>         |                |            |           |           |           |                  |           |           |           |          | 15                  | 3          | 2         |           |           |
| Melastomataceae | <i>Blakea</i> cf. <i>litoralis</i>   |                |            |           |           |           | 45               |           |           |           |          |                     |            |           |           |           |
| Rubiaceae       | <i>Palicourea elata</i>              | 265            | 13         | 7         |           |           | 107              | 8         | 6         |           |          |                     |            |           |           |           |
| Rubiaceae       | <i>Palicourea solitudinum</i>        |                |            |           |           |           | 130              | 7         | 4         | 5         | 1        |                     |            |           |           |           |
| Rubiaceae       | <i>Palicourea tomentosa</i>          | 346            | 77         | 12        | 7         | 5         | 127              | 24        | 8         | 5         | 1        |                     |            |           |           |           |
| Rubiaceae       | <i>Psychotria carthagenensis</i>     | 89             | 15         | 6         | 50        | 10        |                  |           |           |           |          |                     |            |           |           |           |
| Zingiberaceae   | <i>Hedychium coronarium</i>          |                |            |           |           |           |                  |           |           |           |          | 95                  | 4          | 1         | 9         | 5         |
| <b>TOTAL</b>    |                                      | <b>700</b>     | <b>105</b> | <b>16</b> | <b>57</b> | <b>14</b> | <b>527</b>       | <b>43</b> | <b>15</b> | <b>17</b> | <b>3</b> | <b>1404</b>         | <b>125</b> | <b>39</b> | <b>39</b> | <b>15</b> |



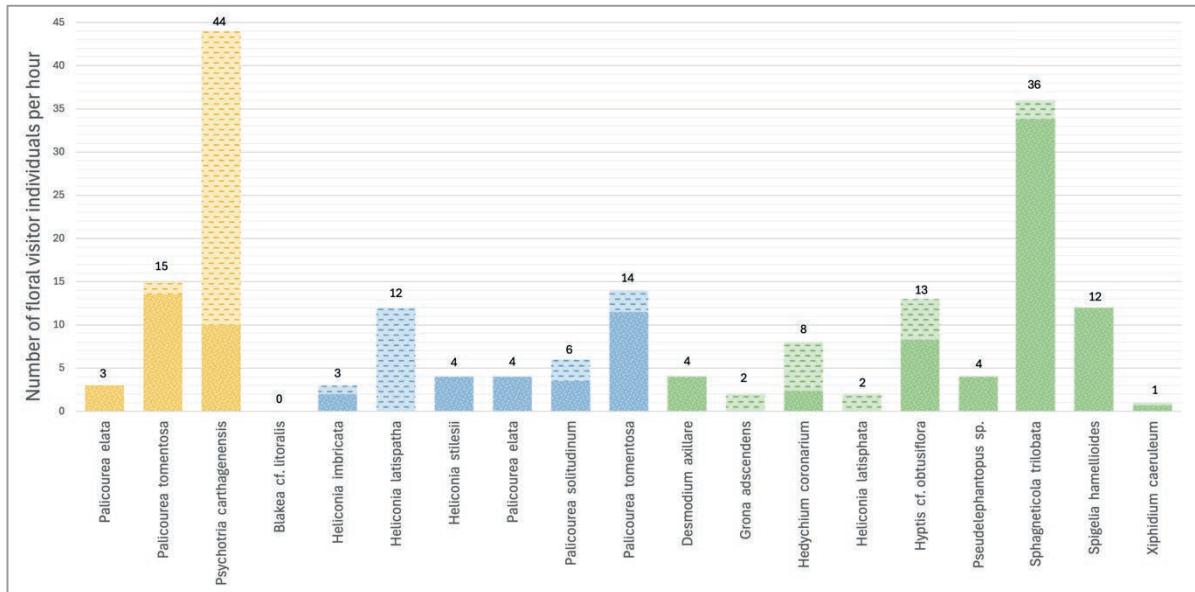
**Figure 10** Total number of observed floral visits (including potential pollinators) per transects in three different habitat types: Primary forest (PF, yellow), old-growth secondary forest (SF, blue), and oil palm plantation (PP, green). PF sites: Fila (*FL\_pf*), Mirador (*ML\_pf*), Tio Marcos (*TL\_pf*), La Torre (*TO\_pf*). SF sites: Bird (*BL\_sf*), Fila (*FL\_sf*), La Bolsa (*LB\_sf*), Manakin (*MA\_sf*), Mirador (*ML\_sf*), Ocelot (*OC\_sf*) [zero observations]. PP sites: Amable 1 & 2 (*A1\_pp*, *A2\_pp*), Will 1, 2 & 3 (*W1\_pp*, *W2\_pp*, *W3\_pp*).

## Visitation frequency on selected plant species

To ensure a reliable comparison of the number of floral visitors, the number of observations per hour was used to standardize differences in the time spent observing each plant species. In addition, this method provides an insight into the frequency of visits. Each observation was attributed to an individual floral visitor. The ratio between potential pollinators and non-pollinating visitors is also visualized in **Figure 11**.

The plant species that attracted the most floral visitor individuals was *Psychotria carthagenensis* in the primary forest, with an average of 44 individuals per hour. *Palicourea tomentosa* attracted approximately 15 floral visitors per hour in PF, and about 14 floral visitors per hour in SF. *Palicourea elata* attracted fewer floral visitors in both habitat types. In the oil palm plantations, *Sphagneticola trilobata* attracted 36 floral visitors per hour. The second most visited plant species in PP was *Hyptis* cf. *obtusiflora*, with approximately 13 floral visitors observed per hour.

The results for *Blakea* cf. *litoralis*, *Heliconia latispatha*, and *H. stilesii* in the SF and the results for *Desmodium axillare*, *Pseudelephantopus* sp., and *Spigelia hamellioides* (Loganiaceae) in the PP, are based on observation times of less than one hour (see **Tab. 6** for obs. time). Consequently, the values were adjusted to reflect a rate per hour. In the case of *Blakea* cf. *litoralis* in the SF, no floral visitors were recorded during the sampling period.

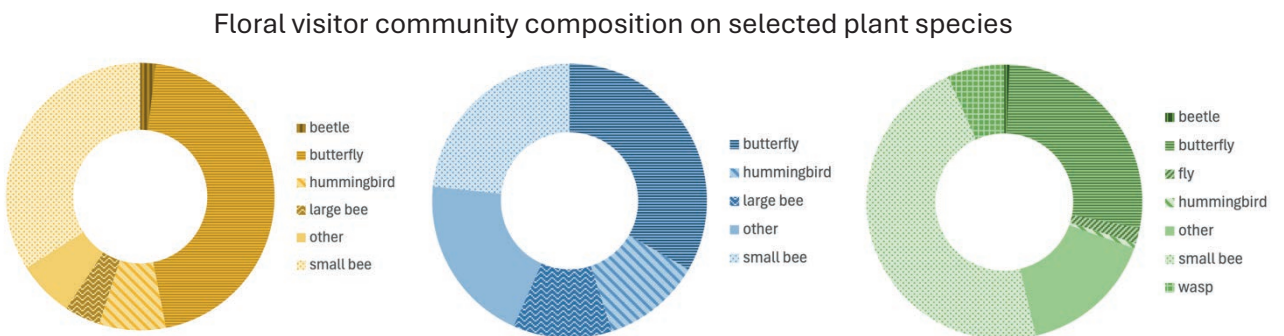


**Figure 11** Total number of observed floral visitors on selected plant species in primary forest (yellow, 3 spp.), old-growth secondary forest (blue, 6 spp.), and oil palm plantation (green, 9 spp.). The proportion of potential pollinator visits is shown in darker shaded pattern; the lighter shaded, dashed pattern indicates non-pollinating visitors.

## Floral visitor community composition

The composition of the floral visitor community differed among the three study habitat types. Six distinct functional groups were identified in the primary rainforest. The most frequently observed functional group was *butterfly*, accounting for 45% of visits (73), followed by *small bee* with 34% (55 visits), and *hummingbird* with 8% (13 visits). In the secondary forest, five functional groups were recorded. As in the PF, *butterfly* was the most represented group, responsible for 33% of visits (20), followed by *small bee* with 23% (14), and *other* (mostly ants) with 20% (13 visits). In contrast to the PF, the functional group *beetle* was not observed in SF. In the oil palm plantations, seven distinct functional groups were documented. The dominant group was *small bee*, accounting for 47% of visits (77), followed by *butterfly* with 27% (45 visits). Unlike in the other two habitats, the functional groups *fly* and *wasp* were present, but *large bee* was absent, and only a single *hummingbird* was observed.

Details on the categorization of species and morphospecies within these functional groups and their orders are provided in the **Appendices II & III**. The differences in floral visitor composition among the habitat types are illustrated in **Figure 12**.



**Figure 12** Composition of functional groups of floral visitors on selected plant species in three different habitat types: Primary forest (yellow), old-growth secondary forest (blue), and oil palm plantation (green). Functional groups of floral visitors: *beetle*, *butterfly*, *hummingbird*, *fly*, *large bee*, *small bee*, *true bug*, *wasp*, and *other*.

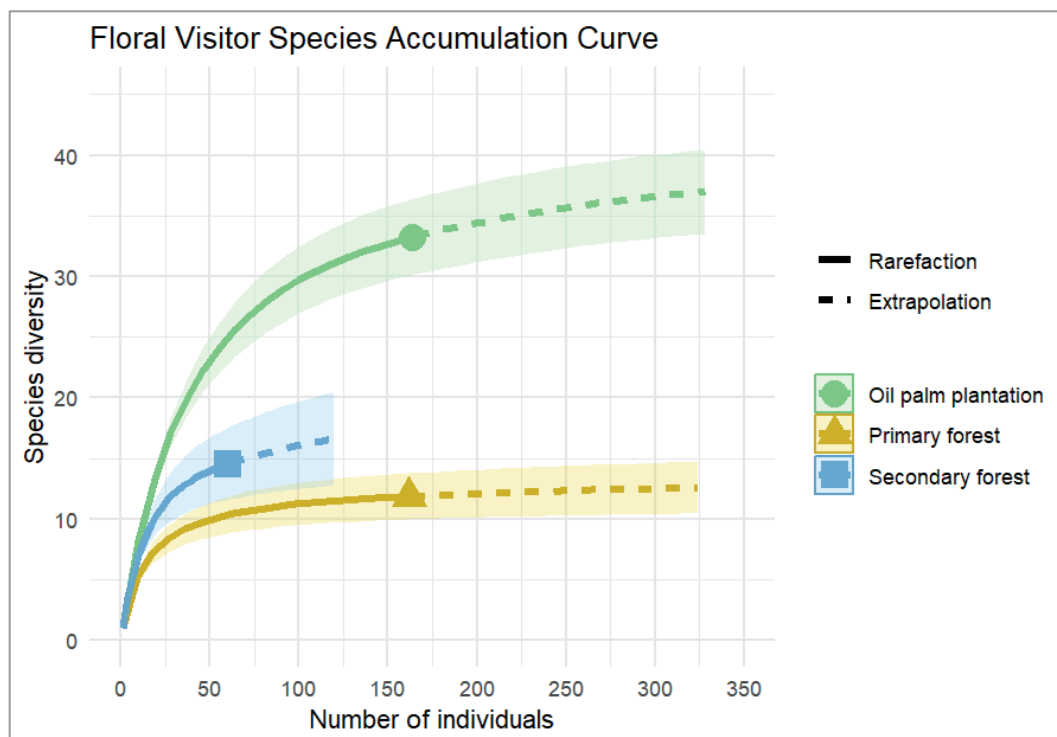
## Floral visitor diversity

The highest species richness was recorded in the oil palm plantations (45 spp.), followed by primary forest (23 spp.), and secondary forest (18 spp.). In terms of total number of individuals, both oil palm plantations and primary forest exhibited higher values than secondary forest. Nevertheless, SF showed the highest species evenness (0,93), closely followed by PP (0,92). These values approached perfect evenness (=1). According to the Shannon Index, oil palm plantations also displayed the highest alpha diversity (3,50), with secondary forest (2,68), and primary forest (2,47) showing lower values. Floral visitor diversity data are shown in **Table 7**.

**Table 7** Shannon Index, Pielou's evenness, species richness, and total number of individuals for floral visitor species in three different habitat types.

| Habitat type                | Primary forest | Secondary forest | Oil palm plantation |
|-----------------------------|----------------|------------------|---------------------|
| Shannon Index (H')          | 2,472642       | 2,676153         | 3,504372            |
| Pielou's evenness (J)       | 0,788597213    | 0,925885396      | 0,920589101         |
| Species richness            | 23             | 18               | 45                  |
| Total number of individuals | 162            | 60               | 164                 |

The species accumulation curve (**Fig. 13**) shows that oil palm plantation had the highest observed floral visitor diversity, with a steep curve and strong extrapolation potential. Secondary forest displayed intermediate diversity, with potential for further species accumulation. Primary forest showed the lowest diversity, with a curve that plateaus early and limited potential for additional species.



**Figure 13** Floral visitor species accumulation curve ( $q = 1$ ,  $CI = 95\%$ ) on selected plant species. Habitat types: Primary forest (yellow), old-growth secondary forest (blue), and oil palm plantation (green).

### 3.2.2. Potential pollinators on selected plant species

The following section summarizes the results of focused observations on selected plant species (see **Tab. 6**), taking into account only those floral visitors identified as potential pollinators. For each habitat type, the number of recorded visits, the composition of pollinators, and the diversity of observed (morpho-)species are presented.



In the primary forest, a total of 105 observations were recorded, involving 16 different species and morphospecies of potential pollinators. These accounted for 65% of all plant–visitor interactions. The identified pollinators belonged to three orders: Lepidoptera, Hymenoptera, and Apodiformes. Lepidoptera dominated with 72 visits (69%), followed by Hymenoptera with 21 visits (20%), and Apodiformes with 12 visits (11%). Most visits by Lepidoptera and Apodiformes (>90%) were classified as potential pollinators, while only 29% of visits by Hymenoptera were.

In the secondary forest, 43 observations were recorded, suggesting that 72% of interactions were made by potential pollinators. A total of 15 different species and morphospecies were identified, again from the same three orders as in the primary forest. Lepidoptera accounted for 20 visits (47%), Hymenoptera for 16 (37%), and Apodiformes for 7 (16%).

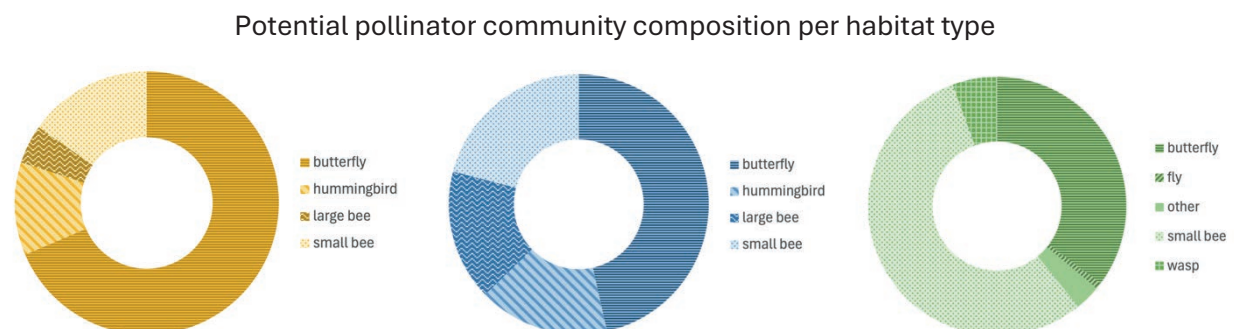
In the oil palm plantations, 125 visits by potential pollinators were recorded, making up 76% of all floral visitor interactions in this habitat type. The observed pollinators belonged to 39 distinct (morpho-) species across four orders: Hymenoptera, Lepidoptera, Orthoptera, and Diptera. Most observations were of Hymenoptera (76 visits, 61%), followed by Lepidoptera (44 visits, 35%), Orthoptera (4 visits, 3%), and Diptera (1 visit, <1%).

**Table 6** (above) shows the number of observations by potential pollinators, as well as the number of potential pollinator species observed for each plant species in each habitat type.

### Potential pollinator community composition

The composition of potential pollinators differed among the habitat types. Four distinct functional groups were identified in the primary forest. The most frequently observed functional group was *butterfly*, accounting for 72 floral visits (69%), followed by *small bee* with 16 visits (15%), and *hummingbird* with 12 visits (11%). The functional group *large bee* was represented by five visits (5%). In the secondary forest transects, the same four functional groups were documented. The group *butterfly* formed the largest group again, responsible for 20 floral visits (47%), followed by small bees with nine visits (21%). *Large bee* and *hummingbird* each accounted for seven visits (16%). In the oil palm plantations, five distinct functional groups were recorded. The most represented functional groups are *small bee*, with 69 visits (55%), followed by *butterfly* with 44 visits (35%). In contrast to the other two habitat types, the functional groups *fly* (1 visit, 1%), *other* (4 visits, 3%), and *wasp* (7 visits, 7%) were also observed. The functional group *large bee*, however, was not recorded in this habitat.

The differences in potential pollinator composition among the habitat types are illustrated in **Figure 14**. Details concerning the categorization of species and morphospecies within these functional groups and their orders are provided in **Appendix III**.



**Figure 14** Composition of functional groups of potential pollinators on selected plant species in three different habitat types: Primary forest (yellow), old-growth secondary forest (blue), and oil palm plantation (green). Functional groups: *butterfly*, *hummingbird*, *fly*, *large bee*, *small bee*, *wasp*, and *other*.

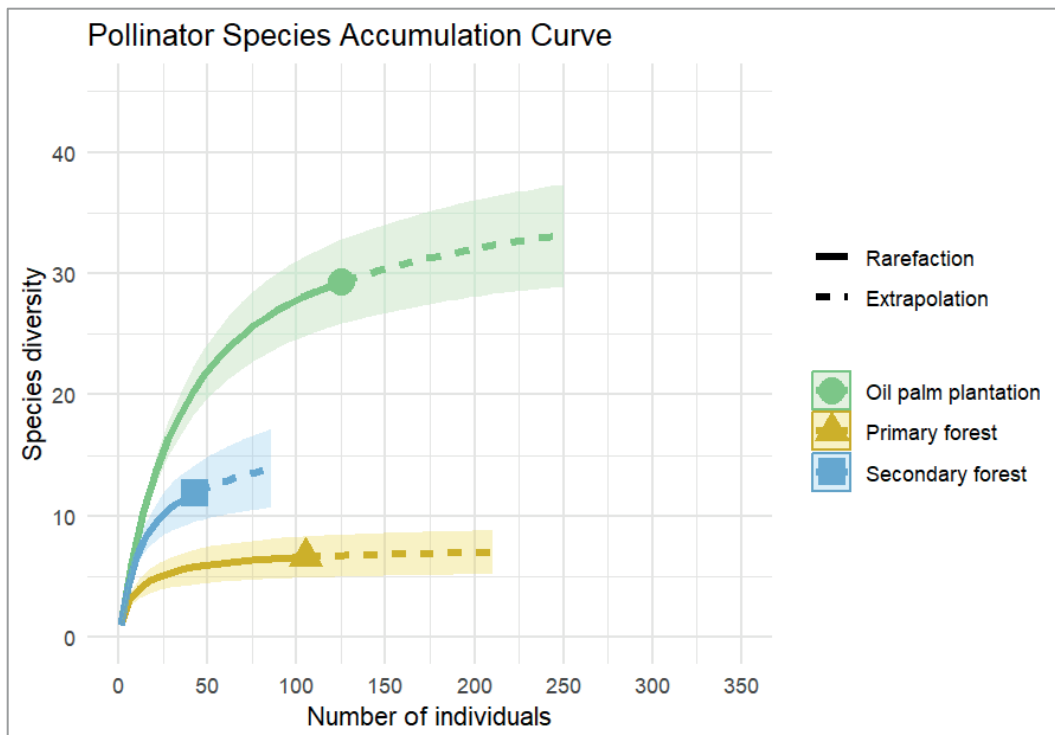
### Potential pollinator diversity

The highest species richness was recorded in oil palm plantations (39 spp.), followed by primary forest (16 spp.), and secondary forest (15 spp.). In terms of total number of individuals, again, both oil palm plantations and primary forest exhibited higher values than secondary forest. Notably, both oil palm plantations and secondary forest showed high species evenness (0,92 PP; 0,91 SF) in contrast to primary forest (0,68). According to the Shannon Index, oil palm plantation also displayed the highest alpha diversity (3,38), with secondary forest (2,47), and primary forest (1,89) showing lower values. Floral visitor diversity data are shown in **Table 8**.

