Research article

Acta Botanica Mexicana

Morphological characterization of extrafloral nectaries in Brazilian Amazonian plant species

Caracterización morfológica de los nectarios extraflorales en especies vegetales de la Amazonia brasileña

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Abstract:

Background and Aims: Extrafloral nectaries (EFNs) are secretory glands of an aqueous solution composed mainly of sugars, amino acids and lipids, frequently used as food resource by ants, which tend to protect their host plants against herbivorous insects. Although the Amazon forest is recognized worldwide for its high plant diversity, few studies have been carried out in the region that characterize the different morphotypes of EFNs. In this context, our main aim was to perform a brief morphological description of EFNs in the Brazilian Amazonian rainforest.

Methods: We established a plot of 6250 m^2 in ten forest fragments situated in the state of Acre, Brazilian Amazon. In these plots, we performed intensive field surveys to locate EFN-bearing plant species. Subsequently, we used scanning electron microscopy images to morphologically characterize the EFNs. The morphological descriptions included information about the life form of EFN-bearing plant species, morphotypes of EFNs and their location in different plant structures.

Key results: We morphologically characterized 67 EFN-bearing plant species, distributed in 28 genera and 19 families. The botanical families with the highest taxonomic representativeness were Fabaceae, Bignoniaceae and Malpighiaceae. Lianas were the life form with the largest number of EFN-bearing plant species, while elevated EFNs were the most frequent morphotype.

Conclusions: The high frequency of elevated EFNs evidences the importance of the ant defense system against herbivory in these Brazilian Amazonian forests, since it has been documented in others works that this morphotype secretes a larger nectar volume, which is an advantage in relation to the attraction potential. Finally, our results indicate the existence of a high diversity of EFN-bearing plant species in this region of the Brazilian Amazon, and an important morphological diversity of associated extrafloral nectaries.

Key words: Brazilian Amazon rainforest, EFN-bearing plant species, morphological characterization.

Resumen:

Antecedentes y Objetivos: Los nectarios extraflorales (NEFs) son glándulas secretoras de una solución acuosa compuesta principalmente de azúcares, aminoácidos y lípidos, frecuentemente utilizada como recurso alimenticio por hormigas, que tienden a proteger sus plantas hospederas contra insectos herbívoros. Aunque la selva amazónica es reconocida mundialmente por su alta diversidad de plantas, pocos estudios se han realizado en la región que caracterizan las diferentes formas de NEFs. En este contexto, nuestro principal objetivo fue realizar una descripción morfológica de los NEFs en una selva amazónica brasileña.

Métodos: Establecimos una parcela de 6250 m^2 en diez fragmentos de bosque situados en el estado de Acre, Amazonía Brasileña. En estas parcelas, realizamos recorridos de campo intensivos para localizar especies de plantas portadoras de NEFs. Posteriormente, utilizamos imágenes de microscopía electrónica de barrido para caracterizar morfológicamente los NEFs. Las descripciones morfológicas incluyeron información sobre la forma de vida de las especies de plantas portadoras de NEFs, morfotipos de NEFs y su ubicación en las diferentes estructuras de la planta.

Resultados clave: Caracterizamos morfológicamente 67 especies de plantas portadoras de NEFs, distribuidas en 28 géneros y 19 familias. Las familias botánicas con mayor representatividad taxonómica fueron Fabaceae, Bignoniaceae y Malpighiaceae. Las lianas fueron la forma de vida que presentó más especies de plantas portadoras de NEFs, mientras que los NEFs de tipo elevado fueron los más frecuentes.

Conclusiones: La mayor frecuencia de NEFs de tipo elevado evidencia la importancia del sistema de defensa de hormigas contra la herbivoria en esta selva amazónica brasileña, ya que se ha documentado en otros trabajos que este morfotipo secreta un mayor volumen de néctar, lo que es una ventaja en relación con el potencial de atracción. Finalmente, nuestros hallazgos indican la existencia de una alta diversidad de especies de plantas portadoras de NEFs en esta región de Amazonía Brasileña, y una importante diversidad morfológica de nectarios extraflorales asociados.

Palabras clave: caracterización morfológica, especies de plantas portadoras de NEFs, selva amazónica brasileña.

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Received: August 10, 2023.
Reviewed: October 4, 2023.
Accepted by Marie-Stéphanie Samain: January 26, 2024.
Published Online first: February 6, 2024.
Published: Acta Botanica Mexicana 131(2024).

