Edible Fruit Plant Species in the Amazon Forest Rely Mostly on Bees and Beetles as Pollinators

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Abstract
Edible fruit plants of tropical forests are important for the subsistence of traditional communities. Understanding the most important pollinators related to fruit and seed production of these plants is a necessary step to protect their pollination service and assure the food security of these communities. However, there are many important knowledge gaps related to floral biology and pollination in megadiverse tropical rainforests, such as the Amazon Forest, due mainly to the high number of plant species. Our study aims to indicate the main pollinators of edible plants (mainly fruits) of the Amazon forest. For this, we adopted a threefold strategy: we built a list of edible plant species, determined the pollination syndrome of each species, and performed a review on the scientific literature searching for their pollinator/visitors. The list of plant species was determined from two specialized publications on Amazon fruit plants, totaling 188 species. The pollination syndrome was determined for 161 species. The syndromes most frequently found among the analyzed species were mellitophily (bee pollination), which was found in 101 of the analyzed plant species (54%) and cantharophily (beetle pollination; 26 species; 14%). We also found 238 pollinator/visitor taxa quoted for 52 (28%) plant species in previous publications, with 124 taxa belonging to Apidae family (bees; 52%), mainly from Meliponini tribe (58 taxa; 47%). Knowledge about pollinators is an important step to help on preserving their ecosystem services and maintaining the productivity of fruit trees in the Amazon.

Graphical Abstract

161 edible plant species analyzed through pollination syndrome:
- 54% rely on bees
- 14% rely on beetles

52 edible plant species analyzed through literature review:
- 124 of their pollinators are bees
- 58 are stingless bees
Brazil holds the largest area covered by tropical forests in the world, and these forests are predominantly in the Amazon biome, which is home to 7,000 to 16,000 species of trees (Gomes et al. 2019). It was proposed that near 220 edible fruit-bearing plants are found only in the Amazon, corresponding to almost 50% of all fruits listed to Brazil (roughly 500 species) (Giacometti 1993). These plant species are important to the subsistence of traditional populations, which is largely based on nature-based systems characterized by small production and manual collection of food (Pinton and Emperaire 2004). However, many of the plants used by indigenous peoples and local communities in the Amazon are still poorly understood regarding their basic biology and their contribution to human well-being (Clement et al. 1982).

Most plant species require animal pollination for fruit and seed production (Ollerton et al. 2011), especially in tropical habitats, where a large number of angiosperms and a wide diversity of pollinators with specific pollination mechanisms are found (Machado and Lopes 2008). Pollination has been extensively studied because of its importance as nature’s contribution to people (NCP) (Diaz et al. 2018) and its utility for sustainable agriculture (Garibaldi et al. 2016) and to the maintenance of biocultural values (Hill et al. 2019). According to the Food and Agricultural Organization (FAO) data, 33% of human food depends to some degree on cultivated species, which are mostly frequently pollinated by bees (Klein et al. 2007). Costanza et al. (1997) carried out the first global assessment of the value of pollination (US$17 billion). This value was later updated (Costanza et al. 2014) and a recent review estimated the total annual value of crop pollination as corresponding to $235–$577 billion (in 2015, U.S. dollars) (IPBES 2016). For Brazil, Giannini et al. (2015a) showed that agricultural pollination had an annual value of US$12 billion (in 2013). For Pará, the second largest state of Brazil and entirely within the Amazon forest biome, the annual value of agricultural pollination (in 2016) corresponds to US$983 million (Borges et al. 2020). In addition, for some crops, flower visitors promote enhancement of fruit quality, which is an indirect benefit of extreme importance for agricultural production, increasing its market value (Giannini et al. 2015a).

Globally, bees are the main pollinators of agricultural crops (Potts et al. 2016). From those, the importance of highly social species such as Apis mellifera Linnaeus, 1758 (Hymenoptera: Apidae) (Potts et al. 2016) and stingless bees (Meliponini tribe) (Slaa et al. 2006; Giannini et al. 2015b, 2020a) is well recognized. Recent data on 23 Brazilian crops showed that 144 bee species were quoted as crop pollinators; from those, social bees comprised 63 species (44%), being Trigona Jurine, 1807 (Hymenoptera: Apidae) and Melipona Illiger, 1806 (Hymenoptera: Apidae) two important genera with the highest number of species quoted (Giannini et al. 2020a).

Pollinator declines have been reported since the mid-20th century (Carson 1962, Buchmann and Nabhan 1997), and nowadays, it is clear that multiple factors can affect pollinators, mainly habitat loss, pathogens, pesticides, and climate change (Potts et al. 2010, 2016). This decline poses an important challenge for global food production (Potts et al. 2016). For Brazil, a previous study showed that the projected climate change will potentially reduce the probability of pollinator occurrence by almost 0.13 by 2050 (Giannini et al. 2017). Considering bees occurring in the Eastern Amazon, recent projections suggested a potential reduction in pollination services, especially regarding crop pollination (Giannini et al. 2020b). However, a supplementary and equally important concern is the lack of knowledge related to insects (Montgomery et al. 2020), especially in tropical areas.

Pollination data from megadiverse tropical forest habitats, such as the Amazon forest, are still scarce (Giannini et al. 2015b, Borges et al. 2020), which represents a challenge to understand crop production and anticipate the potential threat of crop pollinator deficits due to global change. This knowledge gap is critical, especially considering the rapid ongoing degradation in the Amazon forest (Nobre et al. 2016, Paiva et al. 2020), and the high number of species, and the difficulties to conduct field surveys. When analyzing large numbers of tropical plant species, studies on pollination syndromes can be useful, aiming to address the group of pollinators that is the most important for each plant species. Floral characteristics can select floral visitors that have a suitable morphology and behavior, maximizing their chance of acting as pollinators (Stang et al. 2006); those characteristics define the pollination syndrome (Fenster et al. 2004). In the last decade, studies have shown that floral morphology is an important factor in structuring pollination interactions (e.g., Stang et al. 2006, Dalsgaard et al. 2008), since floral structures are adapted to enhance efficiency of pollen vectors (Proctor et al. 1996). In spite of the generalized nature of plant-pollinator interaction (Waser et al. 1996), the pollination syndrome concept was successfully applied to assess the main pollinators in a large number of South African plant species (Johnson and Wester 2017), and in Brazilian tropical forests (Machado and Lopes 2004, Girão et al. 2007), as well seasonal forests (Kinoshita et al. 2006). It was also applied to monitoring restoration (Martins and Antonini 2016), and defining the influence of abiotic factors on flowering phenology (Cortês-Flores et al. 2017). However, determining one specific pollinator taxon, or a set of taxa, is an additional challenge, which can be addressed through a review on scientific literature considering each focused plant species.

Our objective was to indicate the main pollinators of edible plants (mainly fruit trees) of the Brazilian Amazon Tropical Forest. For this, we first built a list of Amazon fruit trees and then determined the pollination syndrome for each species. We also conducted a literature survey to determine whether any specific pollinator/visitor species was previously quoted for each plant species listed.

