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

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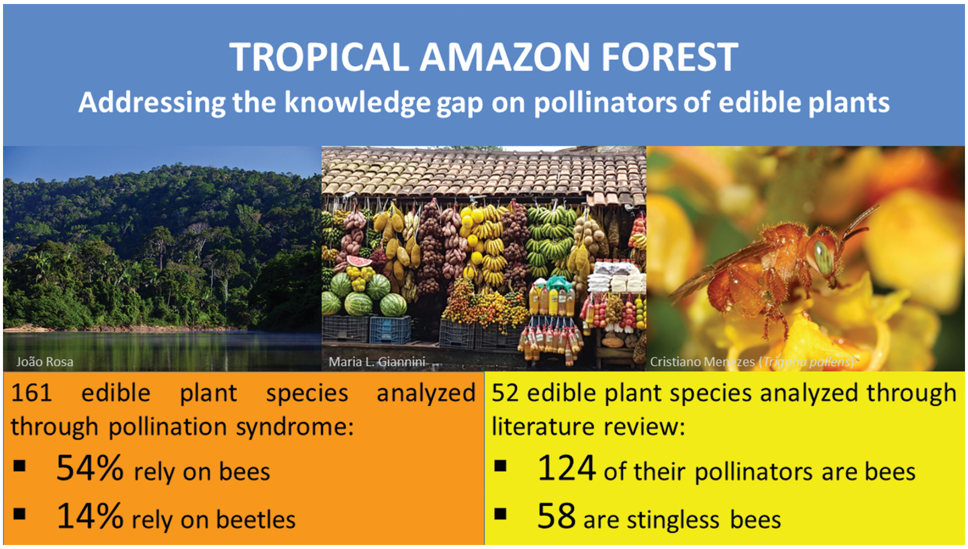
Abstract

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 melittophily (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



Key words: food production, ecosystem service, bee, traditional community, sustainability

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) (Díaz 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 most frequently pollinated by bees (Klein et al. 2007). Costanza et al. (1997) carried out the first global assessment of the value of pollination (US$117 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 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 (Cortés-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

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[a]	Diurnal; nocturnal	Bright colors						Nectar; pollen
Phalaenophily / moths	Nocturnal	White	Moderate; strong / sweet	Bell; brush; tubo	Horizontal; pendent / upright	Medium; large; huge / radial	Absent/ closed	Nectar
Melittophily /bees	Diurnal	Blue; pink; purple; white; yellow	Imperceptible; weak / fresh; sweet	Bell; dish; tubo; flag; gullet	Horizontal; pendent; upright	Small; medium; large / bilateral; radial	Absent; present/ closed; exposed	Fragrance; nectar; oil; pollen; resin
Myophily / flies	Diurnal	Brown; green; white; yellow	Imperceptible; weak / fruity; sour	Bell; dish	Horizontal; upright	Small / radial	Absent; present / exposed	Nectar; pollen
Ornithophily / hummingbirds	Diurnal	Orange; pink; red; yellow	Imperceptible	Brush; tubo; flag; gullet	Horizontal; pendent; upright	Medium; large / bi-lateral; radial	Absent/exposed	Nectar
Psychophily / butterflies and diurnal moths	Diurnal	Blue; orange; pink; red; yellow	Weak / fresh	Bell; brush; tube	Horizontal; upright	Small; medium; large / radial	Absent; present / 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 / bilat-eral; radial	Absent/exposed	Food tissue; nectar; pollen

[a]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 species are native to Brazil and 41 species are exotic. Of the total number of species of fruit plants listed, we determined the pollination syndrome for 161 species; we could not find information for the remaining species (27 species; 14%).

Plant species analyzed (161 species) were classified as having animal pollination syndromes, meaning that they do not exhibit characteristics of wind or water pollination (anemophily and hydrophily, respectively). Most of the studied plants (101 species; 54%) were classified as having a melittophily syndrome (characteristics related to the attraction of bees) (Fig. 1). The other 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 56 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 52 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