**Table 8** Shannon Index, Pielou's evenness, species richness, and total number of individuals for potential pollinator species in three different habitat types.

| Habitat type                | Primary forest | Secondary forest | Oil palm plantation |
|-----------------------------|----------------|------------------|---------------------|
| Shannon Index ( $H'$ )      | 1,886312       | 2,473392         | 3,377014            |
| Pielou's evenness ( $J$ )   | 0,680343242    | 0,913347913      | 0,921784407         |
| Species richness            | 16             | 15               | 39                  |
| Total number of individuals | 105            | 43               | 125                 |

A similar trend is observed in the species accumulation curve (**Fig. 15**) of potential pollinator species, which indicates that oil palm plantation had the highest species diversity with a steep curve and extrapolation potential. The extrapolation also suggests potential for greater species diversity in secondary forest. Primary forest showed the lowest diversity, with a curve that plateaus early and limited potential for additional species.



**Figure 15** Potential pollinator species accumulation curve ( $q = 1$ ,  $CI = 95\%$ ) on selected plant species. Habitat types: Primary forest (yellow), old-growth secondary forest (blue), and oil palm plantation (green).

### 3.2.3. Floral visitors on transect walks (TW)

In addition to focused observations, data on floral visitors were collected during the transect walks. These observations included floral visitor interactions with plants flowering at the time of observation along the entire transect. A total of 56 transect walks were conducted across 15 transects, resulting in 215 observations.

A total of 60 observations were made in the primary forest, and 22 different (morpho-) species of floral visitors were identified. These visitors belonged to three insect orders (Hemiptera, Hymenoptera, and Lepidoptera), one bird order (Apodiformes), and one class of Arachnida. The most represented orders were Lepidoptera and Hymenoptera, with 23 visits each (each 38%), and Apodiformes with 12 visits (20%).

The secondary forest transect walks resulted in a total of 110 observations. The 15 different species and morphotypes of floral visitors were classified in three different insect orders (Diptera, Hymenoptera, and Lepidoptera), and one bird order (Apodiformes). The Hymenoptera order dominated, with a total of 83 visits (75%). Other orders observed included Diptera (12 visits, 11%) Lepidoptera (9 visits, 8%), and Apodiformes (5 visits, 5%).

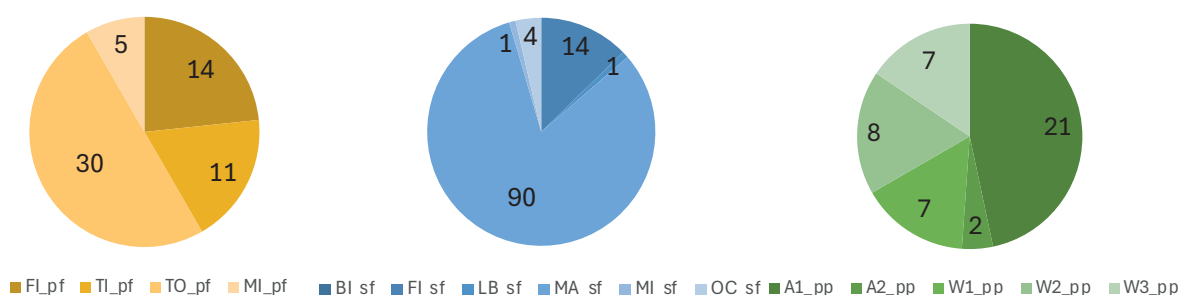
In the oil palm plantations, a total of 45 observations were documented. The floral visitors were classified into 20 different (morpho-) species across six different orders (Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, and Orthoptera). The most represented order was Hymenoptera with 22 visits (49%), followed by Lepidoptera with 13 visits (29%). The remaining four orders had lower numbers: Diptera and Hemiptera with four visits each (each 9%), and Coleoptera and Orthoptera with a single visit (2% each).

The number of visits (V), visitor species (VS), potential pollinators (P), and potential pollinator species (PS) per plant species are presented in **Table 9**. The number of documented flower visits per transect are presented in **Figure 16**. As illustrated below, 83 out of 110 observations (75%) in the secondary forest were documented on two palm species, both of which flowered in the Manakin transect (*MA\_sf*).

**Table 9** Number of potential pollinators (P), potential pollinator species (PS), visits (V), and visitor species (VS) per plant species and habitat type during transect walks (TW). The potential pollinators counts are not included in the visitor counts.

| Plant family    | Plant species                        | Primary forest |           |           |          | Secondary forest |          |           |          | Oil palm plantation |           |          |          |
|-----------------|--------------------------------------|----------------|-----------|-----------|----------|------------------|----------|-----------|----------|---------------------|-----------|----------|----------|
|                 |                                      | P              | PS        | V         | VS       | P                | PS       | V         | VS       | P                   | PS        | V        | VS       |
| Acanthaceae     | <i>Justicia comata</i>               |                |           |           |          |                  |          |           |          | 2                   | 1         | 1        | 1        |
| Arecaceae       | <i>Arecaceae</i> sp. 2               |                |           |           |          |                  |          | 33        | 3        |                     |           |          |          |
| Arecaceae       | <i>Arecaceae</i> sp. 3               |                |           |           |          | 50               | 1        |           |          |                     |           |          |          |
| Asteraceae      | <i>Sphagneticola trilobata</i>       |                |           |           |          |                  |          |           |          | 19                  | 15        | 2        | 2        |
| Costaceae       | <i>Costus</i> cf. <i>laevis</i>      |                |           |           |          | 1                | 1        |           |          |                     |           |          |          |
| Cyperaceae      | <i>Cyperaceae</i> sp. 1              | 4              | 2         |           |          |                  |          |           |          |                     |           |          |          |
| Euphorbiaceae   | <i>Mabea</i> sp.                     | 1              | 1         | 1         | 1        |                  |          |           |          |                     |           |          |          |
| Fabaceae        | <i>Desmodium axillare</i>            |                |           |           |          |                  |          |           |          | 1                   | 1         |          |          |
| Fabaceae        | <i>Grona adscendens</i>              |                |           |           |          |                  |          |           |          | 3                   | 3         |          |          |
| Haemodoraceae   | <i>Xiphidium caeruleum</i>           |                |           |           |          |                  |          |           |          |                     |           | 1        | 1        |
| Heliconiaceae   | <i>Heliconia imbricata</i>           |                |           |           |          | 1                | 1        |           |          |                     |           |          |          |
| Heliconiaceae   | <i>Heliconia irrasa</i>              |                |           | 1         | 1        |                  |          |           |          |                     |           |          |          |
| Heliconiaceae   | <i>Heliconia latispatha</i>          |                |           |           |          |                  |          | 1         | 1        |                     |           |          |          |
| Lamiaceae       | <i>Hyptis</i> cf. <i>obtusiflora</i> |                |           |           |          |                  |          |           |          | 6                   | 3         |          |          |
| Loganiaceae     | <i>Spigelia hamellioides</i>         |                |           |           |          |                  |          |           |          | 2                   | 2         |          |          |
| Marantaceae     | <i>Calathea crotalifera</i>          | 1              | 1         |           |          |                  |          |           |          |                     |           |          |          |
| Melastomataceae | <i>Blakea</i> cf. <i>litoralis</i>   |                |           |           |          |                  |          | 1         | 1        | 1                   | 1         |          |          |
| Melastomataceae | <i>Miconia</i> cf. <i>nervosa</i>    |                |           | 5         | 1        |                  |          | 9         | 2        |                     |           |          |          |
| Melastomataceae | <i>Miconia</i> sp. 3                 |                |           |           |          | 1                | 1        |           |          |                     |           |          |          |
| Melastomataceae | <i>Miconia</i> sp. 6                 |                |           |           |          |                  |          |           |          | 1                   | 1         |          |          |
| Piperaceae      | <i>Piper</i> sp. 1                   |                |           |           |          |                  |          |           |          |                     |           | 4        | 1        |
| Rubiaceae       | <i>Coccocypselum</i> sp.             |                |           |           |          |                  |          |           |          | 1                   | 1         | 1        | 1        |
| Rubiaceae       | <i>Notopleura uliginosa</i>          | 1              | 1         |           |          |                  |          |           |          |                     |           |          |          |
| Rubiaceae       | <i>Palicourea elata</i>              | 12             | 4         | 1         | 1        | 6                | 2        |           |          |                     |           |          |          |
| Rubiaceae       | <i>Palicourea tomentosa</i>          | 25             | 10        |           |          | 3                | 2        | 1         | 1        |                     |           |          |          |
| Rubiaceae       | <i>Psychotria carthagenensis</i>     | 2              | 2         | 6         | 4        |                  |          |           |          |                     |           |          |          |
| Rubiaceae       | <i>Sabicea</i> cf. <i>panamensis</i> |                |           |           |          | 3                | 2        |           |          |                     |           |          |          |
|                 | <b>TOTAL</b>                         | <b>46</b>      | <b>17</b> | <b>14</b> | <b>7</b> | <b>65</b>        | <b>8</b> | <b>45</b> | <b>7</b> | <b>36</b>           | <b>17</b> | <b>9</b> | <b>5</b> |

Total number of floral visits per transect during transect talks (TW)



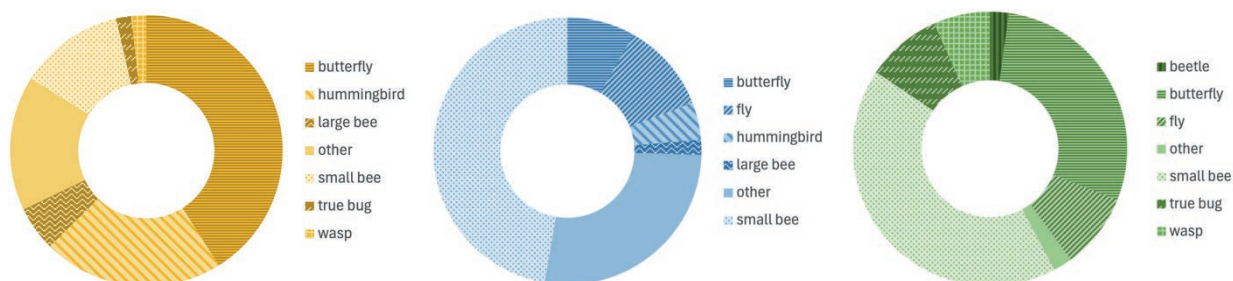
**Figure 16** Total number of observed floral visits (including potential pollinators) during transect walks (TW) in three habitats: Primary forest (PF, yellow), old-growth secondary forest (SF, blue), and oil palm plantation (PP, green). PF sites: Fila (*FI\_pf*), Mirador (*MI\_pf*), Tio Marcos (*TI\_pf*), La Torre (*TO\_pf*). SF sites: Bird (*BI\_sf*) [zero observations], Fila (*FI\_sf*), La Bolsa (*LB\_sf*), Manakin (*MA\_sf*), Mirador (*MI\_sf*), Ocelot (*OC\_sf*). PP sites: Amable 1 & 2 (*A1\_pp*, *A2\_pp*), Will 1, 2 & 3 (*W1\_pp*, *W2\_pp*, *W3\_pp*).

### Floral visitor community composition (transect walks)

The composition of floral visitors differed among the habitat types. A total of seven distinct functional groups were identified in the primary rainforest. The most frequently observed functional group was *butterfly* with 23 visits (38%) recorded, followed by *hummingbird* with 12 visits (20%) and *small bee* with 13 visits (18%). The functional groups *true bug* and *wasp* were both recorded once (2% each). In the secondary forest, six different functional groups have been documented. The most frequently observed group was *small bee*, with 52 flower visits (47%). The second most observed group was *other*, with 30 visits (27%), followed by *fly*, with 12 visits (11%). In comparison to the primary forest (TW), the functional groups *true bug* and *wasp* were not documented. The functional groups documented in the oil palm plantations were classified into seven distinct functional groups. The most represented functional groups are *small bee*, with 19 visits (42%), and *butterfly*, with 13 visits (29%). In comparison to the other two habitat types, *large bee* and *hummingbird* were not observed. The functional groups *fly* and *true bug* were both observed four times (9% each).

The differences in floral visitor composition among the habitat types are illustrated in **Figure 17**. Details concerning the categorization of species and morphospecies within these functional groups and their orders are provided in the **Appendices II & III**.

Floral visitor community composition (TW)



**Figure 17** Composition of functional groups of floral visitors during transect walks (TW) in three different habitat types: Primary forest (yellow), old-growth secondary forest (blue), and oil palm plantation (green). *beetle*, *butterfly*, *fly*, *hummingbird*, *large bee*, *small bee*, *true bug*, *wasp*, and *other*.



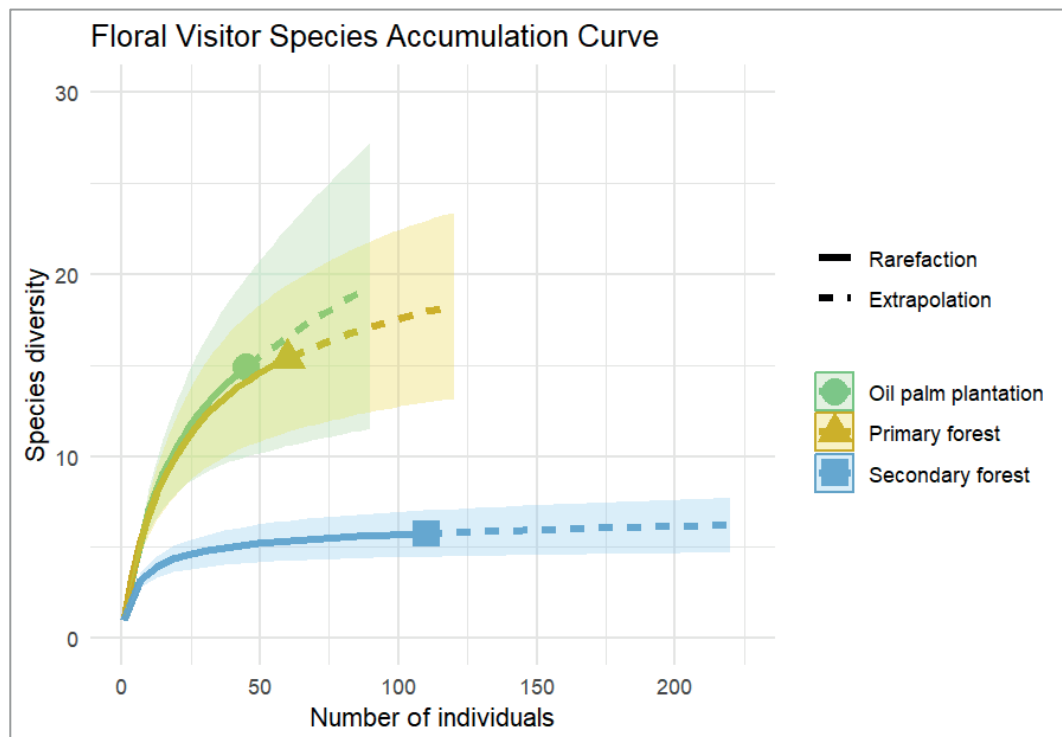
### Floral visitor diversity (transect walks)

The habitat type with the highest species richness was primary forest (22 spp.), followed by oil palm plantation (20 spp.), and secondary forest (15 spp.). Secondary forest sites had the highest total number of individuals. However, this habitat type had the lowest species evenness (0,65). The Shannon Index revealed that the oil palm plantations and primary forest sites have a higher alpha diversity (PP 2,70; PF 2,48) compared to the secondary forest (1,75). The data on floral visitor diversity (TW) are presented in **Table 10**.

**Table 10** Shannon Index, Pielou's evenness, species richness, and total number of individuals for floral visitor species (TW) in three different habitat types.

| Habitat type                | Primary forest | Secondary forest | Oil palm plantation |
|-----------------------------|----------------|------------------|---------------------|
| Shannon Index (H')          | 2,476272       | 1,748488         | 2,701101            |
| Pielou's evenness (J)       | 0,801112258    | 0,645663068      | 0,901649665         |
| Species richness            | 22             | 15               | 20                  |
| Total number of individuals | 60             | 110              | 45                  |

The species accumulation curve (**Fig. 18**) shows that the oil palm plantation and the primary forest have a higher species diversity with steep curves and a potential for greater species diversity. However, the wider confidence intervals show there is more uncertainty in this estimate. Secondary forest showed the lowest diversity, with a curve that plateaus early and limited potential for additional species.



**Figure 18** Floral visitor species accumulation curve ( $q = 1$ , CI = 95%) during transect walks (TW). Habitat types: Primary forest (yellow), old-growth secondary forest (blue), and oil palm plantation (green).

### 3.2.4. Potential pollinators on transect walks (TW)

In the primary forest, a total of 46 observations were recorded, and 17 different animal species and morphotypes of potential pollinators were identified. These account for three quarters (77%) of plant-visitor interactions. The potential pollinators belong to three different orders: Apodiformes, Hymenoptera, and Lepidoptera. The Lepidoptera order dominated with 22 visits (48%), followed by the Hymenoptera and Apodiformes with 12 visits each (26% each).

The results suggest that the majority of floral visits by Lepidoptera and Apodiformes (95 – 100%) were made by potential pollinators, whereas 52% of Hymenoptera floral visits were classified as such.

In the secondary forest, the TW observations resulted in a total of 65 observations by eight distinct (morpho-) species of potential pollinators. These pollinators belong to the same orders as observed in the primary forest: Apodiformes with five visits (8%), Hymenoptera with 52 visits (80%), and Lepidoptera with eight visits (12%). The total number of interactions shows that 59% of interactions were made by potential pollinators in the secondary forest.

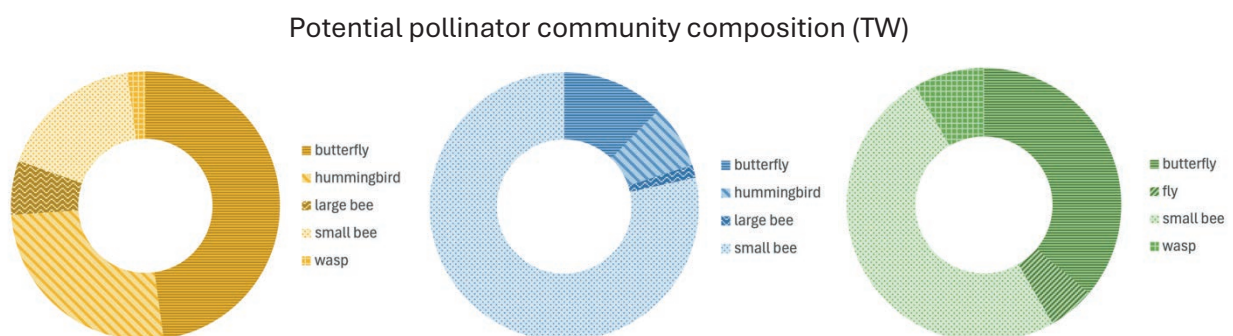
In the oil palm plantations, a total of 36 observations of potential pollinators were documented. This suggests that 80% of interactions were made by potential pollinators. These pollinators were classified into 17 (morpho-) species across three insect orders: Diptera, Hymenoptera, and Lepidoptera. Most observations were recorded for Hymenoptera, with 21 visits (58%), followed by Lepidoptera, with 13 visits (36%), and Diptera with two visits (6%).

**Table 9** (above) shows the number of observations by potential pollinators, as well as the number of potential pollinator species observed during transect walks (TW).

### Potential pollinator community composition (transect walks)

The composition of potential pollinators observed during transect walks differed among the habitat types. A total of five functional groups were identified in the primary rainforest. The most often observed functional group was *butterfly*, with 22 flower visits (48%), followed by *hummingbird*, with twelve visits (26%), and *small bee*, with eight visits (17%). The functional group *large bee* was represented with three recorded visits (7%), and *wasp* completed the composition with one visit (2%). In the secondary forest, four functional groups were documented, with the most represented group being *small bee*, with 51 floral visits and responsible for 78% of the visits by potential pollinators in this habitat type. The second most abundant group was *butterfly*, which visited flowers eight times (12%), followed by *hummingbird*, with five visits (8%), and finally one *large bee* was recorded, accounting for 2%. The functional groups documented in the oil palm plantations were classified into four different functional groups. The most abundant was *small bee*, with 18 visits (50%), and *butterfly*, with 13 visits (36%). Compared to the other two habitat types, the functional groups of *hummingbird* and *large bee* were absent. Like the composition of potential pollinators on selected plant species (see **Fig. 14**), *fly* (2 visits, 6%) and *wasp* (3 visits, 8%) were present instead.

The differences in potential pollinator composition among the habitat types are illustrated in **Figure 19**. Details concerning the categorization of species and morphospecies within these functional groups and their orders are provided in **Appendix III**.



**Figure 19** Composition of functional groups of potential pollinators during transect walks (TW) in three different habitat types: Primary forest (yellow), old-growth secondary forest (blue), and oil palm plantation (green). Functional groups: *beetle*, *butterfly*, *fly*, *hummingbird*, *large bee*, *small bee*, *true bug*, *wasp*, and *other*.