**Materials and Methods**

The list of plant species used in our study was produced from specialized literature on Amazon fruit tree species, and includes the seminal publications of Cavalcante (1996) and Silva (2011), which listed the plants consumed by traditional communities in this biome.

We determined the pollination syndrome of each plant species based on characteristics suggested by Faegri and van der Pijl (1979) and Rosas-Guerrero et al. (2014) (Table 1). The information used to identify the pollination syndromes was based on images available for each plant species, virtual herbaria sources, articles on reproductive and flowering biology, and books that address the region’s flora. Additional details were also obtained, such as the flowering period of each plant species (phenology), plant habit, potential ethnobotanical uses for local Amazon communities, and if species are exotic or native on Brazil.

A survey of previous publications that reported visitors or effective pollinators of plant species quoted here was also conducted. We searched in the Scopus database the scientific name of each plant species and their pollinators and their flowering period was extracted. A survey of previous publications that reported visitors or effective pollinators of plant species quoted here was also conducted. We searched in the Scopus database the scientific name of each plant species and their pollinators and their flowering period was extracted.
Table 1. Pollination syndromes and their characteristics (modified from Faegri and van der Pijl 1979 and Rosas-Guerrero et al. 2014).

| Pollination syndrome | Aperture | Color | Odor strength / type | Shape | Orientation | Size / symmetry | Nectar guide / sexual organ | Reward |
|----------------------|----------|-------|----------------------|-------|-------------|-----------------|--------------------------|--------|
| Anemophily / wind    | Diurnal; nocturnal | Green whitish | Imperceptible | Brush | Upright | Amorpho | Absent | Absent |
| Cantharophily / beetles | Diurnal; nocturnal | Brown; green; white | Strong/fruity; musky | Dish | Horizontal; upright | Large / radial | Absent/exposed | Food tissue; heat; nectar; pollen |
| Entomophily / insect* | Diurnal; nocturnal | Bright colors | Moderate; strong / sweet | Bell; brush; tubo | Horizontal; pendent / upright | Medium; large; huge / radial | Absent / closed | Nectar |
| Phalaenophily / moths | Nocturnal | White | Imperceptible; weak / fresh; sweet | Bell; dish; tubo; flag gullet | Horizontal; pendent; upright | Small / radial | Absent / exposed | Fragrance; nectar; oil; pollen; resin |
| Melittophily / bees  | Diurnal | Blue; pink; purple; white; yellow | Imperceptible; weak / fresh; sweet | Bell; dish; tubo; flag gullet | Horizontal; pendent; upright | Medium; large; huge / radial | Absent / exposed | Nectar; pollen |
| Myophily / flies     | Diurnal | Brown; green; white; yellow | Imperceptible | Bell; dish | Horizontal; upright | Small / radial | Absent / exposed | Nectar; pollen |
| Ornithophily / hummingbirds | Diurnal | Orange; pink; red; yellow | Imperceptible | Brush; tubo; flag gullet | Horizontal; pendent; upright | Medium; large / bilateral; radial | Absent / closed | Nectar |
| Psychophily / butterflies and diurnal moths | Diurnal | Blue; orange; pink; red; yellow | Weak / fresh | Bell; brush; tube | Horizontal; upright | Small; medium; large / radial | Absent / closed | Nectar |
| Chiropterophily / bats | Nocturnal | Dark red; green; white | Moderate; strong / fruity; musky; sour | Bell; brush; dish; gullet | Horizontal; pendent; upright (far ground) | Large; huge / bilateral; radial | Absent / exposed | Food tissue; nectar; pollen |

*The entomophily syndrome is formed by a set of characteristics that characterize flowers attractive to several insects, and it is not possible to determine a particular insect group.
species listed combined with ‘pollination’ OR ‘pollinator’ OR ‘visitor’. As our aim was to identify potential pollinators occurring on Amazon associated to each of the listed plant, we considered only studies conducted in the Amazon biome. If any pollinator/visitor species was quoted in the reference, we inserted this information on our database.

Taxonomy classification for plants and bees followed two Brazilian biodiversity repositories. For plant species, we used Flora do Brasil (http://floradobrasil.jbrj.gov.br) and for bee species we used Catálogo de Abelhas Moure (http://moure.cria.org.br; classification according to Moure et al. 2007).

Results

We compiled a list of 188 species (Table 2). These species belong to 44 botanical families, and the families Arecaceae and Sapotaceae were the most frequent, with 22 and 16 species, respectively. Most species are trees (148 species; 79%). Among the 188 species, 147 were the most frequent, with 22 and 16 species, respectively. Most frequent syndromes were cantharophily (beetles), which was identified for 26 species (14%); chiropterophily (bats), which was identified for 14 species (7%); and phalenophily (moths), which was identified for 13 plant species (7%). These four syndromes represented 82% of all plants analyzed. Considering all insects quoted (bees, beetles, moths, and flies), the total percentage is equal to 78%. Additional information on the flowering period could not be obtained for 36 plant species. A short flowering period was found for 26 species (maximum 2 mo). The other species (106 species) had a flowering period of 3 mo or more (Supp Information 1 [online only]).

Studies conducted by other authors provided data on animal visitors or pollinators for 32 analyzed plant species, accounting for 28% of the total. These studies quoted 238 animal taxa (Supp Information 1 [online only]), of which 124 were bees of the Apidae family (58 Meliponini tribe; 20 species of Centris Fabricius, 1804 (Hymenoptera: Apidae)) (Table 3), 62 Coleoptera, 42 Diptera, four Lepidoptera, one Hemiptera, one Neuroptera and