Table 2. Pollination syndrome of edible plants from Brazilian Amazon

Family	Scientific name	Brazilian vernacular name	Syndrome
Arecaceae	1. *Acrocomia sclerocarpa* Mart.	Mucajá	Undefined
Opilinaceae	2. *Agonandra brasiliensis* Miers ex Benth & Hook. F.	Agonandra	Undefined
Arecaceae	3. *Aiphanes aculeata* Willd.	Cariota-de-espinho	Cantharophily
Rubiaceae	4. *Alibertia 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.	Cajuí	Mellitophily
Anacardiaceae	8. *Anacardium humile* A. St.-Hil	Cajuzinho-do-campo	Mellitophily
Anacardiaceae	9. *Anacardium microcarpum* Ducke	Caju-do-Campo	Mellitophily
Anacardiaceae	10. *Anacardium negrense* Pires & Froés ex Black & Pires	Cajutim	Mellitophily
Anacardiaceae	11. *Anacardium occidentale* L.	Caju	Mellitophily
Bromeliaceae	12. *Ananas comosus* (L.) Merril	Abacaxi	Ornithophily
Annonaceae	13. *Annona crassiflora* Mart.	Araticum-do-cerrado	Cantharophily
Annonaceae	14. *Annona densicoma* Mart.	Araticum-do-Mato	Cantharophily
Annonaceae	15. *Annona montana* Macf.	Araticum	Cantharophily
Annonaceae	16. *Annona muricata* L.	Graviola	Cantharophily
Annonaceae	17. *Annona squamosa* L.	Ata	Cantharophily
Leguminosae	18. *Arachis hypogaea* L.	Amendoim	Mellitophily
Myrsinaceae	19. *Ardisia panurensis* Mez	Cururureçá	Mellitophily
Moraceae	20. *Artocarpus altilis* (S. Parkinson) Fosb.	Fruta-Pão	Mellitophily
Moraceae	21. *Artocarpus heterophyllus* Lam.	Jaca	Cantharophily
Arecaceae	22. *Astrocaryum aculeatum* G. Mey.	Tucumã-do-Amazonas	Undefined
Arecaceae	23. *Astrocaryum jauari* Mart.	Jauari	Undefined
Arecaceae	24. *Astrocaryum murumuru* Mart.	Murumuru	Undefined
Arecaceae	25. *Astrocaryum vulgare* Mart.	Tucumã-do-Pará	Cantharophily
Oxalidaceae	26. *Averrhoa bilimbi* L.	Limão-de-Caiena	Mellitophily
Oxalidaceae	27. *Averrhoa carambola* L.	Carambola	Mellitophily
Arecaceae	28. *Bactris gasipaes* Kunth	Pupunha	Cantharophily
Arecaceae	29. *Bactris maraja* Mart.	Marajá	Cantharophily
Moraceae	30. *Bagassa guianensis* Aubl.	Tatajuba	Mellitophily
Melastomataceae	31. *Bellucia grossularioides* (L.) Triana	Araçá-de-Anta	Mellitophily
Lecitidaceae	32. *Bertholletia excelsa* Bonpland	Castanha-do-Pará	Mellitophily
Bixaceae	33. *Bixa orellana* L.	Urucum	Mellitophily
Malvaceae	34. *Bombacopis glaba* (Pasquale) Robyns	Castanha-do-maranhão	Mellitophily
Apocynaceae	35. *Bonafousia longituba* Markgr.	Paiuetu	Phalenophily
Rubiaceae	36. *Borojoa sorbilis* (Ducke) Cuatr.	Puruí-Grande	Phalenophily
Malpighiaceae	37. *Bunchosia armeniaca* (Cav.) DC	Caferana	Mellitophily