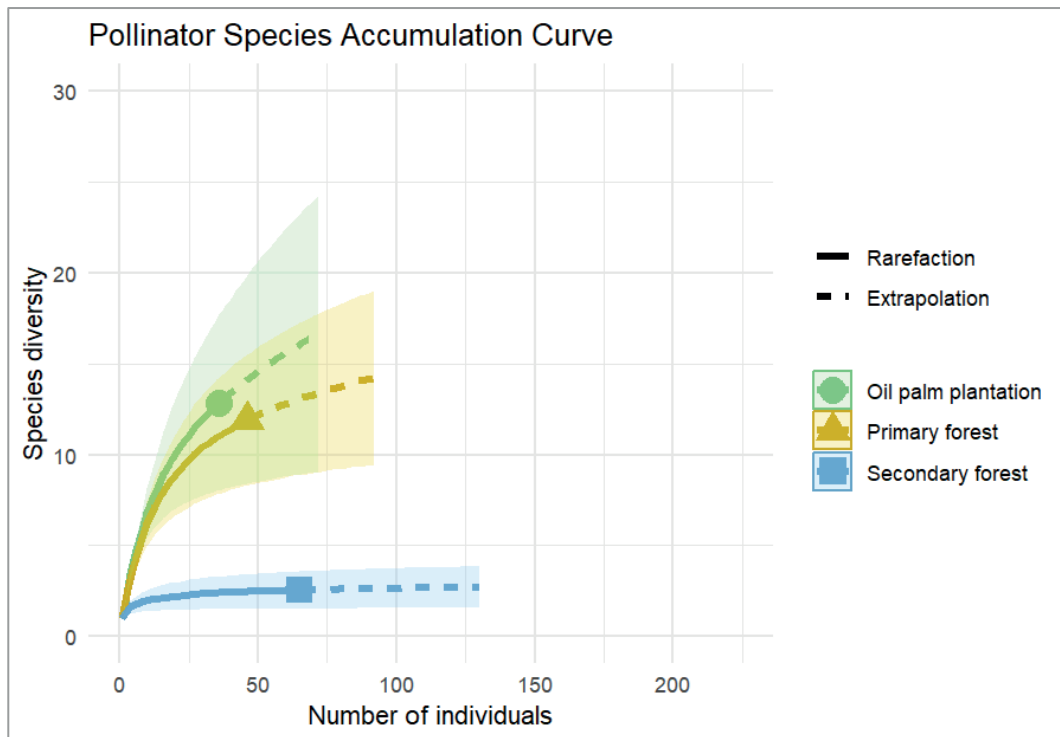
### Potential pollinator diversity (transect walks)

The habitat types sharing the highest species richness were primary forest and oil palm plantation (17 spp. each), followed by secondary forest (8 spp.). Secondary forest sites had the highest total number of individuals. However, secondary forest had the lowest species evenness number (0,45). The Shannon Index reveals that the primary forest and oil palm plantation had a higher alpha diversity (PF 2,73; PP 2,55) compared to the secondary forest (0,93). The potential pollinator diversity data during transect walks are shown in **Table 11**.

**Table 11** Shannon Index, Pielou's evenness, species richness, and total number of individuals of potential pollinators (TW) in three different habitat types.

| Habitat type                | Primary forest | Secondary forest | Oil palm plantation |
|-----------------------------|----------------|------------------|---------------------|
| Shannon Index (H')          | 2,734059       | 0,934698         | 2,554852            |
| Pielou's evenness (J)       | 0,965002867    | 0,449494675      | 0,901750482         |
| Species richness            | 17             | 8                | 17                  |
| Total number of individuals | 46             | 65               | 36                  |

Similar to the species accumulation curve (**Fig. 20**) of floral visitors (TW), the potential pollinator species accumulation curve also indicates that the oil palm plantations and the primary forest sites had a higher species diversity and potential for greater species diversity. Secondary forest showed the lowest diversity, with a curve that plateaus early and limited potential for additional species.



**Figure 20** Potential pollinator species accumulation curve ( $q = 1$ ,  $CI = 95\%$ ) during transect walks (TW). Habitat types: Primary forest (yellow), old-growth secondary forest (blue), and oil palm plantation (green).

### 3.2.5. Floral visitors and potential pollinators in the corridor

Including all observations – on selected plant species with focused observations and during transect walks – the total number of observations was 601 in three habitat types. There were 222 observations in the primary forest, 209 observations in the oil palm plantations, and 170 observations of flower visitors in the old-growth secondary forest. The numbers are shown in **Table 12**.

In the primary forest, most observations of flower visitors were recorded on *Palicourea tomentosa*, *Psychotria carthagenensis*, and *Palicourea elata* (all Rubiaceae). In the secondary forest, most observations of floral visitors were recorded on “Arecaceae sp. 3”, “Arecaceae sp. 2”, and *Palicourea tomentosa*. The highest numbers in floral visitor observations in the oil palm plantations were recorded on *Sphagneticola trilobata* (Asteraceae), *Hyptis* cf. *obtusiflora* (Lamiaceae), and *Xiphidium caeruleum* (Haemodoraceae).

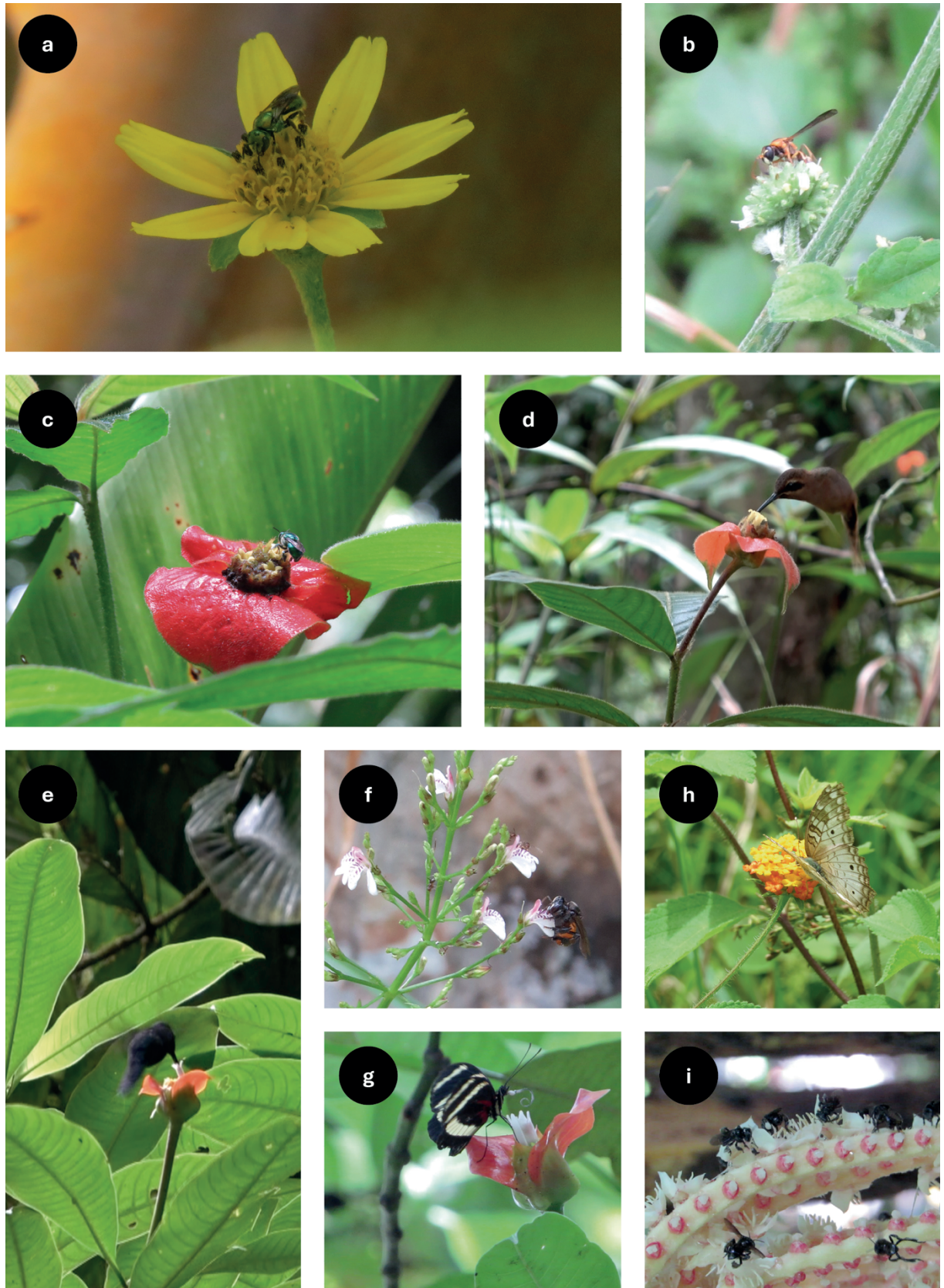
Regarding the number of potential pollinator observations, most observations were documented on *Palicourea tomentosa*, *Palicourea elata*, and *Psychotria carthagenensis* in the primary rainforest. In the old-growth secondary forest, “Arecaceae sp. 3”, *Palicourea tomentosa*, and *Palicourea elata* were the most visited plants. In the oil palm plantations, the plant species with the highest abundances in pollinator observations again were *Sphagneticola trilobata*, *Hyptis* cf. *obtusiflora* and *Xiphidium caeruleum*.

**Table 12** Total number of potential pollinators (P), potential pollinator species (PS), visits (V), and visitor species (VS) per plant species and habitat type summed up for both focused observations and transect walk observations.

| Plant family    | Plant species                        | Primary forest |           |           |           | Secondary forest |           |           |          | Oil palm plantation |           |           |           |
|-----------------|--------------------------------------|----------------|-----------|-----------|-----------|------------------|-----------|-----------|----------|---------------------|-----------|-----------|-----------|
|                 |                                      | P              | PS        | V         | VS        | P                | PS        | V         | VS       | P                   | PS        | V         | VS        |
| Acanthaceae     | <i>Dianthera comata</i>              |                |           |           |           |                  |           |           |          | 2                   | 1         | 1         | 1         |
| Arecaceae       | Arecaceae sp. 2                      |                |           |           |           |                  |           | 33        | 3        |                     |           |           |           |
| Arecaceae       | Arecaceae sp. 3                      |                |           |           |           | 50               | 1         |           |          |                     |           |           |           |
| Asteraceae      | <i>Pseudelephantopus</i> sp.         |                |           |           |           |                  |           |           |          | 1                   | 1         |           |           |
| Asteraceae      | <i>Sphagneticola trilobata</i>       |                |           |           |           |                  |           |           |          | 112                 | 34        | 8         | 3         |
| Costaceae       | <i>Costus</i> cf. <i>laevis</i>      |                |           |           |           | 1                | 1         |           |          |                     |           |           |           |
| Cyperaceae      | Cyperaceae sp. 1                     | 4              | 2         |           |           |                  |           |           |          |                     |           |           |           |
| Euphorbiaceae   | <i>Mabea</i> sp.                     | 1              | 1         | 1         | 1         |                  |           |           |          |                     |           |           |           |
| Fabaceae        | <i>Desmodium axillare</i>            |                |           |           |           |                  |           |           |          | 2                   | 1         |           |           |
| Fabaceae        | <i>Grona adscendens</i>              |                |           |           |           |                  |           |           |          | 3                   | 3         | 5         | 2         |
| Haemodoraceae   | <i>Xiphidium caeruleum</i>           |                |           |           |           |                  |           |           |          | 9                   | 3         | 6         | 5         |
| Heliconiaceae   | <i>Heliconia imbricata</i>           |                |           |           |           | 4                | 2         | 1         | 1        |                     |           |           |           |
| Heliconiaceae   | <i>Heliconia irrasa</i>              |                |           | 1         | 1         |                  |           |           |          |                     |           |           |           |
| Heliconiaceae   | <i>Heliconia latispatha</i>          |                |           |           |           |                  |           | 7         | 3        |                     |           | 6         | 2         |
| Heliconiaceae   | <i>Heliconia stilesii</i>            |                |           |           |           | 1                | 1         |           |          |                     |           |           |           |
| Lamiaceae       | <i>Hyptis</i> cf. <i>obtusiflora</i> |                |           |           |           |                  |           |           |          | 20                  | 7         | 8         | 3         |
| Loganiaceae     | <i>Spigelia hamellioides</i>         |                |           |           |           |                  |           |           |          | 5                   | 3         |           |           |
| Marantaceae     | <i>Calathea crotalifera</i>          | 1              | 1         |           |           |                  |           |           |          |                     |           |           |           |
| Melastomataceae | <i>Blakea</i> cf. <i>litoralis</i>   |                |           |           |           |                  |           | 1         | 1        | 1                   | 1         |           |           |
| Melastomataceae | <i>Miconia</i> cf. <i>nervosa</i>    |                |           | 5         | 1         |                  |           | 9         | 2        |                     |           |           |           |
| Melastomataceae | <i>Miconia</i> sp. 3                 |                |           |           |           | 1                | 1         |           |          |                     |           |           |           |
| Melastomataceae | <i>Miconia</i> sp. 6                 |                |           |           |           |                  |           |           |          | 1                   | 1         |           |           |
| Piperaceae      | <i>Piper</i> sp. 1                   |                |           |           |           |                  |           |           |          |                     |           | 4         | 1         |
| Rubiaceae       | <i>Coccocypselum</i> sp.             |                |           |           |           |                  |           |           |          | 1                   | 1         | 1         | 1         |
| Rubiaceae       | <i>Notopleura uliginosa</i>          | 1              | 1         |           |           |                  |           |           |          |                     |           |           |           |
| Rubiaceae       | <i>Palicourea elata</i>              | 25             | 10        | 1         | 1         | 14               | 6         |           |          |                     |           |           |           |
| Rubiaceae       | <i>Palicourea solitudinum</i>        |                |           |           |           | 7                | 4         | 5         | 1        |                     |           |           |           |
| Rubiaceae       | <i>Palicourea tomentosa</i>          | 102            | 12        | 7         | 5         | 27               | 10        | 6         | 2        |                     |           |           |           |
| Rubiaceae       | <i>Psychotria carthagenensis</i>     | 17             | 8         | 56        | 12        |                  |           |           |          |                     |           |           |           |
| Rubiaceae       | <i>Sabicea</i> cf. <i>panamensis</i> |                |           |           |           | 3                | 2         |           |          |                     |           |           |           |
| Zingiberaceae   | <i>Hedychium coronarium</i>          |                |           |           |           |                  |           |           |          | 4                   | 1         | 9         | 5         |
|                 | <b>TOTAL</b>                         | <b>151</b>     | <b>25</b> | <b>71</b> | <b>18</b> | <b>108</b>       | <b>20</b> | <b>62</b> | <b>8</b> | <b>161</b>          | <b>43</b> | <b>48</b> | <b>17</b> |

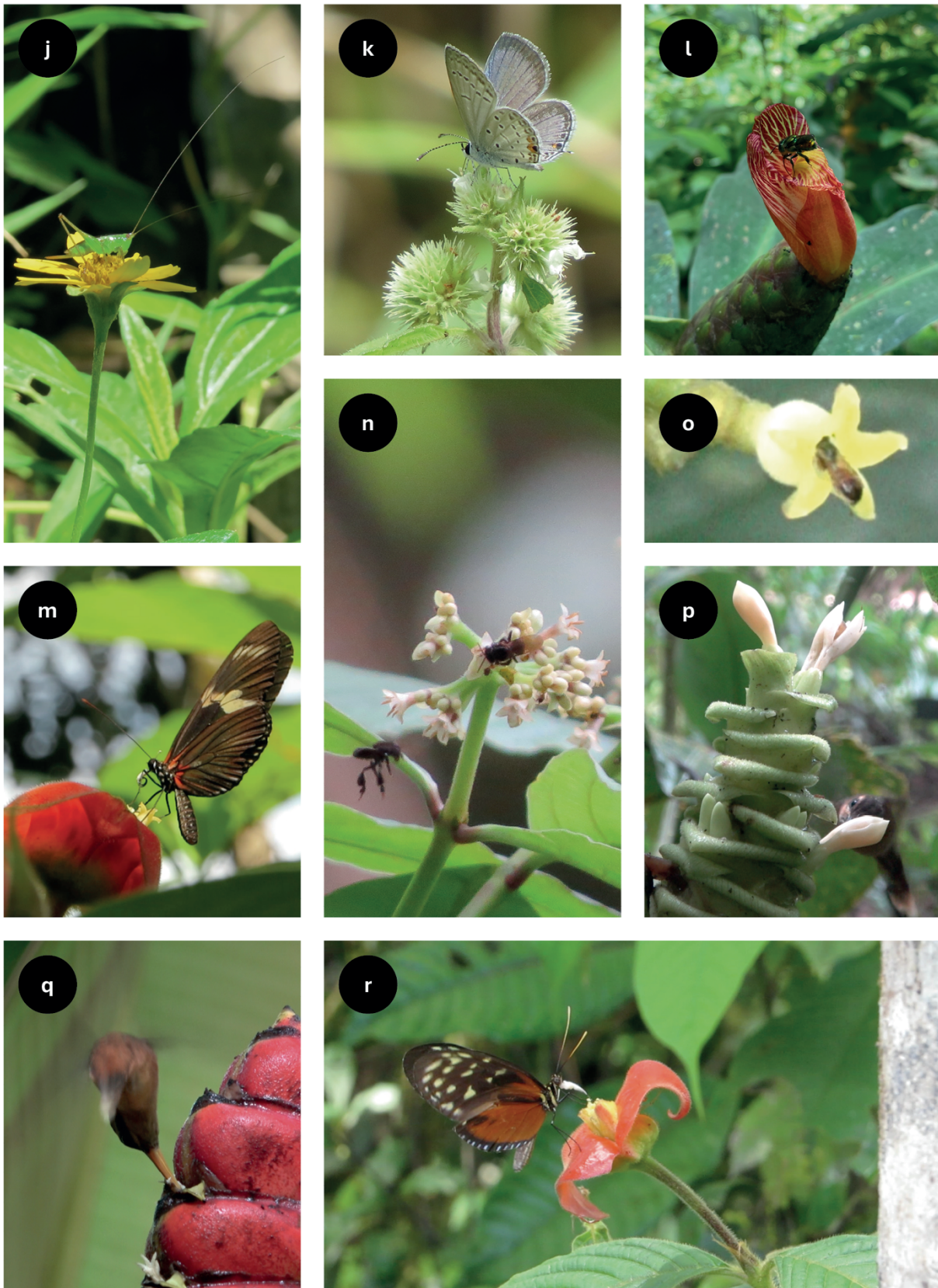
Twenty-six pollinator individuals were sampled in the field for further identification. These included 17 bees (9 bee species in 2 families), 8 butterflies (6 lepidopteran species in 4 families), and one hoverfly. A list of floral visitors present in the three study habitats as well as a list of plant species and their pollinators observed are available in the **Appendices II & III**.





**Figure 21** Selected floral visitors and potential pollinators in three habitat types: Primary forest (PF), old-growth secondary forest (SF), and oil palm plantations (PP). Pictures taken outside of transects are marked with \*. (a) cf. *Augochlora* cf. sp. 1 on *Sphagneticola trilobata* (PP). (b) “Vespidae morphospecies 2” on *Hyptis* cf. *obtusiflora* (PP). (c) *Euglossa* spp. on *Palicourea tomentosa* (SF). (d) *Phaethornis striigularis* on *Palicourea tomentosa* (PF). (e) *Thalurania colombica* on *Palicourea elata* (SF). (f) *Trigona fulviventrīs* on *Dianthera comata* (PP). (g) *Heliconius* cf. *hewitsoni* pollen-feeding on *Palicourea elata* (PF). (h) *Anartia jatrophae* on *Lantana camara* (PP\*). (i) “Meliponini morphospecies 2” on “*Arecaceae* sp. 3” (SF).





**Figure 21 continued** Selected floral visitors and potential pollinators in three habitat types: Primary forest (PF), old-growth secondary forest (SF), and oil palm plantations (PP). Pictures taken outside of transects are marked with \*. (j) Tettigoniidae on *Sphagneticola trilobata* (PP). (k) *Cupido* cf. *comyntas* on *Hyptis* cf. *obtusiflora* (PP). (l) *Euglossa* spp. on *Costus* cf. *laevis* (SF). (m) *Heliconius* cf. *doris* on *Palicourea tomentosa* (PF). (n) Meliponini morphospecies 5 on *Psychotria carthagenensis* (PF). (o) *Ceratina* sp. 2 collected on *Palicourea solitudinum* (SF). (p) Nectar robber *Phaethornis striigularis* piercing *Goeppertia marantifolia* (SF\*). (q) *Phaethornis striigularis* pollinating *Heliconius imbricata* (SF). (r) *Heliconius* cf. *hecale* pollen-feeding on *Palicourea tomentosa* (SF).