To cite as: Miranda, P. N., J. E. Lahoz da Silva Ribeiro, A. Aguirre-Jaimes, I. Brasil and W. Dáttilo. 2024. Morphological characterization of extrafloral nectaries in Brazilian Amazonian plant species. Acta Botanica Mexicana 131: e2241. DOI: https://doi.org/10.21829/abm131.2024.2241

e-ISSN: 2448-7589

Introduction

Among the high diversity of plant species occurring in tropical rainforests (Ribeiro et al., 1999; Giulietti et al., 2005), some species are known for the presence of secretory glands called extrafloral nectaries (EFNs), that can be distributed in different parts of the plants (EFN-bearing plant species) and are not directly involved in pollination processes (Koptur, 1992). These glands secrete an aqueous solution mainly composed of sugars, amino acids, and lipids (Baker and Baker, 1975, 1983; Heil, 2011), frequently used as a food resource by various arthropod groups, particularly ants, spiders, and wasps (Koptur et al., 2010; Schoereder et al., 2010; Heil, 2015; Del-Claro et al., 2016). Among these, ants have been relatively well-studied in the context of insect-plant interactions (Blüthgen et al., 2000; Aguirre et al., 2013). In exchange for the food provided by the EFN-bearing plant species, some ants can protect their host plants against herbivores (Rico-Gray and Oliveira, 2007; Koptur et al., 2010), which can increase plant fitness (De La Fuente and Marquis, 1999).

The global diversity of EFN-bearing plant species is high (Keeler et al., 2023), corresponding to approximately 25% of the angiosperms (Elias, 1983; Koptur, 1992). Approximately 4000 EFN-bearing plant species have been recognized, distributed among 768 genera and 108 families (Weber and Keeler, 2013; Marazzi et al., 2019). Of these 768 genera, 153 are legumes (20% of the total number of legume genera) (Marazzi et al., 2019), and of the 108 families, three of them (Fabaceae, Passifloraceae and Malvaceae) account for approximately 50% of the total species (McKey, 1989; Marazzi et al., 2013; Weber and Keeler, 2013). Part of this diversity occurs in temperate zones, but these EFN-bearing plant species are more common in tropical areas (Koptur, 1992). In tropical regions, EFN-bearing plant species may represent from 5 to 33% of the general floristic diversity (Schupp and Feener, 1991; Fiala and Linsenmair, 1995; Aguirre et al., 2013). Miranda et al. (2022) sampled 93 EFN-bearing plant species in a 3500 ha reserve located in the Atlantic Forest biome, Southeastern Brazil. These plant species correspond to 6% of the 562 plant species previously recorded for the area. According to Morellato and Oliveira (1991), in the Brazilian Amazonian rainforests, depending on the vegetation type ("terra firme" forest, successional forest, palm vegetation and savanna), EFN-bearing plant species may represent 18 to 53% of the total number of woody species.

While these studies reveal a substantial diversity of EFN-bearing plant species in tropical forests, there remains a significant dearth of documentation for these plants in the Brazilian Amazon (Keeler et al., 2023). The "World list of angiosperm species with extrafloral nectaries" (Keeler et al., 2023) reports approximately 400 EFN-bearing plant species recorded for Brazil. However, fewer than 100 of these are documented in publications based on samples collected in the Brazilian Amazon (Arbo, 1972; Gates, 1982; Prance, 1989, 2007; Morellato and Oliveira, 1991; Ribeiro et al., 1999; Secco, 2005; Lohmann, 2006; Nogueira et al., 2012; Dáttilo et al., 2013, 2014; Campos and Camacho, 2014; Coutinho and Meira, 2015; Silva et al., 2017).

Over the last decade, there has been a notable increase in studies examining ecological interactions between ants and EFN-bearing plant species in the Brazilian Amazon (Dáttilo et al., 2014; Falcão et al., 2015; Miranda et al., 2019; Nogueira et al., 2020). These ecological studies often prioritize the collection of samples from non-fertile plants, as all plants hosting ants on their EFNs are recorded (Miranda et al., 2019). However, the absence of reproductive structures poses challenges for species-level identification. Nevertheless, it is crucial to emphasize that some of these studies have identified more than 100 EFN-bearing plant species or morphospecies (Falcão et al., 2015; Miranda et al., 2019), underscoring the remarkable diversity of these plants in the Brazilian Amazon.