Table 2. Continued

Family	Scientific name	Brazilian vernacular name	Syndrome
Malpighiaceae	38. *Byrsonima amazonica* Griseb.	Muruci-Vermelho	Mellitophily
Malpighiaceae	39. *Byrsonima crassifolia* (L.) Rich.	Muruci	Mellitophily
Malpighiaceae	40. *Byrsonima crispa* Jussieu	Muruci-da-Mata	Mellitophily
Malpighiaceae	41. *Byrsonima lancifolia* Jussieu	Muruci-da-Capoeira	Mellitophily
Malpighiaceae	42. *Byrsonima verbascifolia* (L.) Rich. Ex Jussieu	Muruci-Rasteiro	Mellitophily
Myrtaceae	43. *Campomanesia lineatifolia* Ruiz & Pavon	Guabiraba	Mellitophily
Caryocaceae	44. *Carica papaya* L.	Mamão	Phalenophily
Caryocaraceae	45. *Caryocar brasiliense* Camb.	Pequi	Chiropterophily
Caryocaceae	46. *Caryocar villosum* (Aubl.) Pers.	Piquiá	Chiropterophily
Euforbiaceae	47. *Caryodendron amazonicum* Ducke	Castanha-de-Porco	Undefined
Leguminosae	48. *Cassia leiandra* Benth.	Marimari	Mellitophily
Hippocrateaceae	49. *Cheiloclinium cognatum* (Miers) A.C. Smith	Uarutama	Mellitophily
Crisobalanaceae	50. *Chrysobalanus icaco* L.	Ajuru	Mellitophily
Sapotaceae	51. *Chrysophyllum cainito* L.	Camitié	Myophily
Curcubitaceae	52. *Citrullus lanatus* (Thunb.) Matsum. & Nakai	Melancia	Mellitophily
Rutaceae	53. *Citrus* spp.	Citrus	Mellitophily
Crisobalanaceae	54. *Couepia bracteosa* Benth.	Pajurá	Mellitophily
Crisobalanaceae	55. *Couepia edulis* (Prance) Prance	Castanha-de-Cutia	Mellitophily
Crisobalanaceae	56. *Couepia longipendula* Pilger	Castanha-de-Galinha	Mellitophily
Crisobalanaceae	57. *Couepia paraensis* (Mart. & Zucc.) Benth.	Pirauxi	Mellitophily
Crisobalanaceae	58. *Couepia subcordata* Benth. Ex Hook.f.	Umarirana	Mellitophily
Apocynaceae	59. *Couma guianensis* Aubl.	Sorva	Mellitophily
Apocynaceae	60. *Couma macrocarpa* Barb. Rodr.	Sorva-Grande	Mellitophily
Apocynaceae	61. *Couma utilis* (Mart.) Muell. Arg.	Sorvinha	Phalenophily
Curcubitaceae	62. *Cucumis melo* L.	Melão	Mellitophily
Fabaceae	63. *Dipteryx alata* Vogel	Baru	Mellitophily
Humiriaceae	64. *Duckesia verrucosa* (Ducke) Cuatr.	Uxicuruá	Undefined
Annonaceae	65. *Duguetia marcgraviana* Mart.	Pindaeua	Cantharophily
Annonaceae	66. *Duguetia stenantha* R. E. Fries	Jaboti	Cantharophily
Rubiaceae	67. *Duroia macrophylla* Huber	Cabeça-de-Urubu	Phalenophily
Rubiaceae	68. *Duroia saccifera* Hook. F. ex Schum.	Puruí-do-Mata	Phalenophily
Sapotaceae	69. *Ecclinusa guianensis* Eyma	Guajaraí	Undefined
Arecaceae	70. *Elaeis oleifera* (Kunth) Cortés	Caiaué	Undefined
Humiriaceae	71. *Endopleura uchi* (Huber) Cuatrecasas	Uxi	Undefined
Vochysiaceae	72. *Erisma japura* Spruce ex. Warm.	Japurá	Mellitophily
Myrtaceae	73. *Eugenia brasiliensis* Lam.	Grumixama	Mellitophily
Myrtaceae	74. *Eugenia patrisii* Vahl	Ubaia	Mellitophily
Myrtaceae	75. *Eugenia stipitata* McVaugh	Araçá-Boi	Mellitophily
Myrtaceae	76. *Eugenia uniflora* L.	Ginja	Mellitophily
Arecaceae	77. *Euterpe oleraceae* Mart.	Açai	Cantharophily
Arecaceae	78. *Euterpe precatoria* Mart.	Açai-do-Amazonas	Cantharophily
Crisobalanaceae	79. *Exellodendron coriaceum* (Berth.) Prance	Catanharana	Undefined
Salicaceae	80. *Flacourtia jangomas* (Lour.) Raeusch.	Ameixa-de-Madagascar	Mellitophily
Annonaceae	81. *Fusaea longifolia* (Aubl.) Safford	Fusaia	Cantharophily
Rubiaceae	82. *Genipa 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. *Helicostylis tomentosa* (Poepp. & Endl.) Rusby	Inharé	Undefined
Humiriaceae	87. *Humiria balsamifera* Aubl.	Umiri	Mellitophily
Fabaceae	88. *Hymenaea stigonocarpa* Mart. Ex Haine	Jatobá-do-cerrado	Chiropterophily
Leguminosae	89. *Hymenea courbaril* L.	Jutaí	Chiropterophily
Leguminosae	90. *Inga alba* (Sw.) Willd.	Inga-Turi	Chiropterophily
Leguminosae	91. *Inga capitata* Desv.	Ingá-Costela	Chiropterophily
Leguminosae	92. *Inga cinnamomea* Spruce *ex* Benth.	Ingá-Açu	Chiropterophily
Leguminosae	93. *Inga edulis* Mart.	Ingá-Cipó	Chiropterophily
Leguminosae	94. *Inga fagifolia* (L.) Willd. Ex Benth.	Ingá-Cururu	Chiropterophily
Leguminosae	95. *Inga heterophylla* Willd.	Ingá-Xixica	Chiropterophily
Leguminosae	96. *Inga macrophylla* Humb. & Bonpl. Ex Willd	Ingapéua	Chiropterophily
Leguminosae	97. *Inga velutina* Willd.	Ingá-de-Fogo	Chiropterophily
Caryocacee	98. *Jacaratia spinosa* (Aubl.) A. DC.	Jaracatiá	Phalenophily
Sapotaceae	99. *Labatia macrocarpa* Mart.	Cabeça-de-Macaco	Undefined
Apocynaceae	100. *Lacmellea arborescens* (Muell. Arg.) Monach.	Tucujá	Phalenophily
Quiinaceae	101. *Lacunaria jenmani* (Oliv.) Ducke.	Moela-de-Mutum	Mellitophily