## 4. Discussion

This study examines the diversity of flowers and their floral visitors in different habitats along the biological corridor COBIGA (Corredor Biológico La Gamba) in southwestern Costa Rica. The community of co-flowering understory plants and their floral visitors are investigated and compared across multiple study sites in primary forests, old-growth secondary forests, and oil palm plantations. The results reveal a high diversity of floral resources with numerous plant-pollinator interactions in all three habitats, and, specifically, they show that a surprisingly high diversity of plants and pollinators can be found in oil palm plantations, however, composed of a different set of species than in the rainforest understory.

### 4.1. Floral resources

A comparison of the availability, abundance, and diversity of the floral resources in the study area revealed significant differences between the three selected habitat types. The study's findings on species richness and the abundance of open flowers consistently show that the understory of oil palm plantations (PP) is the most diverse and flower-rich habitat type, followed by old-growth secondary forests (SF), and finally, primary forests (PF). Interestingly, the primary forest understory also showed the lowest diversity of plant species flowering at the time of study.

To understand these patterns, it is necessary to consider the underlying influencing factors. Light availability, which is determined by canopy openness or closure, plays a crucial role in all habitats (Li, et al. 2023; Liow, et al. 2001; Dormann, et al. 2020). Plant species richness and diversity are also influenced by habitat heterogeneity and various types of disturbance, such as edge effects and fragmentation (Baptista de Lima, et al. 2020; Li, et al. 2023; Turner & Corlett 1996). In oil palm plantations, the frequency and intensity of anthropogenic disturbances related to management are also important drivers of floral diversity and species richness.

The results of this study are somewhat surprising as they show a higher diversity of flowering understory plants in oil palm plantations than in undisturbed tropical rainforest. However, the story changes considerably when looking at the full picture. Primary and old-growth secondary forests are much taller (30 – 60 m) than oil palm plantations (10 – 15 m), and this study only focuses on the first three meters. Tropical lowland rainforests are characterized by a multilayered vegetation structure (including trees, lianas, and epiphytes) and varied topography (e.g., slopes, ridges, and valleys). As each layer consists of numerous tree species (Terborgh 1985), with crowns producing thousands of flowers, a significant portion of available floral resources in rainforest habitats is missing in this study. In contrast, oil palm plantations do not have a diverse canopy (Foster, et al. 2011), consisting of only one tree species (oil palm, *Elaeis guineensis*), which has inflorescences primarily pollinated by a specialized, introduced African beetle (Greathead 1983). Although we did not study the floral visitors of oil palm inflorescences in La Gamba, they might also represent a considerable pollen source for native insects like bees and other pollen feeders as it has been shown in other studies from Costa Rica and Indonesia (Mayfield 2005; Rizali, et al. 2019).

Furthermore, the closed canopy resulting from the high density of subcanopy and canopy trees in intact, mature forests, such as those in our study's primary and old-growth secondary forest sites, strongly influences the availability of understory plants. Denser canopies restrict understory flowering, a pattern documented in several studies (e.g., Baptista de Lima, et al. 2020; Liow, et al. 2001). Reduced light availability likely limited flowering in the understory of the studied forested sites as well. Li, et al. (2023) observed a positive correlation between canopy openness and both understory flower density and vegetation cover in oil palm plantations.



In line with the “Intermediate Disturbance Hypothesis”, our results indicate that moderate levels of disturbance can maintain or even enhance species richness in ecosystems like oil palm plantations. While major disturbances are often associated with an increase in exotic species and a decline in native species (Ross, et al. 2002), our study shows that exotic species played only a minor role across all three habitat types. The only recorded non-native species were *Murdannia nudiflora* (Commelinaceae) and *Hedychium coronarium* (Zingiberaceae), both found in the oil palm plantations, along with two additional exotic Zingiberaceae species in the old-growth secondary forest.

As Liow, et al. (2001) pointed out, diversity indices do not always accurately reflect a habitat’s ecological status or importance. In our study, primary forest sites are ranked as less diverse according to the calculated indices (see **Tab. 5**), despite potentially having a much higher ecological value. It should be noted that our study represents only a snapshot within a season of the year. Different environmental conditions may exist at other times, which could result in greater diversity and abundance of flowering plants in the primary forest. Finally, potential limitations of our study include sampling bias and non-random transect selection. These factors may have influenced our results as well. Nevertheless, our results indicate that oil palm plantations can harbor a relatively high level and diversity of floral resources in their understory, which likely can contribute to sustaining a community of floral visitors.

### Flowering understory plant community composition

Another objective of this study was to compare and identify differences in the composition of the flowering understory plant community, including terrestrial and epiphytic plants. Based on the results presented in **Table 4**, the floral composition of the understory plants in primary forest was more similar to that in old-growth secondary forest than to oil palm plantations.

Forests with better structure, shadier conditions and fewer edge habitats favor plant populations that need less light to flower (Baptista de Lima, et al. 2020). This was evident in both the primary and old-growth secondary forest habitats in our study. The understory in these habitats was dominated by forest specialists, particularly members of the Rubiaceae and Melastomataceae families. Succulent and broad-leaved herbs from genera such as *Heliconia* (Heliconiaceae), *Calathea* (Marantaceae), *Costus* (Costaceae), and *Dieffenbachia* (Araceae) were also abundant. Epiphytic species like *Philodendron fragrantissimum* (Araceae) and *Guzmania lingulata* (Bromeliaceae) were only recorded in the primary forest. These findings align with the descriptions of flowering plants in deep valleys and ridges of lowland rainforests in the field guide by Weber (2001). Another example of an epiphytic plant is *Blakea* cf. *litoralis* (Melastomataceae), which was found in both the old-growth secondary forest and in oil palm plantations growing on the trunk of an oil palm. Melastomataceae and Rubiaceae were the most species-rich plant families in all three habitat types. Similar compositions of common understory plant families in Neotropical lowland rainforests have been reported in other studies (e.g., da Silva, et al. 2021; Rincon, et al. 1999; Baptista de Lima, et al. 2020; Guariguata, et al. 1997), which supports our findings. Some families, such as Piperaceae, Gesneriaceae, Arecaceae, and Commelinaceae, which are usually common, played a minor role in our study.

More plant species that are adapted to lighter conditions, were found in transects of old-growth secondary forests. According to Baptista de Lima, et al. (2020), the presence of open-area and edge-opportunistic plants may result from reduced forest cover and increased edge effects. Such conditions are commonly found at forest edges and in forest gaps, where most of the SF transects (and *FI\_pf*) were situated. *Palicourea elata* (Rubiaceae) is a species that thrives in light gaps and on forest edges (Weber 2001) and was documented in all but one transect in both forest habitats. According to Skinner (2008), *Costus* cf. *laevis* and *Costus* cf. *pulverulentus*, both of which were observed in the secondary forest, are commonly found in understory clearings and along riverbanks. *Pentagonia* cf. *tinajita* (Rubiaceae), which is typically found in



secondary riparian habitats (Csekits 2008), was recorded in the transect (W2<sub>pp</sub>) that follows the course of a small river within the oil palm plantation. *Heliconia latispatha* (Heliconiaceae), known for its heat and drought tolerance (Weber 2001), was abundant in the secondary forest and was present in both oil palm plantations.

The floristic composition of the oil palm plantations differed drastically from that of the primary forest. Most forest species were not found in this habitat type. Danielsen, et al. (2008) also found that trees, lianas, epiphytic orchids, and indigenous palms were entirely absent from oil palm plantation plots in Asia, whereas they were present in forest plots. A similar pattern was observed in the current study, as the vegetation is dominated by an herbaceous ground layer and plants that cover the palm trunks. The flora in oil palm plantations is adapted to disturbed, simplified, and open environments – conditions that are also typical in pastures, indicating a degree of ecological overlap with such areas. Common pasture plants, according to Weber (2001), that were found in the oil palm plantation sites included two species each of *Cyperus* (Cyperaceae), *Desmodium* (Fabaceae), and *Hyptis* (Lamiaceae), as well as *Lantana camara* (Verbenaceae), *Caperonia* cf. *palustris* (Euphorbiaceae), and *Sphagneticola trilobata* (Asteraceae). A few of these species also appeared in old-growth secondary forest transects, likely due to ongoing disturbances. Oil palm plantations are also characterized by wet conditions. Wetland species recorded in the transects included *Limnocharis flava* (Limnocharitaceae), *Bacopa salzmannii* (Plantaginaceae), *Heteranthera reniformis* (Pontederiaceae), and *Ludwigia* (Onagraceae). Turner & Corlett (1996) and Danielsen, et al. (2008) emphasize that only a few rainforest species tolerate the environmental conditions in agricultural landscapes.

Nevertheless, oil palm plantations were dominated by generalist species that have low conservation value. Additionally, although *Sphagneticola trilobata* and *Limnocharis flava* are native to Costa Rica, both have become naturalized in many tropical regions worldwide (Global Invasive Species Database 2025). *Sphagneticola trilobata* forms a dense ground cover and is listed among the “100 of the World’s Worst Invasive Alien Species” (Lowe, et al. 2004). It was the most dominant plant species in the oil palm plantation transects, accounting for approximately one-third of all recorded individuals and one-quarter of open flowers in this study habitat.

### Pollination systems of flowering understory plants

Another objective of this study concerned the pollination systems found in the three different habitat types and their abundances. Six or more different pollination syndromes were found across all studied plant species (see Fig. 6). The bee pollination syndrome was the most common, consistent with findings from other studies on plant-pollinator interactions in the tropical rainforest (e.g., da Silva, et al. 2021). Common floral rewards provided for bees are nectar and pollen. Plants that produce buzz-pollinated flowers and offer only pollen as a reward are strictly adapted to bees as pollinators, as they are the only known animals that can release pollen by vibrating (“buzz pollination”). In the Golfo Dulce area, buzz pollination involves medium to large bees such as bumble bees and orchid bees. This type of pollination is found on site in the genus *Miconia* (Melastomataceae), in other genera of the family Melastomataceae, and in *Xiphiidium* (Haemodoraceae) (Weber 2008). *Xiphiidium caeruleum* was present in two oil palm plantation transects and *Miconia* in all three habitat types, with the highest species richness of this genus found in the old-growth secondary forest sites.

Bats, birds, and some non-flying mammals, as well as lizards (see Olesen and Valido 2003) are the only known pollen vectors among vertebrates. In Central America, hummingbirds are the most important group of avian pollinators. Pollination by hummingbirds is common in the plant families Acanthaceae, Bromeliaceae, Costaceae, Gesneriaceae, Heliconiaceae, Marantaceae, Rubiaceae, and Zingiberaceae (Bawa 1990; Stiles 1985). These plant families were present in our study sites and are associated with the bird-syndrome. *Palicourea elata* and *P.*

*tomentosa* (syn. *Psychotria*; *Cephaelis*) of the Rubiaceae family, present in the primary and secondary forest sites, are adapted to pollination by birds and bees. Both shrub species have bright red bracts with white tubular corollas. Bird flowers are primarily nectar flowers. Nectar is a critical source of food, drink and energy for hummingbirds. *Heliconia* with its bright red and yellow colors and high nectar production is specialized for hummingbirds (Fuchs & Quesada n.d.; Stiles 1985; Weber 2008). Four species of *Heliconia* were recorded in the old-growth secondary forest. This habitat type had the highest abundance and relatively highest number of ornithophilic plant species, followed by the primary forest. The oil palm plantations had a low number of flowering plants known to be visited and pollinated by hummingbirds. Only nine percent of the plants in PP provided potential resources for hummingbirds in terms of their pollination syndrome. These findings are consistent with those of Friesenbichler (2013). In her research, Friesenbichler (2013) investigated the relationship between oil palm plantations and the local hummingbird population in La Gamba, Costa Rica. Regarding the Costaceae in the study sites, all species are pollinated by hummingbirds, except for *Costus laevis*. This species is adapted to be pollinated by *Euglossa* bees and is rarely – and illegitimately – visited by hummingbirds (Schemske 1983). *Costus* species were documented flowering in the secondary rainforest (and in the primary forest outside of the transects as well as fruiting in the oil palm plantation transects, see **Appendix I**).

According to Weber (2008), bat pollination is relatively rare in the Golfo Dulce area. The only chiropterophilous plant species recorded in the study transects was *Mabea* sp. from the Euphorbiaceae family, found in the primary forest. Floral traits associated with bat pollination include pale or dull-colored flowers, flowers positioned away from branches (and/or cauliflory), and often large, sturdy flowers. The Bromeliaceae family is one of the most species-rich plant families in the Neotropics and has undergone remarkable adaptive radiation, leading to a wide variety of flower morphologies (Göttinger, et al. 2019). This plant family plays a crucial ecological role in bat pollination (Aguilar-Rodriguez, et al. 2019). The two Bromeliaceae species recorded in this study – one in the primary forest and one in the secondary forest – are likely bird-pollinated. The genus *Guzmania* includes species that are pollinated by bats (Göttinger, et al. 2019). However, *Guzmania lingulata*, found on site in the primary forest, exhibits diurnal anthesis, indicating that it is pollinated by hummingbirds rather than bats (Krömer 2003; Stiles 1985). No records exist for *Aechmea pubescens*, and no observations were made in this study. Other species within the *Aechmea* genus are reportedly bird-pollinated (Göttinger, et al. 2019).

Further, primary forests exhibited a high diversity of pollination syndromes that were also evenly distributed across plant species (see **Tab. 3**). This pattern is consistent with Bawa (1990), who suggests that the high species richness of tropical lowland rainforests correlates with a high diversity of pollination mechanisms. Old-growth secondary forests showed a similar number of syndromes (6) but with slightly lower evenness. In contrast, oil palm plantations contained the highest number of pollination syndromes (7), yet their overall diversity was reduced due to low evenness, as the community was dominated by melittophily. As stated by Bawa (1990), the distribution of pollination systems also varies across forest layers; the bee pollination syndrome is more prevalent in the forest canopy layer, whereas in the understory, plants are adapted not only to bees but also to hummingbirds, moths, and beetles. In this study, bird- and beetle-pollinated plants were more strongly represented in both forest habitats compared to oil palm plantations. In contrast, moth-pollinated plants were recorded only in oil palm plantations. The dominance of the bee syndrome in oil palm plantations can be explained by the simplified vegetational structure of this habitat (Foster, et al. 2011).

## 4.2. Floral visitors and potential pollinators

### Visitation frequency of floral visitors

Most of the plant species observed in this study offered nectar and/or pollen as reward, which was consumed and/or collected by multiple animal groups, primarily insects. Overall, the most abundant floral visitors documented during this study were bees, butterflies, ants, and hummingbirds, the latter only recorded from primary and secondary forests. Floral visitation patterns are influenced not only by floral traits but also by floral resource availability. The frequency of visits (measured as observations per hour, see **Fig. 11**) appeared to increase with the number of open flowers, in line with trends reported in previous studies (e.g., Ebeling, et al. 2008; Kato, et al. 2008; Silva, et al. 2022). In the primary forest, *Palicourea tomentosa* and *Psychotria carthagenensis* were present in most transects and, due to high flower abundance, these species were frequently visited. Interestingly, *P. tomentosa* produced only half as many flowers in the old-growth secondary forest, yet visitation frequency remained similar. Other species with high flower numbers in the secondary forest included *Palicourea solitudinum*, which attracted small bees and was frequently visited. In contrast, *Aciotis* cf. *rubricaulis* had high numbers of flowers, yet it received no visits during our study period, and no literature exists on its potential pollinators. In the oil palm plantations, *Sphagneticola trilobata* had the highest number of open flowers and was by far the most frequently visited plant species.

It should be noted that many floral visitor species may forage in the forest canopy (Roubik 1993; Ramlah, et al. 2021), which was not included in this study.

### Visitors vs. pollinators

While the flowers observed during this study attracted a variety of visitors, not all of them may act as effective pollinators (Willmer 2011; Reyes, et al. 2021). Ants are an example of common yet ineffective visitors (Faegri & van der Pijl 1966). In our study, we found that 59-80% of all interactions involved contact with the plant's reproductive organs, suggesting that most visitors were potential pollinators. This classification was determined based on their observed behavior. This included whether the floral visitors made contact with the reproductive organs of the flower. Our data shows that in 81% of plant species, where pollinators were documented (21 out of 26 spp., see **Tab. 12**), the assigned pollination syndrome matched the field observations (see **Tab. 4** for pollination syndromes, ps), but also other insects pollinated the plants. Interestingly, contact with the reproductive organs was recorded in seven plant species despite their floral traits indicating that the respective insects are unlikely effective pollinators. Examples include small bees visiting “Cyperaceae sp. 1” (wind-ps), *Hedychium coronarium* (moth-ps), *Mabea* sp. (bat-ps), and *Xiphidium caeruleum* (bee-ps, but “buzz-pollinated”). Other examples include a wasp visiting *Blakea* cf. *litoralis* (bee-ps; Lumer 1983), a fly visiting *Grona adscendens* (be-ps), and grasshoppers visiting *Sphagneticola trilobata*. However, Drager, et al. (2021) pointed out, insects with low per-visit effectiveness may still contribute to pollination through frequent visits. Winfree, et al. (2011) similarly emphasized that frequent visitors often act as important pollinators. However, since no pollen analysis or measurements of fertilization success were performed, it is uncertain whether a visitor functioned as an effective vector for the respective plant species. As Kamke, et al. (2011) argue, detailed observations should be complemented by tests of pollination effectiveness to better understand the complex dynamics of plant-pollinator interactions.

### Diversity of potential pollinators

We initially assumed that pollinator diversity would be highest in primary forests because usually more specialist pollinators are restricted to this habitat. However, this presumed

higher diversity could not be conclusively demonstrated. The results were dependent on the observation method used. Transect walk (TW) observations revealed higher pollinator diversity indices and a steeper accumulation curve in primary forests (see **Tab. 11** and **Fig. 20**). The results are based on all plant species flowering within transects (PF: 9 spp.; SF and PP: 11 spp. each). In contrast, focused observations on selected plant species revealed the lowest diversity measures and a flattened accumulation curve in primary forests (see **Tab. 8** and **Fig. 15**), likely due to the limited number of observed plant species (PF: 3 spp.; SF: 7 spp.; PP: 8 spp.). Transect walk observations may offer a broader view of floral visitors across habitats, and focused observations may underrepresent the diversity in areas where fewer plant species are available to observe.

In TW observations, pollinator diversity was lowest in the secondary forest, likely due to the mass flowering of a single understory palm species (*Arecaceae* sp. 3). This palm attracted large numbers of one stingless bee species, which accounted for 77% of observations in the SF (see **Tab. 9** and **Fig. 21i**) during a short period during its bloom. As a result, both Shannon and evenness indices were reduced ( $H' = 0,93$ ;  $J = 0,45$ , see **Tab. 11**). Similar patterns of heavy bee activity on flowering palms in forest understories have been reported (Rincon, et al. 1999). In contrast, oil palm plantations showed comparatively high diversity indices ( $H' = 3,38$  on selected plant species, **Tab. 8**;  $H' = 2,55$  during TW, **Tab. 11**). This may be because of the more open structure of palm plantations, which allows more light and a constant floral supply (Nery Silva, et al. 2018). Bee diversity has been shown to be higher in open areas, if they are close to forest patches (Nery Silva, et al. 2018). Power, et al. (2021) also reported that bee visitation declined with distance from the forest. Both oil palm plantation sites are located near forest edges within the COBIGA corridor. This allows forest species to forage in agricultural areas (Liow, et al. 2001; Baptista de Lima, et al. 2020). However, despite the presence of suitable floral resources in proximity to the forest, such as *Xiphidium caeruleum* and *Blakea* cf. *litoralis*, no euglossine bees were recorded in the oil palm plantations. This aligns with findings by Larsen, et al. (2005), who noted that large bees are particularly sensitive to habitat disturbance and habitat loss.

## Community composition of potential pollinators

Faegri & van der Pijl's concept of pollination syndromes (1966) proposes that specific combinations of floral traits are adapted to attract certain types of pollinators. According to this concept, pollinators can be grouped into functional groups that behave similarly when visiting flowers (Fenster, et al. 2004). These interactions are shaped by co-evolution, because shared behaviors create similar selection pressures on flowers (Endress 1996). Floral traits influence not only individual pollinator behavior, but also the structure of entire pollinator communities. As Winfree, et al. (2011, p. 14) stated: "Richness and abundance are simple indices that are useful in evaluating large-scale trends, but they can mask changes in the identity or composition of species"; particularly the replacement of forest-dependent species to disturbance-associated species in response to anthropogenic land use changes. These shifts in composition are often driven by the decline or disappearance of specialist species and the presence of widespread generalist species (Winfree, et al. 2011; Liow, et al. 2001; Brosi, et al. 2008). Resource availability, including food and nesting resources, has been identified as a bottleneck contributing to these changes (e.g., Brosi, et al. 2008; Montoya-Pfeiffer, et al. 2020). Recent work by Janovsky & Stenc (2023) further emphasizes that floral traits and niche breadth of plants both shape plant–pollinator network structure.