| Family            | Scientific name                      | Brazilian vernacular name | Syndrome          |
|-------------------|--------------------------------------|---------------------------|-------------------|
| Arecaceae         | 1. Acrocoma sclerocarpa Mart.        | Muçajá                    | Undefined         |
|                   | 2. Agonandra brasiliensis Miers ex Benth & Hook. F. | Agonandra                | Undefined         |
|                   | 3. Aiphoneas aculeata Willd.         | Carioto-de-espinho        | Cantharophily     |
| Rubiaceae         | 4. Aliberta edulis (Rich.) Rich. Ex DC. | Puruí                     | Phalenophily      |
| Lecitidaceae      | 5. Allantoma lineata (Mart. & Berg) Miers | Ceru                     | Mellitophily      |
| Apocynaceae       | 6. Ambelania acida Aubl.              | Papino-do-Mato            | Phalenophily      |
| Anacardiaceae     | 7. Anacardium giganteum Hanc. Ex Engl. | Caju                     | Mellitophily      |
|                   | 8. Anacardium humile A. St.-Hil      | Cajuizinho-do-campo       | Mellitophily      |
|                   | 9. Anacardium microcarpum Ducke       | Caju-do-Campo             | Mellitophily      |
| Anacardiaceae     | 10. Anacardium negrense Pires & Froés ex Black & Pires | Caju                  | Mellitophily      |
|                   | 11. Anacardium occidentale L.         | Abacaxi                   | Orthinophily      |
| Bromeliaceae      | 12. Ananas comosus (L.) Merril        | Araticum-do-cerrado       | Cantharophily     |
| Annoneaceae       | 13. Annona claviflora Mart.           | Araticum-do-Mato          | Cantharophily     |
| Annoneaceae       | 14. Annona densicoma Mart.            | Araticum                 | Cantharophily     |
|                   | 15. Annona montana Macf.              | Graviola                  | Cantharophily     |
| Annonaceae        | 16. Annona muricata L.                | Ata                      | Cantharophily     |
| Annonaceae        | 17. Annona squamosa L.                | Amendoim                  | Mellitophily      |
| Leguminosae       | 18. Arachis hypogaea L.               | Cururureçá               | Mellitophily      |
| Myrsinaceae       | 19. Ardisia panurenisis Mez           | Fruta-Pão                | Mellitophily      |
| Moraceae          | 20. Artocarpus altis (S. Parkinson) Fosh. | Jaca                    | Cantharophily     |
| Moraceae          | 21. Artocarpus heterophyllus Lam.     | Tucumá-do-Amazonas        | Undefined         |
| Arecaceae         | 22. Astrocyrum aculeatum G. Mey.      | Jauari                   | Undefined         |
| Arecaceae         | 23. Astrocyrum jauri Mart.            | Murumuru                 | Undefined         |
| Oxlalidaceae      | 24. Astrocyrum vulgare Mart.          | Tucumá-do-Pará            | Cantharophily     |
| Oxlalidaceae      | 25. Oxlaelidaceae                     | Limão-de-Caiena           | Mellitophily      |
| Arecaceae         | 26. Averrhoa bilimbi L.               | Carambola                 | Mellitophily      |
| Arecaceae         | 27. Averrhoa carambola L.             | Pupunha                   | Cantharophily     |
| Arecaceae         | 28. Bactris gaspaes Kunth              | Marajá                    | Cantharophily     |
| Arecaceae         | 29. Bactris maraja Mart.              | Tatajuba                  | Mellitophily      |
| Arecaceae         | 30. Bagassa guianensis Aubl.           | Araçá-de-Anta             | Mellitophily      |
| Melastomataceae   | 31. Bellucia grosularioide (L.) Triana | Castanha-do-Pará          | Mellitophily      |
| Bixaceae          | 32. Bertholdia exccela Bonpland        | Urucum                    | Mellitophily      |
| Malvaceae         | 33. Bixa orellana L.                  | Castanha-do-maranhão      | Mellitophily      |
| Apocynaceae       | 34. Bombacopsis glaba (Pasquale) Robyns | Paiuetu                  | Phalenophily      |
| Rubiaceae         | 35. Bignonia longituba Markgr.         | Puruí-Grande              | Phalenophily      |
| Malpighiaceae     | 36. Borreria sorbilis (Ducke) Cuatr.  | Caferana                  | Mellitophily      |
| Malpighiaceae     | 37. Bunchosia armeniaca (Cav.) DC     |
| Family                   | Scientific name                  | Brazilian vernacular name | Syndrome        |
|-------------------------|----------------------------------|---------------------------|-----------------|
| Malpighiaceae           | 38. *Byrsonima amazonica* Griseb. | Muruci-Vermelho           | Mellitophily    |
| Malpighiaceae           | 39. *Byrsonima chrysophylla* (L.) Rich. | Muruci                   | Mellitophily    |
| Malpighiaceae           | 40. *Byrsonima crispifolia* Jussieu | Muruci-da-Mata            | Mellitophily    |
| Malpighiaceae           | 41. *Byrsonima lanceolata* Jussieu | Muruci-da-Capoeira        | Mellitophily    |
| Malpighiaceae           | 42. *Byrsonima verbascifolia* (L.) Rich. Ex Jussieu | Muruci-Rasteiro         | Mellitophily    |
| Myrtaeae                | 43. *Campomanesia lineatifolia* Ruiz & Pavon | Guabiraba               | Mellitophily    |
| Caryocaraceae           | 44. *Carica papaya* L.            | Mamão                     | Phalenophily    |
| Caryocaraceae           | 45. *Caryocar brasiliense* Camb.  | Pequi                     | Chiroterophily  |
| Caryocaraceae           | 46. *Caryocar villosus* (Aubl.) Pers. | Pquiá                    | Chiroterophily  |
| Euforbiaceae            | 47. *Caryodendron amazonicum* Ducke | Castanha-de-Porco        | Undefined       |
| Leguminosae             | 48. *Caesia leiandra* Benth.      | Marimari                  | Mellitophily    |
| Hippocrateaceae         | 49. *Cheiloclinium cognatum* (Miers) A.C. Smith | Urarutama                | Mellitophily    |
| Crisobalanaceae         | 50. *Chrysobalanus icaco* L.      | Ajuru                      | Mellitophily    |
| Sapotaceae              | 51. *Chrysophyllum canito* L.     | Camiti                    | Myophily        |
| Curcurbitaceae          | 52. *Citrus lanatus* (Thunb.) Matsum. & Nakai | Melancia                | Mellitophily    |
| Rutaceae                | 53. *Citrus* spp.                 | Citrus                    | Mellitophily    |
| Crisobalanaceae         | 54. *Conepia bracteosa* Benth.    | Pajurá                    | Mellitophily    |
| Crisobalanaceae         | 55. *Conepia edulis* (Prance) Prance | Castanha-de-Cutia        | Mellitophily    |
| Crisobalanaceae         | 56. *Conepia longipedula* Pilger  | Castanha-de-Galinha       | Mellitophily    |
| Crisobalanaceae         | 57. *Conepia paraisensis* (Mart. & Zucc.) Benth. | Pirauxí                  | Mellitophily    |
| Crisobalanaceae         | 58. *Conepia subcordata* Benth. Ex Hook.f. | Umarirana              | Mellitophily    |
| Apocynaceae             | 59. *Comma guianensis* Aubl.      | Sorva                    | Mellitophily    |
| Apocynaceae             | 60. *Comma macrocarpa* Barb. Rodr. | Sorva-Grande            | Mellitophily    |
| Apocynaceae             | 61. *Comma utilis* (Mart.) Megll. Arg. | Sorvinha               | Phalenophily    |
| Curcurbitaceae          | 62. *Cucumis melo* L.            | Melão                     | Mellitophily    |
| Fabaceae                | 63. *Dipterix alata* Vogel       | Baru                      | Mellitophily    |
| Humiriaceae             | 64. *Ducksea verrucosa* (Ducke) Cuatr. | Uxucuruá                | Undefined       |
| Annonaceae              | 65. *Duqueita marcgraviana* Mart. | Pindaeva                 | Cantanorphyphly |
| Annonaceae              | 66. *Duqueita stenanta* R. E. Fries | Jaboti                   | Cantanorphyphly |
| Rubiaceae               | 67. *Duroia macrophylla* Huber    | Cabeça-de-Urubu           | Phalenophily    |
| Rubiaceae               | 68. *Duroia saccifera* Hook. F. ex Schum. | Purturí-de-Mata        | Phalenophily    |
| Sapotaceae              | 69. *Ecclinsia guianensis* Eyma   | Guarára                | Undefined       |
| Areaceae                | 70. *Elaeis oleifera* (Kunth) Cortés | Caiuá                   | Undefined       |
| Humiriaceae             | 71. *Endopleura uchi* (Huber) Cuatrecasas | Úxi                    | Undefined       |
| Vochysiaceae            | 72. *Ertisja japura* Spruce ex. Warm. | Japarú                   | Mellitophily    |
| Myrtaeae                | 73. *Eugenia brasiliensis* Lam.   | Grumixama                | Mellitophily    |
| Myrtaeae                | 74. *Eugenia patrisii* Vahl       | Ubaia                    | Mellitophily    |