Table 2. Continued

Family	Scientific name	Brazilian vernacular name	Syndrome
Lecitidaceae	102. *Lecythis pisonis* Cambess.subesp *usitata* (Miers) Mori & Prance	Sapucaia	Mellitophily
Arecaceae	103. *Leopoldina major* Wallace	Jará-Açu	Undefined
Crisobalanaceae	104. *Licania tomentosa* (Benth.) Frit.	Oiti	Mellitophily
Moraceae	105. *Maclura tinctoria* (L.) D.Don ex Steud	Taiuva	Undefined
Malpiguiaceae	106. *Malpighia punicifolia* L., M. *retusa* Benth.	Acerola	Mellitophily
Clusiaceae	107. *Mammea americana* L.	Abricó	Mellitophily
Anacardiaceae	108. *Mangifera indica* L.	Manga	Myophily
Sapotaceae	109. *Manilkara huberi* (Ducke) Chevalier	Maçaranduba	Myophily
Sapotaceae	110. *Manilkara zapota* (L.) P. Royen	Sapotilha	Mellitophily
Arecaceae	111. *Mauritia flexuosa* L.f.	Miriti	Cantharophily
Arecaceae	112. *Mauritiella armata* (Mart.) Burr.	Caraná (buriti)	Cantharophily
Arecaceae	113. *Maximiliana maripa* (Aubl.) Drude	Inajá	Cantharophily
Sapindaceae	114. *Melicoccus bijugatus* Jacq.	Pitomba-das-Guianas	Mellitophily
Sapotaceae	115. *Micropholis acutangula* (Ducke) Eyma	Abiu-carambola	Mellitophily
Melastomataceae	116. *Mouriri apiranga* Spruce ex Triana	Apiranga	Mellitophily
Melastomataceae	117. *Mouriri eugeniifolia* Spruce ex Triana	Dauicu	Mellitophily
Malastomataceae	118. *Mouriri ficoides* Morley	Muriri	Mellitophily
Melastomataceae	119. *Mouriri grandiflora* DC.	Camutim	Mellitophily
Melastomataceae	120. *Mouriri guianensis* Aubl.	Gurguri	Phalenophily
Melastomataceae	121. *Mouriri pusa* Gardner	Puçá	Mellitophily
Melastomataceae	122. *Mouriri trunciflora* Ducke	Mirauba	Mellitophily
Polygalaceae	123. *Moutabea chodatiana* Huber	Gogó-de-Guariba	Undefined
Musaceae	124. *Musa* X *paradisiaca* L.	Banana	Chiropterophily
Myrtaceae	125. *Myrcia fallax* (Rich.) DC.	Frutinheira	Mellitophily
Myrtaceae	126. *Myrciaria dubia* (KUNTH) McVaugh	Caçari, camu-camuzeiro	Mellitophily
Sapotaceae	127. *Neoxythece elegans* (A. DC) Aubr	Caramuri	Undefined
Arecaceae	128. *Oenocarpus bacaba* Mart.	Bacaba	Cantharophily
Arecaceae	129. *Oenocarpus bataua* Mart.	Patauá	Cantharophily
Arecaceae	130. *Oenocarpus mapora* Karsten	Bacabinha	Cantharophily
Arecaceae	131. *Oenocarpus minor* Mart.	Bacabi	Cantharophily
Arecaceae	132. *Oenorcapus distichus* Mart.	Bacaba-de-Leque	Cantharophily
Arecaceae	133. *Orbignya phalerata* Mart.	Babaçu	Undefined
Bombacaceae	134. *Pachira aquatica* Aubl.	Mamorana	Chiropterophily
Apocynaceae	135. *Parahancornia amapa* (Hub.) Ducke	Amapá	Phalenophily
Crisobalanaceae	136. *Parinari montana* Aubl.	Pajurá-da-Mata	Mellitophily
Crisobalanaceae	137. *Parinari sprucei* Hook.f.	Uará	Mellitophily
Passifloraceae	138. *Passiflora edulis* Sims f. *flavicarpas* Deg.	Maracujá	Mellitophily
Passifloraceae	139. *Passiflora nitida* Kunth	Maracujá-Suspiro	Mellitophily
Passifloraceae	140. *Passiflora quadrangularis* L.	Maracujá-Açu	Mellitophily
Sapindaceae	141. *Paullinia cupana* H.B.K. var. *sorbilis* (Mart.) Ducke	Guaraná	Mellitophily
Hippocrateaceae	142. *Peritassa laevigata* (Hoffm. Ex Link.) A. C. Smith	Gulosa	Mellitophily
Lauraceae	143. *Persea americana* Mill. Var. *americana* Mill	Abacate	Mellitophily
Solanaceae	144. *Physalis angulata* L.	Camapu	Myophily
Clusiaceae	145. *Platonia insignis* Mart.	Bacuri	Ornithophily
Icacinaceae	146. *Poraqueiba paraensis* Ducke	Umari ou Mari	Mellitophily
Anacardiaceae	147. *Poupartia amazonica* Ducke	Jacaiacá	Undefined
Moraceae	148. *Pourouma cecropiifolia* Mart.	Mapati	Mellitophily
Sapotaceae	149. *Pouteria caimito* (Ruiz & Pavon) Radlk.	Abiu	Mellitophily
Sapotaceae	150. *Pouteria macrocarpa* (Huber) Baenhi	Cutite-Grande	Mellitophily
Sapotaceae	151. *Pouteria macrophylla* (Lam.) Eyma	Cutite	Mellitophily
Sapotaceae	152. *Pouteria pariry* (Ducke) Baehni	Pariri	Undefined
Sapotaceae	153. *Pouteria ramiflora* (Mart.) Radlk	Abiu-do-cerrado	Undefined
Sapotaceae	154. *Pouteria speciosa* (Ducke) Baehni	Pajurá-de-Óbidos	Undefined
Sapotaceae	155. *Pouteria* spp.	Abiurana	Mellitophily
Sapotaceae	156. *Pouteria torta* (Mart.) Ralk	Abiu-Piloso	Mellitophily
Sapotaceae	157. *Pouteria ucuqui* Pires & Schultes	Ucuqui	Mellitophily
Myrtaceae	158. *Psidium acutangulum* DC.	Araçá-Pera	Mellitophily
Myrtaceae	159. *Psidium guajava* L.	Goiaba	Mellitophily
Myrtaceae	160. *Psidium guineense* Swartz	Araçá	Mellitophily
Bombacaceae	161. *Quararibea cordata* (Bonpl.) Visch.	Sapota-do-Solimões	Mellitophily
Quiinaceae	162. *Quiina 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