Our results show that pollinator communities differ less between primary and old-growth secondary forest sites than between oil palm plantations and the two latter habitats. Many members of each functional pollinator group present in the primary forest were also found in the secondary forest (17 out of 34, 50%); however, only some (5 out of 34, 14,7%) of these members were found in oil palm plantations (for more details, see **Appendix II**).



## Interactions between functional key pollinator groups and flowers

The key functional pollinator groups recorded during the study were:

### **hummingbird**

Hummingbirds (family: Trochilidae) are the main bird pollinators in Central America and represent one of the largest avian families in the New World (Bawa, 1990; Stiles, 1985). In our study, they were the only birds visiting flowers. In primary and secondary forest, hummingbirds predominantly visited *Palicourea elata*, *P. tomentosa* and *Heliconia* species (*H. imbricata* and *H. stilesii*) (**Fig. 21q**). In the oil palm plantations, only one random interaction between a hummingbird visiting *Hedychium coronarium* was recorded. This plant species is reportedly pollinated by hawkmoths (Müller 1890).

The co-evolutionary association between hummingbirds and their plants is well documented (e.g., Martín González, et al. 2015; Huber & Weissenhofer 2007). *Palicourea elata* was the dominant floral resource. It had a high abundance of open flowers in the primary and old-growth secondary forest and is known to be adapted to bird pollination (Stiles 1985; Silva & Segura 2015). It produces high amounts of nectar, displays bright red bracts and its tubular corollas match the morphology of hummingbird beaks. Similarly, brightly colored *Heliconia* species, which are also morphologically suited for hummingbirds, provide a critical nectar source during their breeding season (Stiles 1985). These plants offer only a few open flowers per inflorescence each day over extended periods to ensure a constant nectar supply (Huber & Weissenhofer 2007). In Costa Rica, 37 species of *Heliconia* can be found (Fuchs & Quesada n.d.). Of the 38 total hummingbird visits, our study identified two hummingbird species: *Thalurania colombica* and *Phaethornis striigularis*. Both species are typically found in the understory of humid tropical forests, at forest edges and in dense secondary forest (Schuchmann 1999). *Phaethornis striigularis* is also known for nectar robbery by piercing flowers to access nectar without pollinating the plant (Silva, et al. 2022; Schuchmann 1999). This behavior was also randomly observed during this study on *Goeppertia marantifolia* (Marantaceae) in the secondary forest outside transects (**Fig. 21p**). In another study conducted in the same area, it was shown that *Threnetes ruckeri* robs nectar in a similar way from *Calathea lutea*, another Marantaceae species (see Etl, et al. 2019). Hence, such a behaviour might be more common, suggesting that some hummingbird species act as nectar robbers rather than pollinators in Marantaceae.

In contrast to the studied forest habitats, the oil palm plantations showed a lower abundance and diversity of flowering bird-pollinated plant species (see **Fig. 6**). Interestingly, although a few individuals of *Heliconia latispatha* were present in two transects, no hummingbird visitations could be confirmed. Likewise, *H. latispatha* and *H. irrassa* had many open flowers in the old-growth secondary forest, yet they did not attract any hummingbirds either. The absence of hummingbird observations in the secondary forest in our study may be due to the short observation time (30 minutes). A previous study on floral visitors in La Gamba (Lindhuber 2023) identified hummingbirds, small bees, and butterflies as potential pollinators of *H. latispatha*. However, even in that study, low hummingbird activity was documented on this plant, as well as in oil palm plantations in general (see also Friesenbichler 2013). *Phaethornis striigularis* may inhabit vegetation-rich plantations (Schuchmann 1999), but the lack of suitable nectar sources likely limits the diversity, abundance, and foraging behavior of nectarivorous birds.

### **large bee**

The functional group *large bee* was composed only of orchid bees (family: Apidae, tribe: Euglossini), with most individuals (84%) belonging to the genus *Euglossa*, and singular records of *Eulaema* and *Exaerete*. In our study, observations of orchid bees were documented on

*Palicourea tomentosa* and on *Costus* cf. *laevis*, which is known to be pollinated by female *Euglossa* bees (**Fig. 211**) (Schemske 1983). This functional group was exclusively observed in the primary and secondary forest sites, but never in oil palm plantations (**Appendix II**). The absence aligns with findings from Brazil, where oil palm plantations also showed low abundance and species richness of orchid bees (Brito, et al. 2017). The sensitivity of large-bodied bee communities to disturbance and tropical forest fragmentation is well funded. Most species of the tribe Euglossini depend heavily on intact forests due to their specific nesting and floral resource requirements (Larsen, et al. 2005; Montoya-Pfeiffer, et al. 2020; Brosi, et al. 2008). Other studies have shown a decline in orchid bee species richness when sampled outside of forests in sugar cane plantations (Milet-Pinheiro & Schlindwein 2005). Due to their broad foraging behaviors and the wide variety of plant species they pollinate, orchid bees are considered key pollinators in Neotropical ecosystems. They predominantly forage in the forest understory (Bawa 1990; Roubik 1993). While females collect nectar, pollen, and resin for their offspring, males collect nectar and fragrances from various sources (Jarau, et al. 2009).

### **butterfly**

Lepidoptera (butterflies) are highly diverse in Costa Rica (DeVries 1987), yet plants pollinated by butterflies are generally rare in tropical rainforests (Weber 2008). However, in the current study, butterflies represented the most frequently recorded floral visitors in the primary forest transects. Several species of *Heliconius* were regularly observed visiting two Rubiaceae species (*Palicourea tomentosa*, *P. elata*). Similar interactions between *Heliconius* butterflies and the two former mentioned *Palicourea* species were also recorded in old-growth secondary forest transects. The flowers have long, narrow corolla tubes, a floral trait typically associated with butterfly pollination (Fenster, et al. 2004). However, during our observations they were also frequently visited – and most likely pollinated – by hummingbirds and orchid bees (see above), which suggests that they have a mixed pollination system. The abundance of these two Rubiaceae species, coupled with the continuous presence of open flowers corresponded with high levels of butterfly visitations in both forest habitat types. These results support the hypothesis that pollinator abundance in tropical rainforests reflects the availability of flowers (Kato, et al. 2008).

Nymphalid species, especially from the genus *Heliconius*, are particularly common in tropical rainforests (DeVries 1987). Five of the eight *Heliconius* species that occur in the Golfo Dulce region (Krenn, et al. 2010), were recorded mainly as pollinators of *P. tomentosa* and occasionally *P. elata*. in primary and old-growth secondary forest sites. These included *H. doris*, *H. hewitsoni*, *H. pachinus*, *H. hecalesia*, and *H. hecale*, as well as cf. *Hyposcada virginiana*. Another study investigating the pollination biology of *P. elata* reported several *Heliconius* species as pollinators, as well as another nymphalid species (*Hyposcada virginiana*) (Silva & Segura 2015). As *Heliconius* butterflies also feed on pollen, a behavior unique for this genus (Krenn, et al. 2010), they likely visit the flowers of *Palicourea* spp. for nectar and pollen. This behavior was confirmed during the current study (**Fig. 21r**).

In oil palm plantations, no *Heliconius* species were recorded during the study. This absence is likely due to the lack of larval host plants, such as Passifloraceae, which are typically only found in natural forests (Krenn, et al. 2010). The composition of the butterfly community in the oil palm plantations differed from that in forest habitats (see **Appendix II**). Instead of forest-adapted species, butterflies that are typical of disturbed and open habitats (Krenn, et al. 2010) were frequently observed, such as *Anartia fatima*, *A. jatrophae*, and *Anthanasia frisia* (all Nymphalidae). These species are commonly associated with intensely cultivated landscapes like pastures and oil palm plantations (Krenn, et al. 2010). Consistent with Koh's (2008b) findings that ground cover vegetation is a key predictor of butterfly richness in Asian oil palm plantations, both of our study sites had high floral abundances. In addition to Nymphalidae, we recorded butterflies from the families HesperIIDae, Lycaenidae, Riodinidae, and Pieridae.

Abundant species included *Cupido* cf. *comyntas* (Lycaenidae), *Charis anius*, and *Calephelis* sp. (Riodinidae). The most frequently visited flowers were *Sphagneticola trilobata* (Asteraceae) and *Hyptis* cf. *obtusiflora* (Lamiaceae). Additionally, some individuals of butterfly species also visited *Lantana camara* (Verbenaceae) but outside the studied transects (**Fig. 21h**).

### **small bee**

The main representatives of the functional group *small bee* were the stingless bees (Meliponini; Apidae) and sweat bees from the tribe Augochlorini (Halictidae) (**Appendices II & III**). Small bees were the most frequent floral visitors and also accounted for the most frequent potential pollinators considering all the study habitats together. Although, according to Bawa (1990), bee pollination predominantly occurs in the forest canopy, we recorded numerous small bees on understory flowers. Bees are widely recognized as the most important group of pollinators, due to their reliance on food resources such as pollen and nectar (Willmer 2011). Their adaptations, high floral constancy, and foraging frequency make them especially effective as pollinators.

Social stingless bees have a pantropical distribution but are particularly abundant in the Neotropics. Multiple studies in various tropical environments have shown that up to 50% of bee observations involve stingless bees (Grüter 2020; Rincon, et al. 1999). Their abundance and polylectic foraging behavior make them important pollinators in all tropical ecosystems on earth (Arena, et al. 2018; Grüter 2020). However, not all visits by stingless bees result in successful pollination; stingless bees are also known for nectar robbing (e.g., Murphy 2005). In our study, *Psychotria carthagenensis* (Rubiaceae) was predominantly visited by various stingless bee species, yet only about 15% of flower visits involved contact with the reproductive parts. Consolaro, et al. (2011) identified *Bombus* and halictid bees as main pollinators of *P. carthagenensis* in Brazil. Stingless bees were most abundant in primary forest and less abundant in old-growth secondary forest and oil palm plantations. This pattern is likely due to their nesting requirements, especially for those that nest in tree cavities, which requires forest (Brosi, et al. 2008; Rincon, et al. 1999; Eltz, et al. 2003). The fox-colored stingless bee, *Trigona fulvoventris* (Apidae), one of the most widespread species of stingless bees in the region (Jarau, et al. 2009), was recorded in all three habitats. Including the observations outside the transects, this species visited at least 18 different plant species in the corridor.

Small bees were the most abundant pollinators in both secondary forest and oil palm plantations. In the secondary forest, *Palicourea solitudinum* (Rubiaceae) was highly attractive to solitary small bees, which were observed crawling into the flowers to pollinate them (**Fig. 21o**). In oil palm plantations, where melittophilous plants dominate the flora (**Fig. 6**), small bees were the dominant pollinator group. The community there was primarily composed of metallic halictid bees (e.g., *Augochlora* spp.) and other, rather small solitary bees. *Sphagneticola trilobata* (Asteraceae) was highly attractive to small bees (**Tab. 12**). This species produces large, yellow flower heads that are easily accessible – an ideal floral resource for generalist pollinators (**Fig. 21a**).

### **wasp**

The functional group *wasp* was observed in lower numbers. The role of wasps as pollinators is not well studied in general, except for the coevolved mutualism between fig wasps (Agaonidae) and figs (*Ficus*, Moraceae) (Janzen 1979). Usually, most wasp species are generalist flower visitors with short, unspecialized mouthparts, typically visiting flowers with short corollas and exposed rewards (Winfree, et al. 2011; Endress 1996). In our study, we recorded a wasp pollinating *Psychotria carthagenensis* (Rubiaceae) once in the primary forest, and wasps pollinating *Hyptis* cf. *obtusiflora* (Lamiaceae) in the oil palm plantations (**Fig. 21b**). In Panama, wasps have been reported as pollinators of *Hyptis* sp. (Keller & Armbruster 1989).

### **fly**

The functional group *fly* was also observed in lower abundances. According to Endress (1996), flies represent the second most important group of pollinators, though most of them do not depend on flowers for food. Many flies collect nectar from open, unspecialized flowers and can effectively pollinate them (Endress 1996). In our study, we observed flies (Diptera) pollinating *Sphagneticola trilobata* (Asteraceae) in oil palm plantations. Additionally, wasp-like syrphids and other flies with elongated probosces (e.g. Bombyliidae) can exploit tubular flowers, which are usually polyphilic (Endress 1996; Weber 2008). In contrast, flowers associated with the sapromyophily syndrome (e.g., in Araceae) are specialized to flies and emit a smell of rotting organic matter, have huge, dull flowers, and produce heat (Chakraborty & Adhikary 2018).

### **beetle, true bug and other**

The functional groups *beetle* and *true bug* were observed occasionally in our study, and then only as floral visitors. Both groups are known to feed on flowers (Xiao, et al. 2021) and beetles possibly represent one of the most ancient pollinator groups (Gottsberger 1988). In particular, beetles are associated with many aroids and palms, where they act as important pollen vectors (Bawa 1990; Willmer 2011). Similarly, true bugs have recently been identified as effective pollinators of an Araceae species in Costa Rica (Etl, et al. 2022). Within *other*, only grasshoppers were classified as potential pollinators on *Sphagneticola trilobata* (Asteraceae) (Fig. 21j).

### **bat, moth and non-flying mammal**

The functional groups *bat*, *moth*, and *non-flying mammal* were not recorded in any of the habitat types during the study period. Their absence is likely due to their nocturnal foraging behavior (Bawa 1990; Weber 2008) as observations were conducted during the day. In addition, the number of species adapted to bat or moth pollination within the transects was low.

In summary, hummingbirds, orchid bees, and *Heliconius* butterflies were strongly associated with primary and old-growth secondary forests. This reflects their dependence on complex vegetation structures, specific floral resources, and microhabitats. These groups were almost completely absent from the studied oil palm plantations. These findings show that forest degradation and conversion into e.g., oil palm plantations, leads to a loss of many of the numerous, specialized plant-pollinator interactions known from undisturbed tropical rainforests. Small bees, wasps, and generalist butterflies were frequently observed in oil palm plantations, suggesting a greater tolerance to disturbance and simplified landscapes (Winfree, et al. 2011; Brosi, et al. 2008). This contrasting pattern highlights a clear shift in pollinator community composition across the three studied habitat types. The loss of several key pollinator groups (hummingbirds, orchid bees, *Heliconius* butterflies) due to conversion of rainforest into oil palm plantations raises further questions about how the loss of functional groups affect pollination networks and ecosystem resilience in landscapes like oil palm plantations. The results of this study emphasize the importance of primary forest fragments for the conservation of key functional groups (e.g., Montoya-Pfeiffer, et al. 2020). Nevertheless, our results also show that other, seemingly less specialized plant-pollinator interactions can be found inside oil palm plantations. This suggests that some insects and plants can still use this habitat as a place to live, gather food, or travel through.



### 4.3. Implications for conservation

Oil palm (*Elaeis guineensis*) cultivation is expanding worldwide and the demand for palm oil as a vegetable oil for food production or biofuel will continue to rise (Danielsen, et al. 2008; Beggs & Moore 2013). While the expansion of plantations in La Gamba has mainly replaced pastures and rice fields so far and expansion into forests is less likely (Höbinger, et al. 2012), concerns remain regarding habitat loss, landscape simplification, and barriers to species dispersal. Montero, et al. (2021) note that although Costa Rica has successfully reversed deforestation, the increase in monocultures has fragmented habitats and isolated forest patches. This leads to a decline in forest-dependent pollinators, as they rely on intact forest ecosystems for nesting and floral resources (Pots, et al. 2010; Krishnan, et al. 2020). Our study supports these findings, revealing that although oil palm plantations exhibited high floral and pollinator abundances, they lacked forest specialists and the composition of their pollinator community differed drastically from those in forest habitats.

#### Management strategies to improve the ecological value of oil palm plantations

Despite limitations and challenges, oil palm plantations present unique opportunities for biodiversity-friendly management. Current research emphasizes their potential (e.g., Foster, et al. 2011; Luke, et al. 2020; Zemp, et al. 2023; Pots, et al. 2010). Conservation recommendations should focus on how to enhance habitat complexity, increase floral and nesting resources, and integrate plantations into the broader ecological matrix. As Luke, et al. (2020) and Foster, et al. (2011) suggest, the oil palms' long rotation cycles and tree-like structure leave room for improving biodiversity values through management practices. Measures such as reducing herbicide usage in favor of selective manual cutting (or horse grazing in the case of Finca Will), maintaining epiphytes on palm trunks, and promoting native understory growth can enhance habitat heterogeneity, which has been shown to support greater species richness (Aratrakorn, et al. 2006; Ramlah, et al. 2021; de Araujo, et al. 2018). These management practices were also implemented in the studied oil palm plantations and shown here to be effective.

In terms of floral resources, our study found that oil palm plantations had an unexpectedly high plant diversity and abundance, likely due to greater light availability and a more open landscape structure (see also Nery Silva, et al. 2018). However, many of these plant species had bee-adapted or generalist pollination systems (e.g., *Sphagneticola trilobata*, *Piper* spp., *Hyptis* spp., and *Pseudelephantopus* sp.). To increase their conservation value, plantations should be enriched with native, pollinator-attractive plant species, (e.g., our study plants *Palicourea* spp. *Psychotria carthagenensis*, and *Heliconia* spp.). As Martins & Antonini (2016) emphasize, plant traits should be considered in planning to ensure the attraction of diverse pollinators. Specific emphasis can be placed on hummingbird-adapted species with nectar-rich flowers (Friesenbichler 2013; Najera & Simonetti 2010). Lindhuber's (2023) observations within the COBIGA corridor support this, identifying plant species of particularly high ecological value for oil palm plantations based on visitation frequency and floral visitor diversity (e.g. *Heliconia* spp., *Calathea lutea*, *Pentagonia monocalis*). In parallel, enhancing nesting opportunities is equally important. Many forest-dependent bees, such as stingless bees, which rely on hollow tree trunks or other cavities, are scarce in monocultures (Brosi, et al. 2008). Nesting resources can be temporarily supported through artificial shelters (Arena, et al. 2018) and epiphytes, which provide microhabitats for bees and other insects.

However, local habitat improvements within plantations should be part of broader, landscape-scale conservation strategies. Ecological restoration, particularly through the planting of native tree species, can support the recovery of pollinator communities and ecosystem functionality (Li, et al. 2023; Montoya-Pfeiffer, et al. 2020), but it cannot fully replace the ecological value of intact rainforests. As Zemp, et al. (2023) emphasize, restoration strategies

do not replace the protection of remaining forest patches. Only intact and mature tropical rainforest ecosystems provide the full complexity of resources and microhabitats that are required by many forest-restricted pollinators (Brosi, et al. 2008; Nery Silva, et al. 2018). Weissenhofer, et al. (2012) also distinguish between reforestation and ecological restoration: the latter aims to establish diverse, self-sustaining ecosystems that often requires planting over 100 native species per hectare. While these restored areas may eventually offer habitats for sensitive species, they cannot immediately replicate the conservation value of primary forests. As Gutiérrez-Chacón, et al. (2020) demonstrate, recovery takes time. In their study, even after thirteen years of active restoration in riparian forests, pollinator richness and composition remained below reference levels. This underlines the need for long-term commitment. The success of restoration efforts can be evaluated through the return of functional key pollinator groups, such as large bees, which are sensitive to habitat degradation and closely associated with intact forests (Montoya-Pfeiffer, et al. 2020; Larsen, et al. 2005) – a pattern that was also evident in our study. Furthermore, Martins & Antonini (2016) determined that the richness, abundance, and composition of pollination syndromes can evaluate the restoration success.

Finally, biological corridors are essential for mitigating the effects of fragmentation and maintaining ecological connectivity. As shown by Hilty, et al. (2019), corridors facilitate species movement, genetic exchange, and functional ecological interactions. This connectivity is particularly crucial for pollinators such as orchid bees. Brito, et al. (2017) found that the presence of corridors and nearby forest patches can support orchid bee populations, even within oil palm plantations. The proximity of oil palm plantations to rainforests directly influences species richness and pollinator community composition (Ramlah, et al. 2021) and can accelerate the recovery of animal communities (Turner & Corlett 1996). Thus, the COBIGA biological corridor is essential for maintaining ecosystem processes and functional diversity in fragmented tropical landscapes (Höbinger, et al. 2012).

## Conclusions

This study examined plant-pollinator interactions in three habitat types in the tropical lowland rainforest of La Gamba, Costa Rica, comparing oil palm plantations, old-growth secondary forests, and primary forests. The different habitat types within the COBIGA biological corridor host a wide variety of plant species and are used by many floral visitors.