| Myrtaeae                | 75. *Eugenia stipitata* McVaugh  | Aracá-Boi               | Mellitophily    |
| Myrtaeae                | 76. *Eugenia uniflora* L.        | Ginja                    | Mellitophily    |
| Areaceae                | 77. *Euterpe oleracea* Mart.      | Açai                    | Cantanorphyphly |
| Areaceae                | 78. *Euterpe precatoria* Mart.    | Açar-do-Amazonas         | Cantanorphyphly |
| Crisobalanaceae         | 79. *Exellodendron coriaceum* (Benth.) Prance | Catanhariana         | Undefined       |
| Salicaceae              | 80. *Flacourtia jangomas* (Lour.) Raesch. | Ameixa-de-Madagascar   | Mellitophily    |
| Annonaceae              | 81. *Fusaea longifolia* (Aubl.) Safford | Fusaiá                | Cantanorphyphly |
| Rubiaceae               | 82. *Gempa americana* L.         | Jenipapo                | Mellitophily    |
| Gnetaceae               | 83. *Gnetum* spp.                | Ituá                    | Undefined       |
| Malvaceae               | 84. *Guazuma ulmifolia* Lam.     | Mutamba                 | Mellitophily    |
| Apocynaceae             | 85. *Hancornia speciosa* Gomes   | Mangaba                 | Phalenophily    |
| Moraceae                | 86. *Helicostylos tomentosa* (Poeppe. & Endl.) Rusby | Inháré                | Undefined       |
| Humiriaceae             | 87. *Humiria balsamifera* Aubl.  | Umiri                   | Mellitophily    |
| Fabaceae                | 88. *Hymenaea stigonocarpa* Mart. Ex Haine | Jatobá-do-cerrado    | Chiroterophily  |
| Leguminosae             | 89. *Hymenaea courbarill* L.     | Jataí                   | Chiroterophily  |
| Leguminosae             | 90. *Inga alba* (Sw.) Willd.     | Inga-Turi               | Chiroterophily  |
| Leguminosae             | 91. *Inga capitata* Desv.        | Inga-Costela            | Chiroterophily  |
| Leguminosae             | 92. *Inga cinnamomea* Spruce ex Benth. | Inga-Çau               | Chiroterophily  |
| Leguminosae             | 93. *Inga edulis* Mart.          | Inga-Cipó               | Chiroterophily  |
| Leguminosae             | 94. *Inga fagifolia* (L.) Willd. Ex Benth. | Inga-Cururu         | Chiroterophily  |
| Leguminosae             | 95. *Inga heterophylla* Willd.   | Inga-Xixica             | Chiroterophily  |
| Leguminosae             | 96. *Inga macrophylla* Humb. & Bonpl. Ex Willd | Inga-pêuêa        | Chiroterophily  |
| Leguminosae             | 97. *Inga velutina* Willd.       | Inga-de-Fogo            | Chiroterophily  |
| Caryocaraceae           | 98. *Jacaranda spinosa* (Aubl.) A. DC. | Jaracatiá             | Phalenophily    |
| SAPotaceae              | 99. *Labatia macrocarpa* Mart.   | Cabeça-de-Macaco        | Undefined       |
| Apocynaceae             | 100. *Lacamella arborea*ens (Muell. Arg.) Monach. | Tucuú                | Phalenophily    |
| Quinaceae               | 101. *Lacunaria jenni* (Oliv.) Ducée. | Moela-de-Mutum          | Mellitophily    |
| Family | Scientific name | Brazilian vernacular name | Syndrome |
|--------|-----------------|---------------------------|----------|
| Clusiaceae | 102. *Lecythis pisonis* Cambess. subsp. *usitata* (Miers) Mori & Prance | Sapucaia | Mellitophily |
| Arecaceae | 103. *Leopoldina major* Wallace | Jará-Açu | Undefined |
| Crisobalancheae | 104. *Licaria tomentosa* (Benth.) Frit. | Oiti | Mellitophily |
| Moraceae | 105. *Maclura tinctoria* (L.) D.Don ex Steud | Taiuva | Undefined |
| Malpighiaceae | 106. *Malpigia paniculata* L., *M. retusa* Benth. | Acerola | Mellitophily |
| Clusiaceae | 107. *Mameza americana* L. | Abrícó | Mellitophily |
| Anacardiaceae | 108. *Mangifera indica* L. | Manga | Myophily |
| Sapotaceae | 109. *Manilkara huberi* (Ducke) Chevalier | Maçaranuba | Myophily |
| Sapotaceae | 110. *Manilkara zapota* (L.) P. Royen | Sapotilha | Mellitophily |
| Arecaceae | 111. *Mauritia flexuosa* L.f. | Miriri | Cantharophily |
| Arecaceae | 112. *Mauritiella arnott* (Mart.) Burr. | Caraná (buriti) | Cantharophily |
| Arecaceae | 113. *Maximiliana maripa* (Aubl.) Drude | Inajá | Cantharophily |
| Sapindaceae | 114. *Melicoccos bijugatus* Jacq. | Prtomba-das-Guianas | Mellitophily |
| Sapotaceae | 115. *Micropholis acutangula* (Ducke) Eyma | Abú-carambola | Mellitophily |
| Melastomataceae | 116. *Mouriri apiranga* Spruce ex Triana | Aprança | Mellitophily |
| Melastomataceae | 117. *Mouriri egugifolia* Spruce ex Triana | Dauícu | Mellitophily |
| Melastomataceae | 118. *Mouriri ficoides* Morley | Muriri | Mellitophily |
| Melastomataceae | 119. *Mouriri grandiflora* DC. | Camutim | Mellitophily |
| Melastomataceae | 120. *Mouriri guianensis* Aubl. | Gurguri | Phalophily |
| Melastomataceae | 121. *Mouriri pusa* Gardner | Puçá | Mellitophily |
| Melastomataceae | 122. *Mouriri trunciflora* Ducke | Mirauba | Mellitophily |
| Polygalaceae | 123. *Moutaiba chodatiana* Huber | Gogó-de-Guariiba | Undefined |
| Musaceae | 124. *Musa X paradisiaca* L. | Banana | Chirotopheroy |
| Myrtaceae | 125. *Myrcia fallax* (Rich.) DC. | Frutheira | Mellitophily |
| Myrtaceae | 126. *Myrsia rubra* (KUNTZ) McAugh | Caçari, camu-camuzeiro | Mellitophily |
| Sapotaceae | 127. *Neomybece elegans* (A.D. Aubr | Caramuri | Undefined |
| Arecaceae | 128. *Oenocarpus bacoa* Mart. | Bacaba | Cantharophily |
| Arecaceae | 129. *Oenocarpus bataua* Mart. | Batauá | Cantharophily |
| Arecaceae | 130. *Oenocarpus mapora* Karsten | Baciahinha | Cantharophily |
| Arecaceae | 131. *Oenocarpus minor* Mart. | Bacia | Cantharophily |
| Arecaceae | 132. *Oenocarpus duchich* Mart. | Bacia-de-Leque | Cantharophily |
| Arecaceae | 133. *Orbignya phalerata* Mart. | Babaçu | Undefined |
| Bombacaceae | 134. *Pachira aquatica* Aubl. | Mamorana | Chirotopheroy |
| Apocynaceae | 135. *Parahancornia amapa* (Hub.) Ducke | Amapá | Phalenophily |
| Crisobalancheae | 136. *Parnari montana* Aubl. | Pajuí-dá-Mata | Mellitophily |
| Crisobalancheae | 137. *Parnari sprucei* Hook. f. | Uará | Mellitophily |
| Passifloraceae | 138. *Passiflora edulis* Sims f. *flavicans* Deg. | Maracujá | Mellitophily |
| Passifloraceae | 139. *Passiflora nitida* Kunth | Maracujá-Susiro | Mellitophily |
| Passifloraceae | 140. *Passiflora quadrangularis* L. | Maracujá-Açu | Mellitophily |
| Sapindaceae | 141. *Pallodium cupana* H.B.K. var. *sorbo* (Mart.) Ducke | Guaraná | Mellitophily |
| Hippocoraceae | 142. *Peritassa laevigata* (Hoffm. ex Link.) A. C. Smith | Gulosã | Mellitophily |
| Lauraceae | 143. *Persea americana* Mill. var. *americana* Mill | Abacate | Mellitophily |
| Solanaceae | 144. *Physalis angulata* L. | Campau | Myophily |
| Clusiaceae | 145. *Platonia insignis* Mart. | Bacuri | Ornithophily |
| Iacineaceae | 146. *Poraqueiba paraensis* Ducke | Umari ou Marí | Mellitophily |
| Anacardiaceae | 147. *Pourthia amazônica* Ducke | Jacaica | Mellitophily |
| Moraceae | 148. *Pourouma cerifolium* Mart. | Mapati | Mellitophily |
| Sapotaceae | 149. *Potentia cainito* (Ruiz & Pavon) Radlk. | Abú | Mellitophily |
| Sapotaceae | 150. *Potentia macrocarpa* (Huber) Baehni | Cutute-Grande | Mellitophily |
| Sapotaceae | 151. *Potentia macrophylla* (Lam.) Eyma | Cutute | Mellitophily |
| Sapotaceae | 152. *Potentia parryi* (Ducke) Baehni | Pariri | Undefined |
| Sapotaceae | 153. *Potentia ramiflora* (Mart.) Radlk | Abú-do-cerrado | Undefined |
| Sapotaceae | 154. *Potentia especiosa* (Ducke) Baehni | Pajuí-de-Óbidos | Undefined |
| Sapotaceae | 155. *Potentia sagittalis* | Abiarana | Mellitophily |
| Sapotaceae | 156. *Potentia torta* (Mart.) Ralfk | Abú-Pilosó | Mellitophily |
| Sapotaceae | 157. *Potentia ucuqui* Pires & Schultes | Ucuqui | Mellitophily |
| Myrtaceae | 158. *Psidium acutangulam* DC. | Araça-Pera | Mellitophily |
| Myrtaceae | 159. *Psidium guajava* L. | Goiaba | Mellitophily |
| Myrtaceae | 160. *Psidium guineense* Swartz | Araça | Mellitophily |
| Bombacaceae | 161. *Quararibea cordata* (Bonpl.) Visch. | Sapota-do-Solimões | Mellitophily |
| Quinaceae | 162. *Quina florida* Tul. | Pama | Undefined |
| Clusiaceae | 163. *Rheedia acuminata* (Rui & Pav.) Planch. & Triana | Bacurizinho | Mellitophily |
| Clusiaceae | 164. *Rheedia brasiliensis* (Mart. Planch. & Triana | Bacuripari-Liso | Mellitophily |
| Clusiaceae | 165. *Rheedia gardneriana* Miers ex. Planch. & Triana | Bacuri mirim | Mellitophily |
the different insect groups determined by pollination syndrome are responsible for pollinating more than two-thirds of all plant species analyzed. Through the literature review, bee and beetle species were also particularly emphasized.