Table 2. Continued

Family	Scientific name	Brazilian vernacular name	Syndrome
Clusiaceae	166. *Rheedia macrophylla* (Mart.) Planch. & Triana	Bacuripari	Mellitophily
Annonaceae	167. *Rollinia mucosa* (Jacq.) Baill.	Biribá	Cantharophily
Humiriaceae	168. *Sacoglottis guianensis* Benth.	Achuá	Mellitophily
Hippocrateaceae	169. *Salacia impressifolia* (Miers) A.C. Smith	Uaimiratipi	Undefined
Arecaceae	170. *Scheelea phalerata* (Mart.) Burret	Acuri	Undefined
Solanaceae	171. *Solanum sessiliflorum* Dunal.	Cubiu	Undefined
Anacardiaceae	172. *Spondias dulcis* Park.	Cajarana	Mellitophily
Anacardiaceae	173. *Spondias mombin* L.	Taperebá	Mellitophily
Myrtaceae	174. *Syzygium cumini* (L.) Skeels	Ameixa	Mellitophily
Myrtaceae	175. *Syzygium malaccense* (L.) Merr. & L. M. Perry	Jambo	Mellitophily
Myrtaceae	176. *Syzygium samarangense* (Blume) Merr. & L.M. Perry	Jambo-Rosa	Mellitophily
Sapindaceae	177. *Talisia esculenta* (A. St. Hil.) Radlk	Pitomba	Mellitophily
Leguminosae	178. *Tamarindus indica* L.	Tamarindo	Mellitophily
Malvaceae	179. *Theobroma bicolor* Humb. & Bonpl.	Cacacu-do-Peru	Mellitophily
Malvaceae	180. *Theobroma cacao* L.	Cacau	Mellitophily
Malvaceae	181. *Theobroma canumanense* Pires &Fróes ex Cuatrecasas	Cupuaçu-do-Mato	Mellitophily
Sterculiaceae	182. *Theobroma grandiflorum* (Willd. Ex Spreng.) Schum	Cupuaçu	Cantharophily
Malvaceae	183. *Theobroma mariae* (Mart.) Schum.	Cacau-Jacaré	Mellitophily
Malvaceae	184. *Theobroma obovatum* Klotsch ex Bernoulli	Cabeça-de-Urubu	Mellitophily
Malvaceae	185. *Theobroma speciosum* Willd.	Cacauí	Myophily
Malvaceae	186. *Theobroma subincanum* Mart.	Cupuí	Mellitophily
Annonaceae	187. *Xylopia romatica* (Lam.) Mart.	Pimenta-de-Macaco	Cantharophily
Rhamnaceae	188. *Zizyphus mauritiana* Lam.	Dão	Mellitophily