Despite their monocultural character, the oil palm plantations in our study provided high floral resource availability and floral visitor richness. This can be explained by their ecological management, which involves reduced to no use of herbicides and vegetation control through annual mowing or extensive grazing, creating moderate disturbances without suppressing plants. In combination with higher light availability at ground level, these practices support diverse floral resources and visitors. Therefore, oil palm plantations are an important part of the COBIGA biological corridor. However, their plant and pollinator communities were taxonomically and functionally distinct from those in both forest habitats. Oil palm plantations were characterized by generalist pollination systems and pollinators, adapted to disturbed and more open environments. In contrast to this, primary and secondary forests had more specialized, forest-dependent plants and pollinators, such as orchid bees, hummingbirds, and *Heliconius* butterflies, which emphasizes the ecological role of intact forest ecosystems. These findings highlight how species richness and abundance indices alone can mask shifts in community composition (see Winfree, et al. 2011).

In order to support the conservation of biodiversity alongside agricultural landscapes, it is essential to implement a combination of plantation management strategies, long-term ecological restoration using carefully selected diverse native species, and the protection and expansion of biological corridors, such as COBIGA. These measures promote sustainable land use and contribute to the long-term conservation of pollinators and their ecosystem services, through their key role in the reproduction of most plant species (Ebeling, et al. 2008).

While this study provides valuable insights, it represents only a part of the complex plant-pollinator interactions within the COBIGA biological corridor. To gain a comprehensive understanding of the dynamics of floral resources and their relevance to floral visitors and pollinators, future research should expand the observation periods (including nocturnal activity), cover other seasons beside the wet season, and include the canopy layer. Moreover, long-term monitoring of secondary forests and oil palm plantations is essential to evaluate ecological success and restoration progress to gain a fuller picture of pollinator dynamics in fragmented tropical landscapes.

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## 6. Appendix

### I. List of understory plants in the study habitats

List of plant species documented for three habitat types, including the data collected outside of transects (\*). The list is sorted alphabetically by plant family. Plants that were not in bloom during the data collection period were also documented: blooming (blo), budding (bud), faded (fad), fruiting (fru), vegetative (veg).

|                     | Plant family and species                              | Stage | Trail |
|---------------------|-------------------------------------------------------|-------|-------|
| Primary forest (PF) | ACANTHACEAE                                           |       |       |
|                     | <i>Aphelandra sp. 1</i>                               | blo   | *     |
|                     | ACHARIACEAE                                           |       |       |
|                     | <i>Carpotroche sp.</i>                                | fru   | *     |
|                     | ARACEAE                                               |       |       |
|                     | <i>Philodendron fragrantissimum</i>                   | blo   |       |
|                     | Araceae sp. 2                                         | fru   |       |
|                     | Araceae sp. 4                                         | blo   | *     |
|                     | <i>Dieffenbachia cf. oerstedii</i>                    | fru   | *     |
|                     | ARECACEAE                                             |       |       |
|                     | Arecaceae sp. 4                                       | fru   |       |
|                     | Arecaceae sp. 5                                       | veg   |       |
|                     | cf. <i>Geonoma sp.</i>                                | blo   | *     |
|                     | BROMELIACEAE                                          |       |       |
|                     | <i>Guzmania lingulata</i>                             | blo   |       |
|                     | COSTACEAE                                             | blo   | *     |
|                     | <i>Costus sp.</i>                                     | blo   | *     |
|                     | CYPERACEAE                                            |       |       |
|                     | <i>Becquerelia cymosa</i>                             | blo   |       |
|                     | Cyperaceae sp. 1                                      | blo   |       |
|                     | EUPHORBIACEAE                                         |       |       |
|                     | <i>Mabea sp.</i>                                      | blo   |       |
|                     | GESNERIACEAE                                          |       |       |
|                     | <i>Episcia lilacina</i>                               | blo   |       |
|                     | <i>Besleria tambensis</i>                             | blo   | *     |
|                     | HELICONIACEAE                                         |       |       |
|                     | <i>Heliconia irrasa</i>                               | blo   |       |
|                     | <i>Heliconia imbricata</i>                            | blo   | *     |
|                     | MARANTACEAE                                           |       |       |
|                     | <i>Calathea crotalifera</i>                           | blo   |       |
|                     | <i>Goepertia sp. 1</i>                                | blo   | *     |
|                     | <i>Goepertia marantifolia</i> (syn. <i>Calathea</i> ) | fad   | *     |
|                     | MELASTOMATACEAE                                       |       |       |
|                     | cf. <i>Clidemia sp.</i>                               | blo   |       |
|                     | <i>Miconia cf. nervosa</i>                            | blo   |       |



|                     |            |                                                                      |          |   |
|---------------------|------------|----------------------------------------------------------------------|----------|---|
| Primary forest (PF) |            | <i>Miconia cf. secunmexicana</i>                                     | blo      |   |
|                     |            | <i>Miconia sp. 8 (cf. approximata)</i>                               | fru      |   |
|                     |            | Melastomataceae sp. 3                                                | fru      |   |
|                     |            | Melastomataceae sp. 4                                                | fru      |   |
|                     | PIPERACEAE |                                                                      |          |   |
|                     |            | cf. <i>Piper fimbriolatum</i>                                        | blo      | * |
|                     | RUBIACEAE  |                                                                      |          |   |
|                     |            | <i>Carapichea affinis</i>                                            | fru      |   |
|                     |            | cf. <i>Palicourea violacea</i> (syn. <i>Psychotria capitata</i> )    | blo      |   |
|                     |            | <i>Notopleura uliginosa</i>                                          | blo      |   |
|                     |            | <i>Palicourea cf. racemosa</i>                                       | fru      |   |
|                     |            | <i>Palicourea elata</i> (syn. <i>Cephaelis</i> ; <i>Psychotria</i> ) | blo      |   |
|                     |            | <i>Palicourea solitudinum</i>                                        | blo      |   |
|                     |            | <i>Palicourea tomentosa</i> (syn. <i>Psychotria poeppigiana</i> )    | blo      |   |
|                     |            | <i>Psychotria carthagenensis</i>                                     | bud, blo |   |
|                     |            | Rubiaceae sp. 1                                                      | fru      |   |
|                     |            | Rubiaceae sp. 2                                                      | blo      |   |
|                     |            | Rubiaceae sp. 3                                                      | fru      |   |
|                     | UNKNOWN    |                                                                      |          |   |
|                     |            | unidentified plant 1                                                 | blo      |   |

|                                  | Plant family and species             | Stage | Trail |
|----------------------------------|--------------------------------------|-------|-------|
| Old-growth secondary forest (SF) | ACANTHACEAE                          |       |       |
|                                  | <i>Aphelandra cf. golfodulcensis</i> | blo   | *     |
|                                  | <i>Justicia sp. 2</i>                | blo   |       |
|                                  | <i>Ruellia leonardiana</i>           | blo   |       |
|                                  | <i>Sanchezia nobilis</i>             | blo   | *     |
|                                  | <i>Sanchezia sp. 1</i>               | blo   | *     |
|                                  | <i>Thunbergia cf. grandiflora</i>    | blo   | *     |
|                                  | ACHARIACEAE                          |       |       |
|                                  | <i>Carpotroche sp.</i>               | fru   | *     |
|                                  | ACTINIDIACEAE                        |       |       |
|                                  | cf. <i>Saurauia yasicae</i>          | blo   | *     |
|                                  | ARACEAE                              |       |       |
|                                  | <i>Anthurium ravenii</i>             | fru   |       |
|                                  | <i>Anthurium scandens</i>            | fru   |       |
|                                  | <i>Anthurium sp. 2</i>               | fru   |       |
|                                  | <i>Dieffenbachia cf. oerstedii</i>   | blo   |       |
|                                  | Araceae sp. 1                        | fru   |       |
|                                  | Araceae sp. 5                        | blo   | *     |
|                                  | ARECACEAE                            |       |       |
|                                  | Arecaceae sp. 1                      | fru   |       |
|                                  | Arecaceae sp. 2                      | blo   |       |

|                                  |                                                           |          |   |
|----------------------------------|-----------------------------------------------------------|----------|---|
| Old-growth secondary forest (SF) | Arecaceae sp. 3                                           | blo      |   |
|                                  | ASTERACEAE                                                |          |   |
|                                  | <i>Clibadium</i> sp.                                      | blo      |   |
|                                  | BROMELIACEAE                                              |          |   |
|                                  | <i>Aechmea pubescens</i>                                  | blo, fru |   |
|                                  | <i>Araeococcus pectinatus</i>                             | fru      | * |
|                                  | <i>Guzmania lingulata</i>                                 | blo      | * |
|                                  | COMMELINACEAE                                             |          |   |
|                                  | <i>Cochliostema odoeatissimum</i>                         | blo      | * |
|                                  | COSTACEAE                                                 |          |   |
|                                  | <i>Costus</i> cf. <i>laevis</i>                           | blo      |   |
|                                  | <i>Costus</i> cf. <i>pulverulentus</i>                    | blo      |   |
|                                  | <i>Costus</i> sp.                                         | veg      |   |
|                                  | <i>Hellenia</i> cf. <i>speciosa</i> (syn. <i>Costus</i> ) | blo      | * |
|                                  | CYCLANTHACEAE                                             |          |   |
|                                  | <i>Carludovica drudei</i>                                 | blo      |   |
|                                  | CYPERACEAE                                                |          |   |
|                                  | <i>Becquerelia cymosa</i>                                 | blo      | * |
|                                  | <i>Cyperus luzulae</i>                                    | blo      |   |
|                                  | Cyperaceae sp. 2                                          | blo      | * |
|                                  | FABACEAE                                                  |          |   |
|                                  | <i>Desmodium axillare</i>                                 | blo      |   |
|                                  | GESNERIACEAE                                              |          |   |
|                                  | <i>Besleria tambensis</i>                                 | blo      | * |
|                                  | <i>Episcia lilacina</i>                                   | blo      |   |
|                                  | cf. <i>Gasteranthus delphinioides</i>                     | blo      | * |
|                                  | HELICONIACEAE                                             |          |   |
|                                  | <i>Heliconia imbricata</i>                                | blo      |   |
|                                  | <i>Heliconia irrasa</i>                                   | blo      |   |
|                                  | <i>Heliconia latispatha</i>                               | blo      |   |
|                                  | <i>Heliconia longifolia</i>                               | blo      | * |
|                                  | <i>Heliconia stilesii</i>                                 | blo      |   |
|                                  | <i>Heliconia trichocarpa</i>                              | blo      | * |
|                                  | MALVACEAE                                                 |          |   |
|                                  | <i>Malvaviscus arboreus</i>                               | blo      | * |
|                                  | MARANTACEAE                                               |          |   |
|                                  | <i>Calathea crotalifera</i>                               | blo      |   |
|                                  | <i>Calathea lutea</i>                                     | blo      |   |
|                                  | cf. <i>Ctenanthe dasycarpa</i>                            | blo      |   |
|                                  | <i>Goeppertia marantifolia</i> (syn. <i>Calathea</i> )    | blo      |   |
|                                  | <i>Goeppertia</i> sp. 1                                   | blo      |   |
|                                  | MELASTOMATACEAE                                           |          |   |
|                                  | <i>Aciotis</i> cf. <i>rubricaulis</i>                     | blo      |   |

|                                  |                                                                      |          |   |
|----------------------------------|----------------------------------------------------------------------|----------|---|
| Old-growth secondary forest (SF) | <i>Blakea</i> cf. <i>litoralis</i>                                   | blo      |   |
|                                  | <i>Miconia</i> cf. <i>neoepiphytica</i>                              | blo      |   |
|                                  | <i>Miconia</i> cf. <i>nervosa</i>                                    | blo      |   |
|                                  | <i>Miconia</i> cf. <i>secunmexicana</i>                              | blo, fru |   |
|                                  | <i>Miconia</i> sp. 2                                                 | fru      |   |
|                                  | <i>Miconia</i> sp. 3                                                 | blo      |   |
|                                  | <i>Miconia</i> sp. 4 (cf. <i>crenata</i> )                           | fru      |   |
|                                  | <i>Miconia</i> sp. 5                                                 | blo      | * |
|                                  | <i>Miconia</i> sp. 9 (cf. <i>dentata</i> )                           | blo      |   |
|                                  | <i>Miconia</i> sp. 10                                                | blo      | * |
|                                  | Melastomataceae sp. 1                                                | blo      |   |
|                                  | ORCHIDACEAE                                                          |          |   |
|                                  | <i>Erycina pusilla</i>                                               | blo      | * |
|                                  | PHYTOLACCACEAE                                                       |          |   |
|                                  | <i>Phytolacca rivinoides</i>                                         | blo      | * |
|                                  | PIPERACEAE                                                           |          |   |
|                                  | <i>Piper</i> cf. <i>hispidum</i>                                     | blo      | * |
|                                  | <i>Piper</i> sp.                                                     | blo      | * |
|                                  | RUBIACEAE                                                            |          |   |
|                                  | <i>Carapichea affinis</i>                                            | fru      | * |
|                                  | <i>Coccocypselum</i> sp.                                             | blo      | * |
|                                  | <i>Isertia haenkeana</i>                                             | blo      |   |
|                                  | <i>Ixora</i> sp.                                                     | blo      |   |
|                                  | <i>Palicourea</i> cf. <i>acuminata</i>                               | fru      |   |
|                                  | <i>Palicourea elata</i> (syn. <i>Cephaelis</i> ; <i>Psychotria</i> ) | blo      |   |
|                                  | <i>Palicourea</i> cf. <i>pilosa</i>                                  | fad      |   |
|                                  | <i>Palicourea</i> cf. <i>racemosa</i>                                | fru      |   |
|                                  | <i>Palicourea solitudinum</i>                                        | blo      |   |
|                                  | <i>Palicourea tomentosa</i> (syn. <i>Psychotria poeppigiana</i> )    | blo      |   |
|                                  | <i>Psychotria carthagenensis</i>                                     | fad      |   |
|                                  | <i>Sabicea</i> cf. <i>panamensis</i>                                 | blo      |   |
|                                  | <i>Spermacoce</i> sp.                                                | blo      | * |
|                                  | <i>Vismia macrophylla</i>                                            | blo      | * |
|                                  | Rubiaceae sp. 1                                                      | fru      |   |
|                                  | Rubiaceae sp. 4                                                      | blo      | * |
|                                  | SOLANACEAE                                                           |          |   |
|                                  | cf. <i>Witheringia solanacea</i>                                     | blo      | * |
|                                  | VERBENACEAE                                                          |          |   |
|                                  | <i>Stachytarpheta</i> sp.                                            | blo      | * |
|                                  | ZINGIBERACEAE                                                        |          |   |
|                                  | <i>Alpinia</i> cf. <i>purpurata</i>                                  | blo      | * |
|                                  | <i>Etlingera elatior</i>                                             | blo      |   |
|                                  | <i>Zingiber spectabile</i>                                           | blo      |   |

|                          | Plant family and species                         | Stage | Trail |
|--------------------------|--------------------------------------------------|-------|-------|
| Oil plam plantation (PP) | ACANTHACEAE                                      |       |       |
|                          | <i>Dianthera comata</i> (syn. <i>Justicia</i> )  | blo   |       |
|                          | <i>Ruellia</i> cf. <i>simplex</i>                | blo   |       |
|                          | <i>Acanthaceae</i> sp. 1                         | blo   |       |
|                          | AMARANTHACEAE                                    |       |       |
|                          | <i>Amaranthaceae</i> sp. 1                       | blo   |       |
|                          | ARACEAE                                          |       |       |
|                          | <i>Anthurium obtusum</i>                         | blo   | *     |
|                          | ASTERACEAE                                       |       |       |
|                          | <i>Pseudelephantopus</i> sp.                     | blo   |       |
|                          | <i>Sphagneticola trilobata</i>                   | blo   |       |
|                          | CAMPANULACEAE                                    |       |       |
|                          | <i>Hippobroma longiflora</i>                     | blo   | *     |
|                          | COMMELINACEAE                                    |       |       |
|                          | <i>Murdannia nudiflora</i>                       | blo   |       |
|                          | cf. <i>Tripogandra</i> sp.                       | bud   |       |
|                          | COSTACEAE                                        |       |       |
|                          | <i>Costus</i> cf. <i>laevis</i>                  | fru   |       |
|                          | CYPERACEAE                                       |       |       |
|                          | <i>Cyperus luzulae</i>                           | blo   |       |
|                          | <i>Cyperus odoratus</i>                          | blo   |       |
|                          | <i>Eleocharis</i> sp.                            | blo   |       |
|                          | EUPHORBIACEAE                                    |       |       |
|                          | <i>Caperonia</i> cf. <i>palustris</i>            | blo   |       |
|                          | FABACEAE                                         |       |       |
|                          | <i>Desmodium axillare</i>                        | blo   |       |
|                          | <i>Desmodium incanum</i>                         | blo   |       |
|                          | <i>Grona adscendens</i> (syn. <i>Desmodium</i> ) | blo   |       |
|                          | <i>Mimosa pudica</i>                             | blo   | *     |
|                          | <i>Mimosa</i> sp.                                | bud   |       |
|                          | <i>Vigna</i> sp.                                 | blo   | *     |
|                          | GESNERIACEAE                                     |       |       |
|                          | <i>Episcia lilacina</i>                          | blo   |       |
|                          | HAEMODORACEAE                                    |       |       |
|                          | <i>Xiphidium caeruleum</i>                       | blo   |       |
|                          | HELICONIACEAE                                    |       |       |
|                          | <i>Heliconia latispatha</i>                      | blo   |       |
|                          | LAMIACEAE                                        |       |       |
|                          | <i>Hyptis</i> cf. <i>obtusiflora</i>             | blo   |       |
|                          | <i>Hyptis</i> cf. <i>brevipes</i>                | blo   |       |



|                          |                                                                  |          |   |
|--------------------------|------------------------------------------------------------------|----------|---|
| Oil plam plantation (PP) | LIMNOCHARITACEAE                                                 |          |   |
|                          | <i>Limnocharis flava</i>                                         | blo      |   |
|                          | LOGANIACEAE                                                      |          |   |
|                          | <i>Spigelia hamellioides</i>                                     | blo      |   |
|                          | MALVACEAE                                                        |          |   |
|                          | cf. <i>Pavonia cf. schiedeana</i>                                | blo      |   |
|                          | cf. <i>Pavonia sp. 1</i>                                         | blo      |   |
|                          | cf. <i>Sida sp.</i>                                              | bud      | * |
|                          | MARANTACEAE                                                      |          |   |
|                          | <i>Calathea lutea</i>                                            | blo      |   |
|                          | <i>Goeppertia marantifolia</i>                                   | blo      |   |
|                          | MELASTOMATACEAE                                                  |          |   |
|                          | <i>Aciotis cf. rubricaulis</i>                                   | blo      |   |
|                          | <i>Blakea cf. litoralis</i>                                      | blo      |   |
|                          | <i>Miconia cf. dependens</i> (syn. <i>Clidemia capitellata</i> ) | blo      |   |
|                          | <i>Miconia sp. 6</i>                                             | blo      |   |
|                          | <i>Miconia sp. 7</i>                                             | bud      |   |
|                          | ONAGRACEAE                                                       |          |   |
|                          | <i>Ludwigia cf. hyssopifolia</i>                                 | blo      |   |
|                          | <i>Ludwigia cf. octovalvis</i>                                   | blo      |   |
|                          | <i>Ludwigia sp. 3</i>                                            | blo      | * |
|                          | <i>Ludwigia sp. 4</i>                                            | blo      | * |
|                          | PIPERACEAE                                                       |          |   |
|                          | <i>Piper cf. aduncum</i>                                         | blo      |   |
|                          | <i>Piper sp. 1</i>                                               | blo      |   |
|                          | <i>Piper sp. 2</i>                                               | blo      | * |
|                          | PLANTAGINACEAE                                                   |          |   |
|                          | <i>Bacopa salzmännii</i>                                         | blo      |   |
|                          | PONTEDERIACEAE                                                   |          |   |
|                          | <i>Heteranthera reniformis</i>                                   | blo      |   |
|                          | RUBIACEAE                                                        |          |   |
|                          | <i>Coccocypselum sp.</i>                                         | blo, fru |   |
|                          | <i>Pentagonia cf. tinajita</i>                                   | blo      |   |
|                          | <i>Sabicea cf. villosa</i>                                       | blo      |   |
|                          | <i>Spermacoce sp.</i>                                            | blo      |   |
|                          | URTICACEAE                                                       |          |   |
|                          | <i>Urera sp.</i>                                                 | blo      |   |
|                          | VERBENACEAE                                                      |          |   |
|                          | <i>Lantana camara</i>                                            | blo      |   |
|                          | ZINGIBERACEAE                                                    |          |   |
|                          | <i>Hedychium coronarium</i>                                      | blo      |   |