As already stated, bees are widely considered as important crop pollinators, especially highly social bees (Slaa et al. 2006, Giannini et al. 2020a). Traditional communities and indigenous people also acknowledge the importance of bees (Potts et al. 2016). In the Amazon, the importance of bees for indigenous people was documented among Kayapó tribe (Posey 1985, Posey and Camargo 1985), and other indigenous people (Athayde et al. 2016), mainly for honey and wax hunting and beekeeping practices. Bee diversity is also recognized by them as representing a key aspect (Athayde et al. 2016).

Native bees are especially important to pollination and they are considered as being more efficient for crop pollination than exotic species, such as the honey bee (Garibaldi et al. 2013). Competition between native bees and honey bees was demonstrated in forests of Mexico (Roubik and Villanueva-Gutierrez 2009). However, there is no study about competition conducted within Amazon forests, and we still have scarce data about the role of honey bees in this biome. Previous studies showed that honey bees are more prevalent on deforested areas than inside the closed forests of south-western Amazon (Brown et al. 2016). Nevertheless, they were reported as an important alternative pollinator on deforested lands (Dick et al. 2003, Ricketts 2004). The Amazon harbor a rich diversity of native stingless bees (ca. 190 species, Pedro 2014). These bees present a wide diet breadth (Ramalho 2013). The Primitivism is also recognized by them as representing a key aspect (Athayde et al. 2016).

**Discussion**

Results obtained through pollination syndrome showed that half of all edible fruit plant species analyzed exhibit melittophily syndrome, indicating the importance of bees. Our data also showed that all four Chiroptera (Fig. 2; Supp Information 1 [online only]). Honey bee (Apis mellifera Linnaeus, 1758) was highlighted as being associated with the largest number of plant species. Stingless bees belonging to the genera Trigona Jurine 1807 (Hymenoptera: Apidae), Ptilomelipona Schwarz 1939 (Hymenoptera: Apidae), Melipona Illiger 1806 (Hymenoptera: Apidae), and Trigona lasiogaster Moure 1950 (Hymenoptera: Apidae) were also emphasized as exhibiting the highest number of species quoted as pollinators. Trigona pallens (Fabricius, 1778) (Hymenoptera: Apidae) and T. fulviventris Guérin, 1844 (Hymenoptera: Apidae) are also noteworthy, exhibiting the highest number of interacting plant species (Fig. 3).