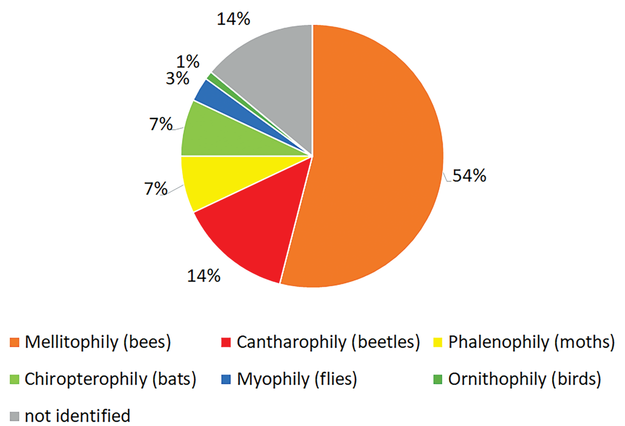


Fig. 1. Percentage of pollination syndromes of 188 edible fruit plant species in the Amazon Tropical Forest.

four Chiroptera (Fig. 2; Supp Information 1 [online only]). Honey bee (*Apis mellifera* Linnaeus, 1758) was highlighted as being associated to the largest number of plant species. Stingless bees belonging to the genera *Trigona* Jurine 1807 (Hymenoptera: Apidae), *Partamona* Schwarz 1939 (Hymenoptera: Apidae), *Melipona* Illiger 1806 (Hymenoptera: Apidae), and *Trigonisca* Moure 1950 (Hymenoptera: Apidae) were also emphasized as exhibiting the highest number of species quoted as pollinators. *Trigona pallens* (Fabricius, 1798) (Hymenoptera: Apidae) and *T. fulviventris* Guérin, 1844 (Hymenoptera: Apidae) are also noteworthy, exhibiting the highest number of interacting plant species (Fig. 3).

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 the different insect groups determined by pollination syndrome are responsible for pollinating more than two-third 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 2004, Lichtenberg et al. 2017) and are considered as key pollinators of forests (Bawa 1990). For Brazil, other bee species are also recognized as important effective pollinators, as the solitary bee species *Centris* Fabricius, 1804 (Hymenoptera: Apidae) and *Xylocopa* Latreille, 1802 (Hymenoptera: Apidae) and the primitively eusocial *Bombus* Latreille, 1802 (Hymenoptera: Apidae) (Giannini et al. 2020a). Important non-bee insects reported as crop pollinators in Brazil were beetles (Curculionidae and