## II. Floral visitors in the study habitats (present-absent)

List of floral visitors present (x) or absent ( ) in the study habitats (primary forest (PF), old-growth secondary forest (SF), and oil palm plantations (PP)), inspired by Guitierrez-Chacon et al. (2019). Floral visitors classified as potential pollinators in bold. Data collected outside transects is marked with (\*).

| Order       | Family        | Species                          | Funct. group | PF | SF | PP |
|-------------|---------------|----------------------------------|--------------|----|----|----|
| Apodiformes | Trochilidae   | <i>Phaethornis striigularis</i>  | hummingbird  | x  | x  |    |
| Apodiformes | Trochilidae   | <i>Thalurania colombica</i>      | hummingbird  | x  | x  |    |
| Apodiformes | Trochilidae   | Trochilidae                      | hummingbird  | x  | x  | x  |
| Coleoptera  | Curculionidae | Curculionidae                    | beetle       |    | x* |    |
| Coleoptera  | unknown       | Coleoptera                       | beetle       | x  |    | x  |
| Diptera     | Asilidae      | Diogmites                        | fly          |    |    | x  |
| Diptera     | unknown       | Nematocera                       | fly          |    |    | x  |
| Diptera     | Syrphidae     | Syrphidae                        | fly          |    | x* |    |
| Diptera     | unknown       | Brachycera                       | fly          |    | x  | x  |
| Hemiptera   | unknown       | Fulgoromorpha                    | true bug     | x  |    |    |
| Hemiptera   | unknown       | Heteroptera                      | true bug     |    | x* | x  |
| Hymenoptera | Apidae        | <i>Apis mellifera scutellata</i> | small bee    |    |    | x* |
| Hymenoptera | Apidae        | <i>Ceratina sp. 1</i>            | small bee    |    |    | x  |
| Hymenoptera | Apidae        | <i>Ceratina sp. 2</i>            | small bee    |    | x  |    |
| Hymenoptera | Apidae        | <i>Euglossa spp.</i>             | large bee    | x  | x  |    |
| Hymenoptera | Apidae        | <i>Eulaema sp.</i>               | large bee    |    | x  |    |
| Hymenoptera | Apidae        | <i>Exaerete sp.</i>              | large bee    |    | x  |    |
| Hymenoptera | Apidae        | Euglossini                       | large bee    | x  |    | x* |
| Hymenoptera | Apidae        | Meliponini                       | small bee    |    | x* | x* |
| Hymenoptera | Apidae        | Meliponini morphospecies 1       | small bee    | x  |    | x  |
| Hymenoptera | Apidae        | Meliponini morphospecies 2       | small bee    |    | x  |    |
| Hymenoptera | Apidae        | Meliponini morphospecies 3       | small bee    | x  |    | x  |
| Hymenoptera | Apidae        | Meliponini morphospecies 4       | small bee    | x  |    |    |
| Hymenoptera | Apidae        | Meliponini morphospecies 5       | small bee    | x  |    |    |
| Hymenoptera | Apidae        | Meliponini morphospecies 6       | small bee    | x  |    |    |
| Hymenoptera | Apidae        | Meliponini morphospecies 8       | small bee    |    |    | x  |
| Hymenoptera | Apidae        | <i>Paratrigona opaca</i>         | small bee    |    | x* |    |
| Hymenoptera | Apidae        | <i>Tetragona cf. perangulata</i> | small bee    |    | x  |    |
| Hymenoptera | Apidae        | <i>Tetragona cf. zigleri</i>     | small bee    | x  |    |    |
| Hymenoptera | Apidae        | <i>Trigona fulviventris</i>      | small bee    | x  | x  | x  |
| Hymenoptera | Formicidae    | Attini                           | other        |    |    | x  |
| Hymenoptera | Formicidae    | <i>Camponotus sericeiventris</i> | other        |    | x  |    |
| Hymenoptera | Formicidae    | Formicidae                       | other        | x  | x  | x  |
| Hymenoptera | Halictidae    | (cf.) <i>Augochlora sp. 1</i>    | small bee    |    |    | x  |
| Hymenoptera | Halictidae    | cf. <i>Augochlora sp. 2</i>      | small bee    |    |    | x  |
| Hymenoptera | Halictidae    | (cf.) <i>Augochlora sp. 3</i>    | small bee    |    |    | x  |
| Hymenoptera | Halictidae    | Augochlorini morphospecies 1     | small bee    | x  |    |    |
| Hymenoptera | Halictidae    | Augochlorini morphospecies 2     | small bee    |    |    | x  |

|             |             |                                                 |           |   |    |    |
|-------------|-------------|-------------------------------------------------|-----------|---|----|----|
| Hymenoptera | Halictidae  | <i>Augochloropsis auriventris</i>               | small bee |   | x* |    |
| Hymenoptera | Halictidae  | <i>Lasioglossum sp.</i>                         | small bee |   | x  |    |
| Hymenoptera | Vespidae    | Vespidae                                        | wasp      | x |    | x  |
| Hymenoptera | Vespidae    | Vespidae morphospecies 1                        | wasp      |   |    | x  |
| Hymenoptera | Vespidae    | Vespidae morphospecies 2                        | wasp      |   |    | x  |
| Hymenoptera | unknown     | Anthophila                                      | small bee | x | x  | x  |
| Hymenoptera | unknown     | Anthophila morphospecies 1                      | small bee | x | x  |    |
| Hymenoptera | unknown     | Anthophila morphospecies 2                      | small bee | x | x  |    |
| Hymenoptera | unknown     | Anthophila morphospecies 3                      | small bee | x |    |    |
| Hymenoptera | unknown     | Anthophila morphospecies 4                      | small bee | x |    |    |
| Hymenoptera | unknown     | Anthophila morphospecies 5                      | small bee | x |    |    |
| Hymenoptera | unknown     | Anthophila morphospecies 6                      | small bee |   | x* |    |
| Hymenoptera | unknown     | Anthophila morphospecies 7                      | small bee |   | x* |    |
| Hymenoptera | unknown     | Anthophila morphospecies 8                      | small bee |   | x* |    |
| Hymenoptera | unknown     | Anthophila morphospecies 9                      | small bee |   |    | x* |
| Hymenoptera | unknown     | Anthophila morphospecies 10                     | small bee |   |    | x  |
| Hymenoptera | unknown     | Anthophila morphospecies 11                     | small bee |   |    | x  |
| Hymenoptera | unknown     | Anthophila morphospecies 12                     | small bee |   |    | x  |
| Hymenoptera | unknown     | Anthophila morphospecies 13                     | small bee |   |    | x  |
| Hymenoptera | unknown     | Anthophila morphospecies 14                     | small bee |   |    | x  |
| Hymenoptera | unknown     | Anthophila morphospecies 15                     | small bee |   |    | x  |
| Hymenoptera | unknown     | Anthophila morphospecies 16                     | small bee |   |    | x  |
| Hymenoptera | unknown     | Anthophila morphospecies 17                     | small bee |   |    | x  |
| Hymenoptera | unknown     | Anthophila morphospecies 18                     | small bee |   |    | x  |
| Hymenoptera | unknown     | Anthophila morphospecies 19                     | small bee |   |    | x  |
| Hymenoptera | unknown     | Anthophila morphospecies 20                     | small bee |   |    | x  |
| Hymenoptera | unknown     | Anthophila morphospecies 21                     | small bee |   |    | x  |
| Lepidoptera | Hesperiidae | cf. <i>Aeromachus sp.</i>                       | butterfly |   |    | x  |
| Lepidoptera | Hesperiidae | <i>Apaustus gracilis</i>                        | butterfly |   |    | x  |
| Lepidoptera | Hesperiidae | cf. <i>Burnsius sp.</i>                         | butterfly |   |    | x  |
| Lepidoptera | Hesperiidae | cf. <i>Xenophanes sp.</i>                       | butterfly |   |    | x  |
| Lepidoptera | Hesperiidae | Hesperiidae morphospecies 1                     | butterfly |   |    | x  |
| Lepidoptera | Lycaenidae  | <i>Cupido cf. comyntas</i>                      | butterfly |   |    | x  |
| Lepidoptera | Nymphalidae | <i>Actinote cf. antea</i>                       | butterfly |   |    | x* |
| Lepidoptera | Nymphalidae | <i>Aeria sp.</i>                                | butterfly | x |    |    |
| Lepidoptera | Nymphalidae | <i>Anartia fatima</i>                           | butterfly |   |    | x  |
| Lepidoptera | Nymphalidae | <i>Anartia jatrophae</i>                        | butterfly |   |    | x  |
| Lepidoptera | Nymphalidae | <i>Anthanassa sp.</i>                           | butterfly |   |    | x  |
| Lepidoptera | Nymphalidae | <i>Heliconius cf. doris</i>                     | butterfly | x | x  |    |
| Lepidoptera | Nymphalidae | <i>Heliconius cf. hecale</i>                    | butterfly | x | x  |    |
| Lepidoptera | Nymphalidae | <i>Heliconius cf. hecalesia subsp. formosus</i> | butterfly | x | x  |    |
| Lepidoptera | Nymphalidae | <i>Heliconius cf. hewitsoni</i>                 | butterfly | x | x  |    |
| Lepidoptera | Nymphalidae | <i>Heliconius cf. pachinus</i>                  | butterfly | x | x  |    |
| Lepidoptera | Nymphalidae | <i>Heliconius spp.</i>                          | butterfly | x | x  |    |

|                |               |                                                        |           |    |    |    |
|----------------|---------------|--------------------------------------------------------|-----------|----|----|----|
| Lepidoptera    | Nymphalidae   | cf. <i>Hyposcada virginiana</i> subsp. <i>evanides</i> | butterfly | x  |    |    |
| Lepidoptera    | Pieridae      | <i>Abaeis</i> sp.                                      | butterfly |    | x  |    |
| Lepidoptera    | Pieridae      | cf. <i>Eurema daira</i>                                | butterfly |    |    | x  |
| Lepidoptera    | Pieridae      | Coliadinae morphospecies 1                             | butterfly |    |    | x  |
| Lepidoptera    | Riodinidae    | cf. <i>Charis anius</i>                                | butterfly |    |    | x  |
| Lepidoptera    | Riodinidae    | <i>Calephelis</i> sp.                                  | butterfly |    |    | x  |
| Lepidoptera    | Riodinidae    | <i>Eurybia</i> sp.                                     | butterfly |    | x  |    |
| Lepidoptera    | unknown       | Lepidoptera                                            | butterfly | x  | x  | x  |
| Lepidoptera    | unknown       | Lepidoptera morphospecies 1                            | butterfly |    |    | x  |
| Lepidoptera    | unknown       | Lepidoptera morphospecies 2                            | butterfly | x  | x  |    |
| Lepidoptera    | unknown       | Lepidoptera morphospecies 3                            | butterfly |    |    | x  |
| Orthoptera     | Tettigoniidae | Orthoptera                                             | other     |    |    | x  |
| Cl. Arachnida  | unknown       | Arachnida                                              | other     | x  |    |    |
| Class Insecta  | unknown       | Insect                                                 | other     |    | x  | x  |
| SUM of "x"     |               |                                                        |           | 34 | 37 | 56 |
| Transects only |               |                                                        |           | 34 | 28 | 51 |

### III. List of plant species and their floral visitors

List of the floral visitors observed on each study plant for the three study habitat types divided into (potential) pollinators, visitors (= non-pollinating visitor), and incidental pollinators (= observations of both behaviors on same plant species). Data collected outside of transects is marked with (\*). The list is inspired by Kress & Beach (1994).

|                     | Plant fam. & species        | Animal species                         | Animal order  | Funct.group | Floral visit   | * |
|---------------------|-----------------------------|----------------------------------------|---------------|-------------|----------------|---|
| Primary forest (PF) | CYPERACEAE                  |                                        |               |             |                |   |
|                     | Cyperaceae sp. 1            | Meliponini morphosp. 3                 | Hymenoptera   | small bee   | pollinator     |   |
|                     |                             | <i>Trigona fulviventris</i>            | Hymenoptera   | small bee   | pollinator     |   |
|                     | EUPHORBIACEAE               |                                        |               |             |                |   |
|                     | <i>Mabea</i> sp.            | <i>Tetragona</i> cf. <i>zigleri</i>    | Hymenoptera   | small bee   | incid. pollin. |   |
|                     | HELICONIACEAE               |                                        |               |             |                |   |
|                     | <i>Heliconia irrasa</i>     | Arachnida                              | Cl. Arachnida | other       | visitor        |   |
|                     | MARANTACEAE                 |                                        |               |             |                |   |
|                     | <i>Calathea crotalifera</i> | Anthophila                             | Hymenoptera   | small bee   | pollinator     |   |
|                     | MELASTOMATACEAE             |                                        |               |             |                |   |
|                     | <i>Miconia nervosa</i>      | Formicidae                             | Hymenoptera   | other       | visitor        |   |
|                     | RUBIACEAE                   |                                        |               |             |                |   |
|                     | <i>Notopleura uliginosa</i> | Anthophila                             | Hymenoptera   | small bee   | pollinator     |   |
|                     | <i>Palicourea elata</i>     | Anthophila morphosp.1                  | Hymenoptera   | small bee   | pollinator     |   |
|                     |                             | Euglossini                             | Hymenoptera   | large bee   | pollinator     |   |
|                     |                             | <i>Heliconius</i> cf. <i>hewitsoni</i> | Lepidoptera   | butterfly   | pollinator     |   |
|                     |                             | <i>Heliconius</i> cf. <i>pachinus</i>  | Lepidoptera   | butterfly   | pollinator     |   |
|                     |                             | <i>Heliconius</i> spp.                 | Lepidoptera   | butterfly   | pollinator     |   |
|                     |                             | Lepidoptera                            | Lepidoptera   | butterfly   | pollinator     |   |



|                     |                                  |                                                           |               |             |                |
|---------------------|----------------------------------|-----------------------------------------------------------|---------------|-------------|----------------|
| Primary forest (PF) | <i>Palicourea tomentosa</i>      | Lepidoptera morphosp. 2                                   | Lepidoptera   | butterfly   | pollinator     |
|                     |                                  | <i>Phaethornis striigularis</i>                           | Apodiformes   | hummingbird | pollinator     |
|                     |                                  | <i>Thalurania colombica</i>                               | Apodiformes   | hummingbird | pollinator     |
|                     |                                  | Trochilidae                                               | Apodiformes   | hummingbird | pollinator     |
|                     |                                  | <i>Aeria sp.</i>                                          | Lepidoptera   | butterfly   | visitor        |
|                     |                                  | Arachnida                                                 | Cl. Arachnida | other       | visitor        |
|                     |                                  | <i>Euglossa spp.</i>                                      | Hymenoptera   | large bee   | pollinator     |
|                     |                                  | <i>Euglossa spp. ♀</i>                                    | Hymenoptera   | large bee   | pollinator     |
|                     |                                  | <i>Euglossa spp. ♂</i>                                    | Hymenoptera   | large bee   | incid. pollin. |
|                     |                                  | Formicidae                                                | Hymenoptera   | other       | visitor        |
|                     |                                  | <i>Heliconius cf. doris</i>                               | Lepidoptera   | butterfly   | pollinator     |
|                     |                                  | <i>Heliconius cf. hecale</i>                              | Lepidoptera   | butterfly   | pollinator     |
|                     |                                  | <i>Heliconius cf. hecalesia</i><br>subsp. <i>formosus</i> | Lepidoptera   | butterfly   | pollinator     |
|                     |                                  | <i>Heliconius cf. hewitsoni</i>                           | Lepidoptera   | butterfly   | pollinator     |
|                     |                                  | <i>Heliconius cf. pachinus</i>                            | Lepidoptera   | butterfly   | pollinator     |
|                     |                                  | <i>Heliconius spp.</i>                                    | Lepidoptera   | butterfly   | pollinator     |
|                     |                                  | <i>cf. Hyposcada virginiana</i><br>subsp. <i>evanides</i> | Lepidoptera   | butterfly   | pollinator     |
|                     |                                  | Lepidoptera                                               | Lepidoptera   | butterfly   | pollinator     |
|                     |                                  | <i>Phaethornis striigularis</i>                           | Apodiformes   | hummingbird | pollinator     |
|                     |                                  | <i>Thalurania colombica</i>                               | Apodiformes   | hummingbird | pollinator     |
|                     |                                  | Trochilidae                                               | Apodiformes   | hummingbird | pollinator     |
|                     | <i>Psychotria carthagenensis</i> | Anthophila                                                | Hymenoptera   | small bee   | pollinator     |
|                     |                                  | Anthophila morphosp.2                                     | Hymenoptera   | small bee   | incid. pollin. |
|                     |                                  | Anthophila morphosp. 3                                    | Hymenoptera   | small bee   | incid. pollin. |
|                     |                                  | Anthophila morphosp. 4                                    | Hymenoptera   | small bee   | visitor        |
|                     |                                  | Anthophila morphosp. 5                                    | Hymenoptera   | small bee   | visitor        |
|                     |                                  | Augochlorini morphosp.1                                   | Hymenoptera   | small bee   | pollinator     |
|                     |                                  | Coleoptera                                                | Coleoptera    | beetle      | visitor        |
|                     |                                  | Formicidae                                                | Hymenoptera   | other       | visitor        |
|                     |                                  | Fulgoromorpha                                             | Hemiptera     | true bug    | visitor        |
|                     |                                  | Meliponini morphosp. 1                                    | Hymenoptera   | small bee   | visitor        |
|                     |                                  | Meliponini morphosp. 4                                    | Hymenoptera   | small bee   | incid. pollin. |
|                     |                                  | Meliponini morphosp. 5                                    | Hymenoptera   | small bee   | visitor        |
|                     |                                  | Meliponini morphosp. 6                                    | Hymenoptera   | small bee   | incid. pollin. |
|                     |                                  | <i>Trigona fulviventrís</i>                               | Hymenoptera   | small bee   | incid. pollin. |
|                     |                                  | Vespidae                                                  | Hymenoptera   | wasp        | pollinator     |

|                                  | Plant fam. & species              | Animal species                    | Animal order  | Funct.group | Floral visit | * |
|----------------------------------|-----------------------------------|-----------------------------------|---------------|-------------|--------------|---|
| Old-growth secondary forest (SF) | ACANTHACEAE                       |                                   |               |             |              |   |
|                                  | <i>Sanchezia nobilis</i>          | <i>Trigona fulviventris</i>       | Hymenoptera   | small bee   | pollinator   | * |
|                                  | ACTINIDIACEAE                     |                                   |               |             |              |   |
|                                  | <i>cf. Saurauia yasicae</i>       | <i>Augochloropsis auriventris</i> | Hymenoptera   | small bee   | pollinator   | * |
|                                  |                                   | Brachycera                        | Diptera       | fly         | pollinator   | * |
|                                  |                                   | Formicidae                        | Hymenoptera   | other       | visitor      | * |
|                                  |                                   | <i>Paratrigona opaca</i>          | Hymenoptera   | small bee   | pollinator   | * |
|                                  |                                   | <i>Trigona fulviventris</i>       | Hymenoptera   | small bee   | pollinator   | * |
|                                  | ARECACEAE                         |                                   |               |             |              |   |
|                                  | Arecaceae sp. 2                   | Brachycera                        | Diptera       | fly         | visitor      |   |
|                                  |                                   | Formicidae                        | Hymenoptera   | other       | visitor      |   |
|                                  |                                   | <i>Tetragona cf. perangulata</i>  | Hymenoptera   | small bee   | visitor      |   |
|                                  | Arecaceae sp. 3                   | Meliponini morphosp. 2            | Hymenoptera   | small bee   | pollinator   |   |
|                                  | COMMELINACEAE                     |                                   |               |             |              |   |
|                                  | <i>Cochliostema odoeatissimum</i> | <i>Euglossa spp.</i>              | Hymenoptera   | large bee   | pollinator   | * |
|                                  |                                   | <i>Trigona fulviventris</i>       | Hymenoptera   | small bee   | visitor      | * |
|                                  | COSTACEAE                         |                                   |               |             |              |   |
|                                  | <i>Costus cf. laevis</i>          | Curculionidae                     | Coleoptera    | beetle      | visitor      | * |
|                                  |                                   | <i>Euglossa spp.</i>              | Hymenoptera   | large bee   | pollinator   |   |
|                                  | <i>Costus cf. speciosus</i>       | Formicidae                        | Hymenoptera   | other       | visitor      | * |
|                                  | HELICONIACEAE                     |                                   |               |             |              |   |
|                                  | <i>Heliconia imbricata</i>        | Formicidae                        | Hymenoptera   | other       | visitor      |   |
|                                  |                                   | <i>Phaethornis striigularis</i>   | Apodiformes   | hummingbird | pollinator   |   |
|                                  |                                   | Trochilidae                       | Apodiformes   | hummingbird | pollinator   |   |
|                                  | <i>Heliconia stilesii</i>         | Trochilidae                       | Apodiformes   | hummingbird | pollinator   |   |
|                                  | <i>Heliconia latispatha</i>       | <i>Eurybia sp.</i>                | Lepidoptera   | butterfly   | visitor      |   |
|                                  |                                   | Insect                            | Class Insecta | other       | visitor      |   |
|                                  |                                   | Formicidae                        | Hymenoptera   | other       | visitor      |   |
|                                  | MALVACEAE                         |                                   |               |             |              |   |
|                                  | <i>Malvaviscus arboreus</i>       | <i>Heliconius cf. hecale</i>      | Lepidoptera   | butterfly   | visitor      | * |
|                                  |                                   | <i>Trigona fulviventris</i>       | Hymenoptera   | small bee   | pollinator   | * |
|                                  |                                   | Trochilidae                       | Apodiformes   | hummingbird | pollinator   | * |
|                                  | MARANTACEAE                       |                                   |               |             |              |   |
|                                  | <i>Goeppertia marantifolia</i>    | Trochilidae                       | Apodiformes   | hummingbird | visitor      | * |
|                                  |                                   | <i>Trigona fulviventris</i>       | Hymenoptera   | small bee   | visitor      | * |
|                                  | MELASTOMATACEAE                   |                                   |               |             |              |   |
|                                  | <i>Blakea cf. litoralis</i>       | Insect                            | Class Insecta | other       | visitor      |   |