![Figure 1. Percentage of pollination syndromes of 188 edible fruit plant species in the Amazon Tropical Forest.](https://academic.oup.com/jee/advance-article/doi/10.1093/jee/toaa284/6095396)
Table 3. Bee species previously quoted in the literature as pollinator/visitor of analyzed edible plant species in the Brazilian Amazon Forest (classification according to Moure et al. 2007) (complete information can be found in the Supp Information 1 [online only])

| Family     | Tribe          | Bee species                             | Brazilian vernacular name of plant species |
|------------|----------------|-----------------------------------------|-------------------------------------------|
| Apidae     | Meliponini     | 1. Aparatrigona impunctata (Ducke, 1916) | cupuaçu; açai                              |
| Apidae     | Apini          | 2. *Apis mellifera* Linnaeus, 1758       | caui; tucumã-do-pará; melão; araçá-boi;   |
|            |                |                                         | manga; caçari; abacate; araçá-pera; goiaba; |
|            |                |                                         | tapereba; muruci; açai                    |
| Apidae     | Augochlorini   | 3. *Augochlora* Smith, 1853              | açai                                      |
| Apidae     | Augochlorini   | 4. *Augochlorodes* Moure, 1958           |                                          |
| Apidae     | Augochlorini   | 5. *Augochloropsis crassigena* Moure, 1943 | muruci                                   |
| Apidae     | Augochlorini   | 6. *Augochloropsis* Cockerell, 1897      | açai                                      |
| Apidae     | Bombini        | 7. *Bombus brevivulculus* Franklin 1913  | castanha-do-pará                         |
| Apidae     | Bombini        | 8. *Bombus transversalis* (Olivier, 1789) | castanha-do-pará; urucum                 |
| Apidae     | Meliponini     | 9. *Celerigona longicornis* (Friese, 1903) | açai                                     |
| Apidae     | Centridini     | 10. *Centris sp* Fabricius, 1804         | caju                                     |
| Apidae     | Centridini     | 11. *Centris aenea* Lepeletier, 1841     | goiaba                                   |
| Apidae     | Centridini     | 12. *Centris americana* Klogg, 1810      | castanha-do-pará; acerola                |
| Apidae     | Centridini     | 13. *Centris bicolor* Lepeletier, 1841   | muruci                                   |
| Apidae     | Centridini     | 14. *Centris leuconoe* Mahlmann & Oliveira sp. n | muruci                               |
| Apidae     | Centridini     | 15. *Centris carrikeri* Cockerell, 1919 | castanha-do-pará                         |
| Apidae     | Centridini     | 16. *Centris xaxenses* (Ducke 1907)      | muruci                                   |
| Apidae     | Centridini     | 17. *Centris decolorata* Lepeletier, 1841 | muruci                               |
| Apidae     | Centridini     | 18. *Centris denudans* Lepeletier, 1841 | castanha-do-pará                         |
| Apidae     | Centridini     | 19. *Centris ferruginea* Lepeletier, 1841 | castanha-do-pará                         |
| Apidae     | Centridini     | 20. *Centris flavifrons* Fabricius, 1775 | acerola; muruci                           |
| Apidae     | Centridini     | 21. *Centris fuscata* Lepeletier, 1841   | muruci                                   |
| Apidae     | Centridini     | 22. *Centris longimana* Fabricius, 1804  | acerola; muruci                           |
| Apidae     | Centridini     | 23. *Centris rhodopreta* Mou & Seabra, 1960 | acerola; muruci                           |
| Apidae     | Centridini     | 24. *Centris similis* Fabricius, 1804    | castanha-do-pará                         |
| Apidae     | Centridini     | 25. *Centris spilopoda* Mou, 1969        | muruci                                   |
| Apidae     | Centridini     | 26. *Centris sponsa* Smith, 1854         | muruci                                   |
| Apidae     | Centridini     | 27. *Centris tarsata* Smith, 1874        | acerola                                  |
| Apidae     | Centridini     | 28. *Centris terminata* Smith, 1874      |                                          |
| Apidae     | Centridini     | 29. *Centris trigonoides* Lepeletier, 1841 | muruci                               |
| Apidae     | Meliponini     | 30. *Cephalotrigona capitata* (Smith, 1854) | açai                                     |
| Apidae     | Meliponini     | 31. *Geratina* Lateville, 1802           | açai                                     |
| Apidae     | Meliponini     | 32. *Dialictus Robertson*, 1902          | açai                                     |
| Apidae     | Anthidini      | 33. *Dicanthidium arenarium* (Ducke, 1907) | muruci                                   |
| Apidae     | Meliponini     | 34. *Dolichotrigona longitarsis* (Ducke, 1916) | açai                                     |
| Apidae     | Centridini     | 35. *Epicharis affinis* Smith, 1874      | castanha-do-pará; urucum                |
| Apidae     | Centridini     | 36. *Epicharis analis* Lepeletier, 1841  | muruci                                   |
| Apidae     | Centridini     | 37. *Epicharis bicolor* Smith, 1854      | muruci                                   |
| Apidae     | Centridini     | 38. *Epicharis conica* Smith, 1874       | castanha-do-pará                         |
| Apidae     | Centridini     | 39. *Epicharis flavia* Friese, 1900      | castanha-do-pará; urucum; muruci       |
| Apidae     | Centridini     | 40. *Epicharis rustica* Friese, 1900     | castanha-do-pará; urucum                |
| Apidae     | Centridini     | 41. *Epicharis umbraculata* Friese, 1900 | castanha-do-pará; muruci                |
| Apidae     | Centridini     | 42. *Epicharis zonata* Smith 1854        | castanha-do-pará                         |
| Apidae     | Euglossini     | 43. *Euglossini* Latreille, 1802         | mangaba                                  |
| Apidae     | Euglossini     | 44. *Eulaema bambiformia* (Packard, 1869) | açai                                     |
| Apidae     | Euglossini     | 45. *Eufriesea flavicenticrus* (Friese, 1899) | castanha-do-pará                         |
| Apidae     | Euglossini     | 46. *Eufriesea purpurata* (Mocsáry, 1896) | castanha-do-pará                          |
| Apidae     | Euglossini     | 47. *Eulaema cingulata* Moure, 1950      | castanha-do-pará; urucum                |
| Apidae     | Euglossini     | 48. *Eulaema meriana* (Olivier, 1789)    | castanha-do-pará; urucum                |
| Apidae     | Euglossini     | 49. *Eulaema mocsaryi* (Friese, 1899)    | castanha-do-pará; araçá-boi              |
| Apidae     | Euglossini     | 50. *Eulaema nigritia* Lepeletier, 1841   | castanha-do-pará; cubiu                 |
| Apidae     | Exomalopsini   | 51. *Exomalopsis Spinola*, 1853          | açai                                     |
| Apidae     | Exomalopsini   | 52. *Exomalopsis aurifilosa Spinola*, 1853 | açai                                     |
| Apidae     | Meliponini     | 53. *Friesomelitta longipes* (Smith, 1854) | açai                                     |
| Apidae     | Meliponini     | 54. *Friesomelitta portoi* (Friese, 1900) | açai                                     |
| Apidae     | Meliponini     | 55. *Geotrigona sequinocialis* (Ducke, 1925) | açai                                     |
| Apidae     | Halictini      | 56. *Habralictus Moure*, 1941            | açai                                     |
| Apidae     | Hylaeini       | 57. *Hylaeus Fabricius*, 1793            | açai                                     |
| Apidae     | Meliponini     | 58. *Leuotrigona pusilla* Moure & Camargo, in Moure et al. 1988 | cupuaçu                                |
| Apidae     | Tapinotaspidini| 59. *Lophopedia pygmaea* (Schrottky, 1902) | muruci                                   |
| Apidae     | Megachilini    | 60. *Megachile Latreille*, 1802          | caju                                     |
### Table 3. Continued