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; açaí
Apidae	Apini	2. *Apis mellifera* Linnaeus, 1758	cauí; tucumã-do-pará; melão; araçá-boi; manga; caçari; abacate; araçá-pera; goiaba; taperebá; muruci; açai
Apidae	Augochlorini	3. *Augochlora* Smith, 1853	açaí
Apidae	Augochlorini	4. *Augochlorodes* Moure, 1958	açaí
Apidae	Augochlorini	5. *Augochloropsis crassigena* Moure, 1943	muruci
Apidae	Augochlorini	6. *Augochloropsis* Cockerell, 1897	açaí
Apidae	Bombini	7. *Bombus brevivilus* Franklin 1913	castanha-do-pará
Apidae	Bombini	8. *Bombus transversalis* (Olivier, 1789)	castanha-do-pará; urucum
Apidae	Meliponini	9. *Celetrigona longicornis* (Friese, 1903)	açaí
Apidae	Centridini	10. *Centris* sp Fabricius, 1804	caju
Apidae	Centridini	11. *Centris aenea* Lepeletier, 1841	goiaba
Apidae	Centridini	12. *Centris americana* Klug, 1810	castanha-do-pará; acerola
Apidae	Centridini	13. *Centris bicolor* Lepeletier, 1841	muruci
Apidae	Centridini	14. *Centris byrsonimae* Mahlmann & Oliveira sp. n	muruci
Apidae	Centridini	15. *Centris carrikeri* Cockerell, 1919	castanha-do-pará
Apidae	Centridini	16. *Centris caxienses* (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 rhodoprocta* Moure & Seabra, 1960	acerola; muruci
Apidae	Centridini	24. *Centris similis* Fabricius, 1804	castanha-do-pará
Apidae	Centridini	25. *Centris spilopoda* Moure, 1969	muruci
Apidae	Centridini	26. *Centris sponsa* Smith, 1854	muruci
Apidae	Centridini	27. *Centris tarsata* Smith, 1874	muruci
Apidae	Centridini	28. *Centris terminata* Smith, 1874	acerola
Apidae	Centridini	29. *Centris trigonoides* Lepeletier, 1841	muruci
Apidae	Meliponini	30. *Cephalotrigona capitata* (Smith, 1854)	açai
Apidae	Xylocopini	31. *Ceratina* Latreille, 1802	açai
Apidae	Halictini	32. *Dialictus* Robertson, 1902	açai
Apidae	Anthidiini	33. *Dicranthidium 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 flava* 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 bombiformis* (Packard, 1869)	araçá-pera
Apidae	Euglossini	45. *Eufriesea flaviventris* (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 nigrita* Lepeletier, 1841	castanha-do-pará; cubiu
Apidae	Exomalopsini	51. *Exomalopsis* Spinola, 1853	açai
Apidae	Exomalopsini	52. *Exomalopsis auropilosa* Spinola, 1853	caçari
Apidae	Meliponini	53. *Frieseomelitta longipes* (Smith, 1854)	açai
Apidae	Meliponini	54. *Frieseomelitta portoi* (Friese, 1900)	açai
Apidae	Meliponini	55. *Geotrigona aequinoctialis* (Ducke, 1925)	açai
Apidae	Halictini	56. *Habralictus* Moure, 1941	açai
Apidae	Hylaeini	57. *Hylaeus* Fabricius, 1793	açai
Apidae	Meliponini	58. *Leurotrigona 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 fasciculata* Smith, 1854	urucum; caçari; taperebá
Apidae	Meliponini	67. *Melipona flavolineata* Friese, 1900	caçari; taperebá; açaí
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 dutrae* (Friese, 1901)	açai
Apidae	Meliponini	72. *Nannotrigona punctata (*Smith, 1854)	caçari; muruci; açaí
Apidae	Meliponini	73. *Nannotrigona schultzei* (Friese, 1901)	açai
Apidae	Augochlorini	74. *Neocorynura* Schrottky, 1910	açai
Apidae	Meliponini	75. *Oxytrigona ignis* Camargo, 1984	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 peltata* (Spinola, 1853)	açai
Apidae	Meliponini	81. *Partamona ailyae* Camargo, 1980	açai
Apidae	Meliponini	82. *Partamona cupira* (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	caçari
Apidae	Meliponini	86. *Partamona testacea* (Klug, 1807)	jambo; 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	muruci
Apidae	Meliponini	91. *Plebeia minima* (Gribodo, 1893)	Cupuaçu; açai
Apidae	Meliponini	92. *Plebeia* Schwarz, 1938	açai
Apidae	Diphaglossini	93. *Ptiloglossa lucernarum* Cockerell, 1923	guaraná
Apidae	Meliponini	94. *Ptilotrigona lurida* (Smith, 1854)	araçá-boi; açai
Apidae	Meliponini	95. *Scaptotrigona postica* (Latreille, 1807)	taperebá; muruci; açai
Apidae	Meliponini	96. *Scaura latitarsis* (Friese, 1900)	açai
Apidae	Meliponini	97. *Scaura tenuis* (Ducke, 1916)	açai
Apidae	Augochlorini	98. *Temnosoma* Smith 1853	açai
Apidae	Meliponini	99. *Tetragona beebei* (Schwarz, 1938)	muruci
Apidae	Meliponini	100. *Tetragona clavipes* (Fabricius, 1804)	acerola
Apidae	Meliponini	101. *Tetragonisca 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	caçari; jambo; açai
Apidae	Meliponini	105. *Trigona dallatorreana* Friese, 1900	jambo
Apidae	Meliponini	106. *Trigona fulviventris* Guérin, 1844	cubiu; taperebá; cupuaçu; muruci
Apidae	Meliponini	107. *Trigona fuscipennis* Friese, 1900	taperebá; muruci; açai
Apidae	Meliponini	108. *Trigona guianae* Cockerell, 1910	açai
Apidae	Meliponini	109. *Trigona pallens* (Fabricius, 1798)	cupuaçu; caçari; taperebá; muruci; açai
Apidae	Meliponini	110. *Trigona recursa* Smith, 1863	caçari; açai
Apidae	Meliponini	111. *Trigona* Jurine, 1807	carambola
Apidae	Meliponini	112. *Trigona williana* Friese, 1900	jambo
Apidae	Meliponini	113. *Trigonisca dobzhanskyi* (Moure, 1950)	açai
Apidae	Meliponini	114. *Trigonisca extrema* Albuquerque & Camargo, 2007	muruci
Apidae	Meliponini	115. *Trigonisca hirticornis* Albuquerque & Camargo, 2007	açai
Apidae	Meliponini	116. *Trigonisca nataliae* (Moure, 1950)	açai
Apidae	Meliponini	117. *Trigonisca pediculana* (Fabricius, 1804)	muruci
Apidae	Meliponini	118. *Trigonisca unidentata* Albuquerque & Camargo, 2007	açai
Apidae	Meliponini	119. *Trigonisca vitrifrons* Albuquerque & Camargo, 2007	açai
Apidae	Tapinotaspidini	120. *Tropidopedia punctifrons* (Smith, 1879)	muruci
Apidae	Tapinotaspidini	121. *Xanthopedia globulosa* (Friese, 1899)	muruci
Apidae	Xylocopini	122. *Xylocopa aurulenta* (Fabricius, 1804)	urucum
Apidae	Xylocopini	123. *Xylocopa frontalis* Olivier, 1789	castanha-do-pará; urucum
Apidae	Xylocopini	124. *Xylocopa* Latreille, 1802	goiaba