|                                  |                               |                                                        |             |             |            |   |
|----------------------------------|-------------------------------|--------------------------------------------------------|-------------|-------------|------------|---|
| Old-growth secondary forest (SF) | <i>Miconia cf. nervosa</i>    | <i>Camponotus sericeiventris</i>                       | Hymenoptera | other       | visitor    |   |
|                                  |                               | Formicidae                                             | Hymenoptera | other       | visitor    |   |
|                                  | <i>Miconia sp. 3</i>          | Anthophila                                             | Hymenoptera | small bee   | pollinator |   |
|                                  | PHYTOLACCACEAE                |                                                        |             |             |            |   |
|                                  | <i>Phytolacca rivinoides</i>  | Anthophila                                             | Hymenoptera | small bee   | pollinator | * |
|                                  |                               | <i>Trigona fulviventris</i>                            | Hymenoptera | small bee   | pollinator | * |
|                                  | PIPERACEAE                    |                                                        |             |             |            |   |
|                                  | <i>Piper cf. hispidum</i>     | Anthophila morphosp. 6                                 | Hymenoptera | small bee   | pollinator | * |
|                                  |                               | Anthophila morphosp. 7                                 | Hymenoptera | small bee   | pollinator | * |
|                                  |                               | Anthophila morphosp. 8                                 | Hymenoptera | small bee   | pollinator | * |
|                                  |                               | Heteroptera                                            | Hemiptera   | true bug    | visitor    | * |
|                                  |                               | Syrphidae                                              | Diptera     | fly         | visitor    | * |
|                                  | RUBIACEAE                     |                                                        |             |             |            |   |
|                                  | <i>Palicourea elata</i>       | Anthophila morphosp.1                                  | Hymenoptera | small bee   | pollinator |   |
|                                  |                               | <i>Heliconius cf. hecalesia</i> subsp. <i>formosus</i> | Lepidoptera | butterfly   | pollinator |   |
|                                  |                               | <i>Heliconius cf. pachinus</i>                         | Lepidoptera | butterfly   | pollinator |   |
|                                  |                               | <i>Heliconius spp.</i>                                 | Lepidoptera | butterfly   | pollinator |   |
|                                  |                               | <i>Thalurania colombica</i>                            | Apodiformes | hummingbird | pollinator |   |
|                                  |                               | Trochilidae                                            | Apodiformes | hummingbird | pollinator |   |
|                                  | <i>Palicourea solitudinum</i> | Anthophila morphosp. 1                                 | Hymenoptera | small bee   | pollinator |   |
|                                  |                               | Anthophila morphosp. 2                                 | Hymenoptera | small bee   | pollinator |   |
|                                  |                               | <i>Ceratina sp. 2 ♀</i>                                | Hymenoptera | small bee   | pollinator |   |
|                                  |                               | Formicidae                                             | Hymenoptera | other       | visitor    |   |
|                                  |                               | <i>Lasioglossum sp.</i>                                | Hymenoptera | small bee   | pollinator |   |
|                                  | <i>Palicourea tomentosa</i>   | <i>Abaeis sp.</i>                                      | Lepidoptera | butterfly   | pollinator |   |
|                                  |                               | <i>Euglossa spp. ♂</i>                                 | Hymenoptera | large bee   | pollinator |   |
|                                  |                               | <i>Eulaema sp.</i>                                     | Hymenoptera | large bee   | pollinator |   |
|                                  |                               | <i>Exaerete sp.</i>                                    | Hymenoptera | large bee   | visitor    |   |
|                                  |                               | <i>Heliconius cf. doris</i>                            | Lepidoptera | butterfly   | pollinator |   |
|                                  |                               | <i>Heliconius cf. hecale</i>                           | Lepidoptera | butterfly   | pollinator |   |
|                                  |                               | <i>Heliconius cf. hewitsoni</i>                        | Lepidoptera | butterfly   | pollinator |   |
|                                  |                               | <i>Heliconius cf. pachinus</i>                         | Lepidoptera | butterfly   | pollinator |   |
|                                  |                               | <i>Heliconius spp.</i>                                 | Lepidoptera | butterfly   | pollinator |   |
|                                  |                               | Lepidoptera morphosp. 2                                | Lepidoptera | butterfly   | pollinator |   |
|                                  |                               | <i>Trigona fulviventris</i>                            | Hymenoptera | small bee   | visitor    |   |
|                                  |                               | Trochilidae                                            | Apodiformes | hummingbird | pollinator |   |

|  |                               |                             |             |           |            |   |
|--|-------------------------------|-----------------------------|-------------|-----------|------------|---|
|  | <i>Sabicea cf. panamensis</i> | <i>Heliconius spp.</i>      | Lepidoptera | butterfly | pollinator |   |
|  |                               | Lepidoptera                 | Lepidoptera | butterfly | pollinator |   |
|  | ZINGIBERACEAE                 |                             |             |           |            |   |
|  | <i>Etlingera elatior</i>      | <i>Trigona fulviventris</i> | Hymenoptera | small bee | pollinator | * |
|  | <i>Zingiber spectabile</i>    | <i>Trigona fulviventris</i> | Hymenoptera | small bee | pollinator | * |

|                          | Plant fam. & species           | Animal species                | Animal order | Funct. group | Floral visit | * |
|--------------------------|--------------------------------|-------------------------------|--------------|--------------|--------------|---|
| Oil palm plantation (PP) | ACANTHACEAE                    |                               |              |              |              |   |
|                          | <i>Justicia comata</i>         | Anthophila                    | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | Anthophila morphosp. 9        | Hymenoptera  | small bee    | pollinator   | * |
|                          |                                | Brachycera                    | Diptera      | fly          | visitor      |   |
|                          |                                | <i>Trigona fulviventris</i>   | Hymenoptera  | small bee    | pollinator   | * |
|                          | ASTERACEAE                     |                               |              |              |              |   |
|                          | <i>Pseudelephantopus sp.</i>   | Anthophila morphosp. 10       | Hymenoptera  | small bee    | pollinator   |   |
|                          | <i>Sphagneticola trilobata</i> | cf. <i>Aeromachus sp.</i>     | Lepidoptera  | butterfly    | pollinator   |   |
|                          |                                | <i>Anartia fatima</i>         | Lepidoptera  | butterfly    | pollinator   |   |
|                          |                                | <i>Anartia jatrophae</i>      | Lepidoptera  | butterfly    | pollinator   |   |
|                          |                                | <i>Anthanassa sp.</i>         | Lepidoptera  | butterfly    | pollinator   |   |
|                          |                                | Anthophila                    | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | Anthophila morphosp. 10       | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | Anthophila morphosp. 11       | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | Anthophila morphosp. 12       | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | Anthophila morphosp. 13       | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | Anthophila morphosp. 14       | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | Anthophila morphosp. 15       | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | Anthophila morphosp. 16       | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | Anthophila morphosp. 17       | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | Anthophila morphosp. 18       | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | <i>Apastus gracilis</i>       | Lepidoptera  | butterfly    | pollinator   |   |
|                          |                                | <i>Augochlora sp. 1 ♂</i>     | Hymenoptera  | small bee    | pollinator   | * |
|                          |                                | cf. <i>Augochlora sp. 1</i>   | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | cf. <i>Augochlora sp. 2 ♀</i> | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | <i>Augochlora sp. 3</i>       | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | cf. <i>Augochlora sp. 3 ♀</i> | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | Augochlorini morphosp. 2      | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | Brachycera                    | Diptera      | fly          | pollinator   |   |
|                          |                                | cf. <i>Burnsius sp.</i>       | Lepidoptera  | butterfly    | pollinator   |   |
|                          |                                | <i>Calephelis sp.</i>         | Lepidoptera  | butterfly    | pollinator   |   |
|                          |                                | <i>Ceratina sp. 1</i>         | Hymenoptera  | small bee    | pollinator   |   |
|                          |                                | cf. <i>Charis anius</i>       | Lepidoptera  | butterfly    | pollinator   |   |



|                          |                               |                             |             |           |                |   |
|--------------------------|-------------------------------|-----------------------------|-------------|-----------|----------------|---|
| Oil palm plantation (PP) |                               | Coleoptera                  | Coleoptera  | beetle    | visitor        |   |
|                          |                               | Coliadinae morphosp. 1      | Lepidoptera | butterfly | pollinator     |   |
|                          |                               | <i>Cupido cf. comyntas</i>  | Lepidoptera | butterfly | pollinator     |   |
|                          |                               | Diogmites                   | Diptera     | fly       | visitor        |   |
|                          |                               | <i>cf. Eurema daira</i>     | Lepidoptera | butterfly | pollinator     |   |
|                          |                               | Hesperiidae morphosp.1      | Lepidoptera | butterfly | pollinator     |   |
|                          |                               | Lepidoptera                 | Lepidoptera | butterfly | pollinator     |   |
|                          |                               | Lepidoptera morphosp. 1     | Lepidoptera | butterfly | pollinator     |   |
|                          |                               | Lepidoptera morphosp. 3     | Lepidoptera | butterfly | pollinator     |   |
|                          |                               | Meliponini morphosp. 3      | Hymenoptera | small bee | pollinator     |   |
|                          |                               | Orthoptera                  | Orthoptera  | other     | pollinator     |   |
|                          |                               | Nematocera                  | Diptera     | fly       | pollinator     |   |
|                          |                               | <i>cf. Xenophanes sp.</i>   | Lepidoptera | butterfly | pollinator     |   |
|                          | CAMPANULACEAE                 |                             |             |           |                |   |
|                          | <i>Hippobroma longiflora</i>  | <i>Trigona fulviventris</i> | Hymenoptera | small bee | visitor        | * |
|                          | FABACEAE                      |                             |             |           |                |   |
|                          | <i>Desmodium axillare</i>     | <i>Trigona fulviventris</i> | Hymenoptera | small bee | pollinator     |   |
|                          | <i>Grona adscendens</i>       | Anthophila                  | Hymenoptera | small bee | pollinator     |   |
|                          |                               | Attini                      | Hymenoptera | other     | visitor        |   |
|                          |                               | Brachycera                  | Diptera     | fly       | pollinator     |   |
|                          |                               | <i>Trigona fulviventris</i> | Hymenoptera | small bee | incid. pollin. |   |
|                          | HAEMODORACEAE                 |                             |             |           |                |   |
|                          | <i>Xiphidium caeruleum</i>    | Anthophila morphosp. 19     | Hymenoptera | small bee | incid. pollin. |   |
|                          |                               | Anthophila morphosp. 20     | Hymenoptera | small bee | incid. pollin. |   |
|                          |                               | Anthophila morphosp. 21     | Hymenoptera | small bee | pollinator     |   |
|                          |                               | Brachycera                  | Diptera     | fly       | visitor        |   |
|                          |                               | Formicidae                  | Hymenoptera | other     | visitor        |   |
|                          |                               | Nematocera                  | Diptera     | fly       | visitor        |   |
|                          | HELICONIACEAE                 |                             |             |           |                |   |
|                          | <i>Heliconia latispatha</i>   | Formicidae                  | Hymenoptera | other     | visitor        |   |
|                          |                               | Lepidoptera                 | Lepidoptera | butterfly | visitor        |   |
|                          | LAMIACEAE                     |                             |             |           |                |   |
|                          | <i>Hyptis cf. obtusiflora</i> | <i>Anartia jatrophae</i>    | Lepidoptera | butterfly | pollinator     |   |
|                          |                               | Anthophila                  | Hymenoptera | small bee | pollinator     |   |
|                          |                               | <i>Cupido cf. comyntas</i>  | Lepidoptera | butterfly | pollinator     |   |
|                          |                               | Formicidae                  | Hymenoptera | other     | visitor        |   |
|                          |                               | <i>Trigona fulviventris</i> | Hymenoptera | small bee | pollinator     |   |
|                          |                               | Vespidae                    | Hymenoptera | wasp      | incid. pollin. |   |
|                          |                               | Vespidae morphosp.1         | Hymenoptera | wasp      | incid. pollin. |   |
|                          |                               | Vespidae morphosp.2         | Hymenoptera | wasp      | pollinator     |   |

|                          |                                |                                  |               |             |                |   |
|--------------------------|--------------------------------|----------------------------------|---------------|-------------|----------------|---|
| Oil palm plantation (pp) | <i>Hyptis cf. brevipes</i>     | <i>Apis mellifera scutellata</i> | Hymenoptera   | small bee   | pollinator     | * |
|                          | LOGANIACEAE                    |                                  |               |             |                |   |
|                          | <i>Spigelia hamelioides</i>    | <i>Anartia jatrophae</i>         | Lepidoptera   | butterfly   | pollinator     |   |
|                          |                                | Meliponini morphosp. 1           | Hymenoptera   | small bee   | pollinator     |   |
|                          |                                | <i>Trigona fulviventr</i>        | Hymenoptera   | small bee   | pollinator     |   |
|                          | MELASTOMATACEAE                |                                  |               |             |                |   |
|                          | <i>Blakea cf. litoralis</i>    | Vespidae                         | Hymenoptera   | wasp        | pollinator     |   |
|                          | <i>Miconia sp. 6</i>           | <i>Trigona fulviventr</i>        | Hymenoptera   | small bee   | pollinator     |   |
|                          | ONAGRACEAE                     |                                  |               |             |                |   |
|                          | <i>Ludwigia cf. octovalvis</i> | Meliponini                       | Hymenoptera   | small bee   | pollinator     | * |
|                          | PIPERACEAE                     |                                  |               |             |                |   |
|                          | <i>Piper sp. 1</i>             | Heteroptera                      | Hemiptera     | true bug    | visitor        |   |
|                          | <i>Piper sp. 2</i>             | <i>Apis mellifera scutellata</i> | Hymenoptera   | small bee   | pollinator     | * |
|                          |                                | Euglossini                       | Hymenoptera   | large bee   | pollinator     | * |
|                          |                                | <i>Trigona fulviventr</i>        | Hymenoptera   | small bee   | pollinator     | * |
|                          | RUBIACEAE                      |                                  |               |             |                |   |
|                          | <i>Coccocypselum sp.</i>       | <i>Anartia jatrophae</i>         | Lepidoptera   | butterfly   | pollinator     |   |
|                          |                                | <i>Trigona fulviventr</i>        | Hymenoptera   | small bee   | visitor        |   |
|                          | VERBENACEAE                    |                                  |               |             |                |   |
|                          | <i>Lantana camara</i>          | <i>Actinote cf. antea</i>        | Lepidoptera   | butterfly   | pollinator     | * |
|                          |                                | <i>Anartia fatima</i>            | Lepidoptera   | butterfly   | pollinator     | * |
|                          |                                | <i>Anartia jatrophae</i>         | Lepidoptera   | butterfly   | pollinator     | * |
|                          |                                | Anthophila                       | Hymenoptera   | small bee   | pollinator     | * |
|                          | ZINGIBERACEAE                  |                                  |               |             |                |   |
|                          | <i>Hedygium coronarium</i>     | Formicidae                       | Hymenoptera   | other       | visitor        |   |
|                          |                                | Insect                           | Class Insecta | other       | visitor        |   |
|                          |                                | Meliponini morphosp. 8           | Hymenoptera   | small bee   | incid. pollin. |   |
|                          |                                | <i>Trigona fulviventr</i>        | Hymenoptera   | small bee   | visitor        |   |
|                          |                                | Trochilidae                      | Apodiformes   | hummingbird | visitor        |   |

## 7. Zusammenfassung

Tropische Regenwälder sind durch Abholzung und Lebensraumfragmentierung stark bedroht. Der Verlust tropischer Wälder und rapide Veränderungen in der Landnutzung haben erhebliche Auswirkungen auf viele Pflanzenarten und ihre Bestäuber. Durch die Wiederanbindung isolierter Waldflächen an Regenwaldgebiete, trägt die Wiederaufforstung bzw. die Renaturierung dazu bei, die Mobilität von Wildtieren zu ermöglichen. Landwirtschaftlich genutzte Flächen, wie beispielsweise Palmölplantagen, können ebenfalls zur Vernetzung fragmentierter Lebensräume beitragen. Das Naturschutzprojekt „COBIGA“ (Biologischer Korridor La Gamba) hat sich zum Ziel gesetzt, einen biologischen Korridor zu schaffen, der den Bergregenwald der „Fila Cal“ mit dem Tieflandregenwald der Golfo Dulce Region im Süden Costa Ricas verbindet. In tropischen Regenwäldern hängt die Reproduktion von Pflanzen hauptsächlich von Tieren als Pollen- und Samenüberträgern ab. Eine Zunahme der Mobilität von Tieren gewährleistet daher auch einen besseren Genfluss zwischen Pflanzenpopulationen. Über die Vielfalt der Bestäuber und ihrer besuchten Pflanzen in den Tropen entlang biologischer Korridore ist jedoch wenig bekannt. Diese Masterarbeit untersucht die Vielfalt und den Bestand an Blütenressourcen, die innerhalb des biologischen Korridors COBIGA verfügbar sind, sowie die wichtigsten Bestäubergruppen, die diese Blüten besuchen. Unter den untersuchten Bestäubergruppen sind Bienen (auch Prachtbienen und Stachellose Bienen), Schmetterlinge, Kolibris, Käfer, Wespen und Fliegen. Die Zusammensetzung der Blütenpflanzengemeinschaften sowie ihre Blütenbesucher und potenziellen Bestäuber wurden in drei Lebensraumtypen im Korridor verglichen: Primärwald (PF), alter Sekundärwald (10 bis 40 Jahre nach der Wiederaufforstung, SF) und Palmölplantagen (PP). Ich habe die Blütenbesucher von einigen, häufig vorkommenden Pflanzenarten über einen Zeitraum von zwei Monaten beobachtet. Meine Ergebnisse zeigten, dass die Blütenpflanzen in allen drei Lebensraumtypen von einer Vielzahl an Blütenbesuchern und potenziellen Bestäubern besucht wurden. Palmölplantagen wiesen eine hohe Vielfalt und Menge an Blüten und Blütenbesuchern auf. Das bedeutet, dass sie eine wertvolle Funktion im biologischen Korridor spielen könnten, sofern die Diversität und Abundanz der Blütenressourcen erhalten bleibt. Die Zusammensetzung der Pflanzen- und Bestäubergemeinschaften der Palmölplantagen unterschieden sich taxonomisch und funktionell jedoch stark von denen im Primär- und Sekundärwald. Im Gegensatz zu den Plantagen, beherbergten die beiden Waldlebensräume auch verschiedene spezialisierte Bestäubungssysteme und die entsprechenden Bestäubergruppen. Das betont die ökologische Bedeutung natürlicher und naturnaher tropischer Wälder für den Schutz von Blütenpflanzen und ihren Bestäubern. Es werden Maßnahmen vorgeschlagen, um den ökologischen Nutzen von Palmölplantagen innerhalb des biologischen Korridors zu erhöhen. Diese Erkenntnisse werden den Schutz von Bestäubern unterstützen, indem sie die Verfügbarkeit von Ressourcen verbessern und eine einfachere Migration durch die Plantagen ermöglichen. Darüber hinaus liefern die Ergebnisse wertvolle Erkenntnisse für zukünftige Renaturierungsmaßnahmen, indem sie die ökologische Bedeutung vielfältiger Pflanzenressourcen in verschiedenen Lebensräumen verdeutlichen.

**Schlagwörter:** Costa Rica, Naturschutz, biologischer Korridor, tropischer Tieflandregenwald, Palmölplantage, Bestäubung