| Family               | Tribe                        | Bee species                           | Brazilian vernacular name of plant species |
|----------------------|------------------------------|---------------------------------------|-------------------------------------------|
| Apidae               | Augochlorini                 | 61. Megalopta aeneicollis Friese, 1926 | guaraná                                    |
| Apidae               | Augochlorini                 | 62. Megalopta amoena (Spinola, 1853)  | guaraná                                    |
| Apidae               | Augochlorini                 | 63. Megalopta sodalis (Vachal, 1904)  | guaraná                                    |
| Apidae               | Meliponini                   | 64. Melipona brachychaeta Moure, 1950 | jambo                                      |
| Apidae               | Meliponini                   | 65. Melipona compressipes Smith, 1854 | caçari                                     |
| Apidae               | Meliponini                   | 66. Melipona fasciiculata Smith, 1854 | urucum; caçari; taperebá                  |
| Apidae               | Meliponini                   | 67. Melipona flavolineata Friese, 1900| caçari; taperebá; açai                    |
| Apidae               | Meliponini                   | 68. Melipona melanoventer Schwarz, 1932| urucum                                     |
| Apidae               | Meliponini                   | 69. Melipona paraenses Ducke, 1916    | acerola                                    |
| Apidae               | Meliponini                   | 70. Melipona seminigra Friese, 1903   | caçari; taperebá; jambo                    |
| Apidae               | Meliponini                   | 71. Nannotrigona dactyloptera (Friese, 1901) | açai                                      |
| Apidae               | Meliponini                   | 72. Nannotrigona punctata (Smith, 1854) | açai; muruci; açai                        |
| Apidae               | Meliponini                   | 73. Nannotrigona schultzei (Friese, 1901) | açai                                      |
| Apidae               | Augochlorini                 | 74. Neocorynura Schrottky, 1910       | açai                                      |
| Apidae               | Meliponini                   | 75. Oxytrigona ignis Camargo, 1964    | açai                                      |
| Apidae               | Meliponini                   | 76. Oxytrigona Cockerell, 1917        | açai                                      |
| Apidae               | Tapinotaspidini              | 77. Paratetrapedia Moure, 1941        | açai                                      |
| Apidae               | Tapinotaspidini              | 78. Paratetrapedia leucostoma (Cockerell, 1923) | muruci                                   |
| Apidae               | Tapinotaspidini              | 79. Paratetrapedia testacea (Smith, 1854) | muruci                                   |
| Apidae               | Meliponini                   | 80. Paratrigona pellata (Spinola, 1853) | açai                                      |
| Apidae               | Meliponini                   | 81. Partamona aiyae Camargo, 1960     | açai                                      |
| Apidae               | Meliponini                   | 82. Partamona cupra (Smith, 1863)     | caçari                                    |
| Apidae               | Meliponini                   | 83. Partamona mourei Camargo, 1980    | jambo                                     |
| Apidae               | Meliponini                   | 84. Partamona pearsoni (Schwarz, 1938) | jambo; açai                               |
| Apidae               | Meliponini                   | 85. Partamona Schwarz, 1939           | açai                                      |
| Apidae               | Meliponini                   | 86. Partamona testacea (Klug, 1807)   | açai; açai                                |
| Apidae               | Meliponini                   | 87. Partamona vicina Camargo, 1980    | açai                                      |
| Apidae               | Meliponini                   | 88. Pereirapis Moure 1943             | açai                                      |
| Apidae               | Meliponini                   | 89. Plebeia alvarengai Moure 1994     | açai                                      |
| Apidae               | Meliponini                   | 90. Plebeia fallax Hibbs              | açai; muruci                              |
| Apidae               | Meliponini                   | 91. Plebeia minima (Gribodo, 1893)    | Cupuáçu; açai                             |
| Apidae               | Meliponini                   | 92. Plebeia Schwarz, 1938             | açai                                      |
| Apidae               | Diphasoglossini             | 93. Psilomma lucernaria Cockerell, 1923 | guaraná                                   |
| Apidae               | Meliponini                   | 94. Psilomma lucernaria (Smith, 1854) | açai; boi; açai                           |
| Apidae               | Meliponini                   | 95. Scaptotrigona postica (Latreille, 1807) | taperebá; muruci; açai                   |
| Apidae               | Meliponini                   | 96. Scaura lattarsis (Friese, 1900)   | açai                                      |
| Apidae               | Meliponini                   | 97. Scaura tenuis (Ducke, 1916)       | açai                                      |
| Apidae               | Augochlorini                 | 98. Temnostoma Smith 1853             | açai                                      |
| Apidae               | Meliponini                   | 99. Tetragona beebei (Schwarz, 1938)  | muruci                                    |
| Apidae               | Meliponini                   | 100. Tetragona clavipes (Fabricius, 1804) | acerola                                 |
| Apidae               | Meliponini                   | 101. Tetragona angustula (Latreille, 1811) | cupuaçu                                  |
| Apidae               | Meliponini                   | 102. Tetrapedia diversipes Klug, 1810 | muruci                                    |
| Apidae               | Meliponini                   | 103. Trigona amazonenses (Ducke, 1916) | jambo                                     |
| Apidae               | Meliponini                   | 104. Trigona branneri Cockerell, 1912 | açai; jambo; açai                         |
| Apidae               | Meliponini                   | 105. Trigona dallatorrensia Friese, 1900 | açai                                      |
| Apidae               | Meliponini                   | 106. Trigona fulviventris Guérin, 1844 | açai; taterebá; cupuaçu; muruci           |
| Apidae               | Meliponini                   | 107. Trigona fuscipennis Friese, 1900 | taterebá; muruci; açai                    |
| Apidae               | Meliponini                   | 108. Trigona guianae Cockerell, 1910  | açai                                      |
| Apidae               | Meliponini                   | 109. Trigona pallens (Fabricius, 1798) | cupuaçu; açai; taterebá; muruci; açai     |
| Apidae               | Meliponini                   | 110. Trigona recurva Smith, 1863      | açai; açai                                |
| Apidae               | Meliponini                   | 111. Trigona Jurine, 1807             | carambola                                  |
| Apidae               | Meliponini                   | 112. Trigona williana Friese, 1900    | jambo                                     |
| Apidae               | Meliponini                   | 113. Trigona dohrbanskyi (Moore, 1950) | açai                                      |
| Apidae               | Meliponini                   | 114. Trigona extrema Albuquerque & Camargo, 2007 | muruci                                   |
| Apidae               | Meliponini                   | 115. Trigona hirticornis Albuquerque & Camargo, 2007 | açai                                      |
| Apidae               | Meliponini                   | 116. Trigona nitidulae (Moore, 1950)  | açai                                      |
| Apidae               | Meliponini                   | 117. Trigona pediculana (Fabricius, 1804) | muruci                                   |
| Apidae               | Meliponini                   | 118. Trigona unidentata Albuquerque & Camargo, 2007 | açai                                      |
| Apidae               | Meliponini                   | 119. Trigona vitrifrons Albuquerque & Camargo, 2007 | açai                                      |
| Apidae               | Tapinotaspidini              | 120. Tropidopedia punctifrons (Smith, 1879) | muruci                                   |
| Apidae               | Tapinotaspidini              | 121. Xanthotepida globolosa (Friese, 1899) | muruci                                   |
| Apidae               | Xylocopini                   | 122. Xylocopa aurulenta (Fabricius, 1804) | urucum                                   |
| Apidae               | Xylocopini                   | 123. Xylocopa frontalis Oliver, 1789  | castana-do-pará; urucum                   |
| Apidae               | Xylocopini                   | 124. Xylocopa Latreille, 1802         | goiaba                                    |
Chrysomelidae) and flies (Syrphidae) (Giannini et al. 2015a), playing a significant role as crop pollinators globally and providing potential insurance against bee decline (Rader et al. 2016).