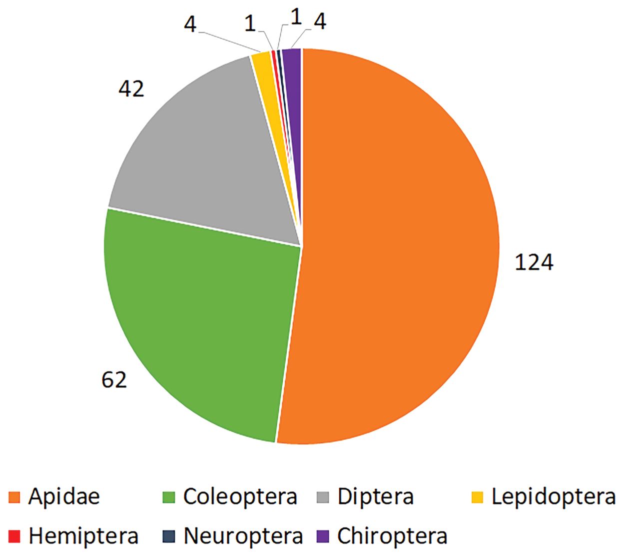


Fig. 2. Number of taxa cited in previous works about pollinator/visitor in 52 of the analyzed edible fruit plant species in the Amazon Tropical Forest. Taxa of Apidae family are quoted on Table 3. All taxa can be found in the Supp Information 1 (online only).

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

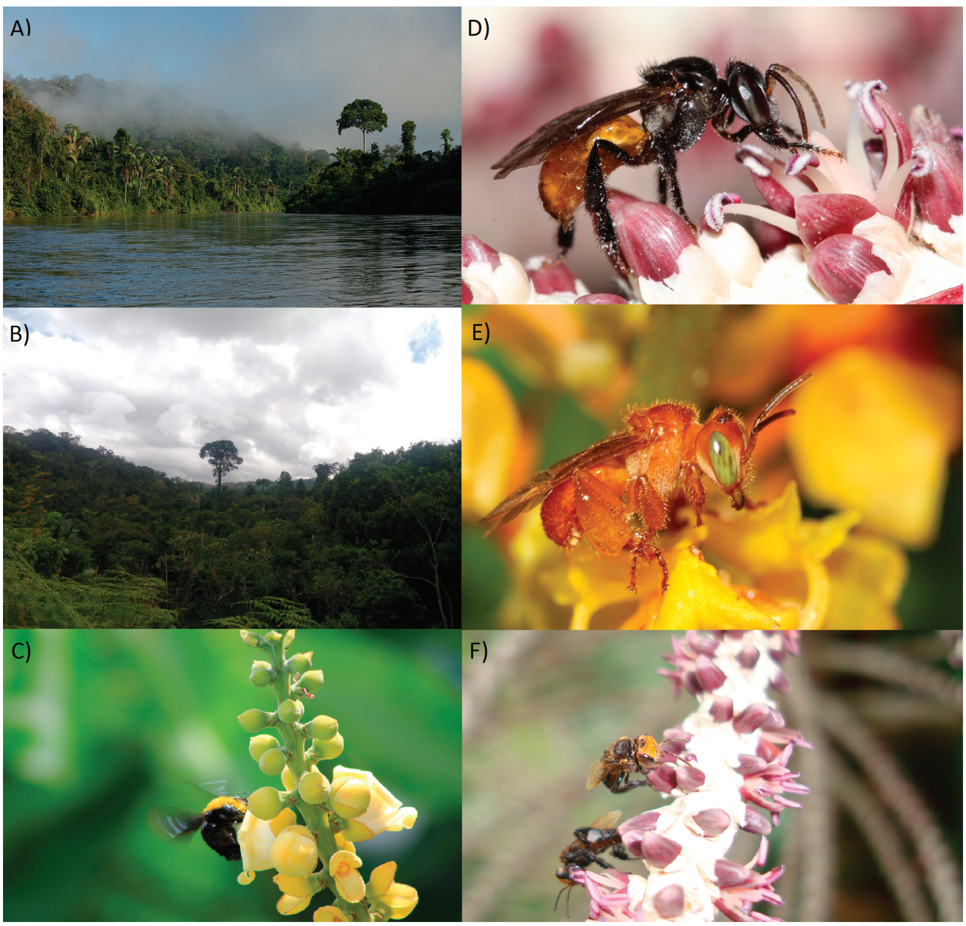


Fig. 3. (A and B) Aspects of the Amazon Forest with the striking view of Brazil nut tree (*Bertholletia excelsa*) with its high stature and straight trunk (Photos: João Rosa and Rafael M. Brito, respectively); (C) Carpenter bee (*Xylocopa frontalis* Olivier, 1789 (Hymenoptera: Apidae)) on Brazil nut blossom (Photo: Marcia M. Maués); (D) *Trigona fulviventris* (male) on muruci (*Byrsonima crassifolia*) flower (Photo: Cristiano Menezes); (E) *Trigona palllens* (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); *Belopeus carmelitus* (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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