Among the Amazon plant species that depend on bees, *Bertholletia excelsa* HBK (Cavalcante et al. 2018), which is popularly known as the Brazil nut tree, is noteworthy, because its nuts present high nutritional and economic value (Kainer et al. 2018). Bee pollinators include two species of primitively social *Bombus* Latreille, 1802 (Hymenoptera: Apidae) and 18 species of solitary bees. Another native species with high economic value is passion fruit (*Passiflora edulis* Sims f. *flavicarpa* Deg), mainly pollinated by larger solitary bees such as *Xylocopa* Latreille, 1802 (Hymenoptera: Apidae) (Yamamoto et al. 2012); however, no study was found about passion fruit pollination in the Amazon forest. This species is cultivated in all states of Brazil, with a total production of more than 550,000 tons (2017 data from the Brazilian Institute of Geography and Statistics - IBGE), and it is highly dependent on pollination to produce its fruits; thus, in the absence of pollinators, production does not occur (Yamamoto et al. 2012).

The second most important pollinator group were beetles, with plants displaying specific adaptations for beetle pollination classified as cantharophilous. This pollination syndrome was primarily

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**Fig. 2.** Number of taxa cited in previous works about pollinator/visitor in 52 of the analyzed edible fruit plant species in the Amazon Tropical Forest. Taxa of Apidae family are quoted on Table 3. All taxa can be found in the Supp Information 1 (online only).

**Fig. 3.** (A and B) Aspects of the Amazon Forest with the striking view of Brazil nut tree (*Bertholletia excelsa*) with its high stature and straight trunk (Photos: João Rosa and Rafael M. Brito, respectively); (C) Carpenter bee (*Xylocopa frontalis* Olivier, 1789 [Hymenoptera: Apidae]) on Brazil nut blossom (Photo: Marcia M. Maués); (D) *Trigona fulviventris* (male) on muruci (*Byrsonima crassifolia*) flower (Photo: Cristiano Menezes); (E) *Trigona pallens* (Hymenoptera: Apidae) on açaí (*Euterpe oleracea*) inflorescence (Photo: Cristiano Menezes); and (F) *Oxytrigona* sp. (Hymenoptera: Apidae) on açaí (*Euterpe oleracea*) inflorescence (Photo: Alistair J. Campbell).
associated with Amazon palm species, such as the inajá (Maximiliana maripa (Aubl.) Drude) and bacaba (Oenocarpus bacaba Mart.). Beetles reported here included Cyclocephala distincta Burmeister, 1847 (Coleoptera: Scarabaeidae); Beloepeus carmeli tus (Germar, 1824) (Coleoptera: Curculionidae); and species of Epitragini tribe. The beetles that pollinate these species of palm trees are attracted by the floral scents produced by thermogenesis of the inflorescences (Oliveira et al. 2003), and such an interaction has been previously documented in other species, as those belonging to the Araceae family (Gottsberger 1990; Maia et al. 2010, 2013). Beetles of both sexes are attracted by the fragrance of flowers, which they use as a mating site, thus enabling pollination (Gottsberger 1986, Bernhardt 2000).

Despite providing an important indication of the main pollinators for each plant species, especially for megadiverse habitats, the pollination syndrome concept has received criticism, mainly because many plants can be pollinated by different pollinators, and it has been suggested that results should be better understood as working hypotheses (Quintero et al. 2017). Two cases here are noteworthy since the analyzed plants exhibit a complex pollination syndrome. One of them is açaí palm (Euterpe oleracea Mart.) that was classified here as predominately pollinated by beetles. However, a recent study determined over 100 species acting as pollinators, including, besides beetles, bees, flies, wasps, and ants (Campbell et al. 2018). Another example is cocoa (Theobroma cacao L.) that was considered here as being mainly pollinated by bees, but also presents a complex pollination system recently reviewed (Toledo-Hernández et al. 2017). For this last species, no study was conducted in the Amazon forest for determining its main pollinators. Both crops (açaí and cocoa) presented the highest value of crop pollination service in Pará (Borges et al. 2020), being also dependent on pollinators (Toledo-Hernández et al. 2017; Campbell et al. 2018). Thus, complex pollination systems require caution when being analyzed through pollination syndromes. Future work could emphasize priority edible plant species to be analyzed through detailed fieldwork, cocoa being one of the main priorities.

Protecting local animal diversity is of extreme importance for fruit production, especially in forested habitats. Increasing the knowledge about insects is also a key factor, especially considering their high diversity in tropical habitats and the historical disregarding of their ecological importance. Habitat heterogeneity is key since more heterogeneous environments can support more species through niche partitioning (Tilman 1982, Chesson 2000, Tscharntke et al. 2012, Moreira et al. 2015), and a higher pollinator diversity can directly affect the reproduction of cultivated and wild plants by increasing pollen transfer and fruit and seed production (Kremen et al. 2002, Klein et al. 2003, Hoehn et al. 2008, Garibaldi et al. 2013). Restoration of degraded land programs, especially on the region of Amazon Arc of Deforestation (south and eastern Amazon), can also benefit from a rich diversity of native plant species, and the list provided here is particularly useful for agroforestry projects aiming to associate restoration with sustainable development (Garrity 2004).

We conclude that the Amazon plant species that produce edible fruits are pollinated mainly by bees, especially stingless bees, but other insects are also important, such as beetles and moths. Animal pollinators underpin food security in traditional communities in the Amazon forest and should be protected. There are still few studies on the reproductive biology of edible plant species, and this knowledge is essential for understanding the level of dependence of plants on their pollinators and for helping on decision-making processes for pollinator protection and sustainability.

Supplementary Data
Supplementary data are available at Journal of Economic Entomology online.

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