The high diversity of EFN-bearing plant species matches the morphological diversity of these glands, which can be classified into two main groups: non-structural and structural nectaries (Marazzi et al., 2019). In non-structural nectaries, the nectar is secreted from tissues without structural specialization (Elias, 1983). On the contrary, structural nectaries are characterized by the presence of specialized nectar-secreting tissues (Nepi, 2007). These structural glands can be classified into trichomatic EFNs and parenchymatic EFNs (secretory tissue formed by small, densely packed thin-walled cells, with a dense and glandular cytoplasm) (Marazzi et al., 2019). In relation to their location on the plant body, these glands occur in both vegetative and reproductive structures (Elias, 1983). On leaves, for example, the EFNs occur on the petiole, the rachis of compound leaves, the upper and lower surfaces of the blade, the leaf margin and on stipules (Koptur, 1992). However, EFNs located in reproductive structures are also called "extrafloral" because they are not directly involved with pollination (Koptur, 1992). They can occur on buds, calyx, inflorescence axis, flower peduncles and fruits (Rico-Gray and Thien, 1989; Rico-Gray, 1993; Rico-Gray et al., 2004). Thus, based on the studies published up to the present moment, we can conclude that EFNs are very diverse in terms of morphology, location, structure, and physiology.

To date, a considerable number of studies have focused on the morphological description of EFNs (Elias and Gelband, 1976; Pascal et al., 2000; Blüthgen and Reifenrath, 2003; Díaz-Castelazo et al., 2005; Aguirre et al., 2013; Rodríguez-Morales et al., 2016; Marazzi et al., 2019). In Brazil, despite its megadiverse status (Frehse et al., 2016), research on the morphological characterization of these glands has primarily concentrated on the Cerrado biome (Oliveira and Leitão-Filho, 1987; Machado et al., 2008; Melo et al., 2010). Thus, considering the significant knowledge gap concerning EFN-bearing plant species in the Brazilian Amazon, one of the world's most diverse regions, it is essential not to dismiss botanical samples from ecological studies. These samples can make valuable contributions to our understanding, particularly regarding the morphological diversity of these glands, even if they do not facilitate taxonomic identification. This importance is amplified when we consider the limited financial resources and logistical challenges associated with conducting scientific research in this region, primarily due to the difficulties in accessing study areas.

The state of Acre, located in the Southwestern Brazilian Amazon, is well-known for its bamboo forests (*Guadua weberbaueri* Pilg.) (Silveira, 2005; de Polari Alverga et al., 2021), quite uncommon in other regions of the Brazilian Amazon (Silveira, 2005). Botanical surveys carried out in the state of Acre have recorded approximately 4350 plant species, and a much larger number may possibly make up the total flora of the state, since large areas are still superficially sampled (Medeiros et al., 2014). Therefore, based on the plant species recorded, between 200 and 1400 EFN-bearing plant species may be expected to occur in the region, considering the proportion that these plant species represent in relation to the general floristic diversity in tropical forests, as mentioned above. The research in less-explored regions is of paramount importance, as it significantly enriches our comprehension of megadiverse ecosystems like the Amazon and the complex web of ecological and evolutionary relationships they harbor. In these circumstances, our main aim was to perform a brief morphological description of EFNs in bamboo forests, based on botanical samples from the only ecological study about ant-plant interactions mediated by EFNs carried out in state of Acre (Miranda et al., 2019); and discuss the results found in the ant-plant interactions context. The morphological descriptions include information about the life form of the EFN-bearing plant species, morphotypes of EFNs and location on the plant body.

Material and Methods

Study site

The state of Acre, whose territory represents 4% of the Brazilian Amazon, is divided into five regions, which follow the distribution of the hydrographic basins of the main rivers (Acre, 2010). The present study was carried out in 10 forest fragments, ranging in size from approximately 5 to 3000 ha, all belonging to a single region called Regional Baixo Acre (Fig. 1, Supplementary Material 1). This region, whose predominant vegetation is bamboo forest (Silveira, 2005), represents 14% of the territory of the state (Acre, 2010), and is undoubtedly the most studied in floristic terms (Medeiros et al., 2014), since the Federal University of Acre and other research institutes are located there. According to the Köppen climate classification (Köppen, 1936), our study area is classified as having a monsoon climate (Peel et al., 2007), with an average rainfall of 1450 mm per year (Macêdo et al., 2013) and marked seasonality, with most rain falling between November and March (Acre, 2010). The average annual temperature is 24 °C (INMET, 2016), with daily variation of around 9 °C (Acre, 2010). The region's elevation varies between 110 and 270 m (Acre, 2010). The predominant

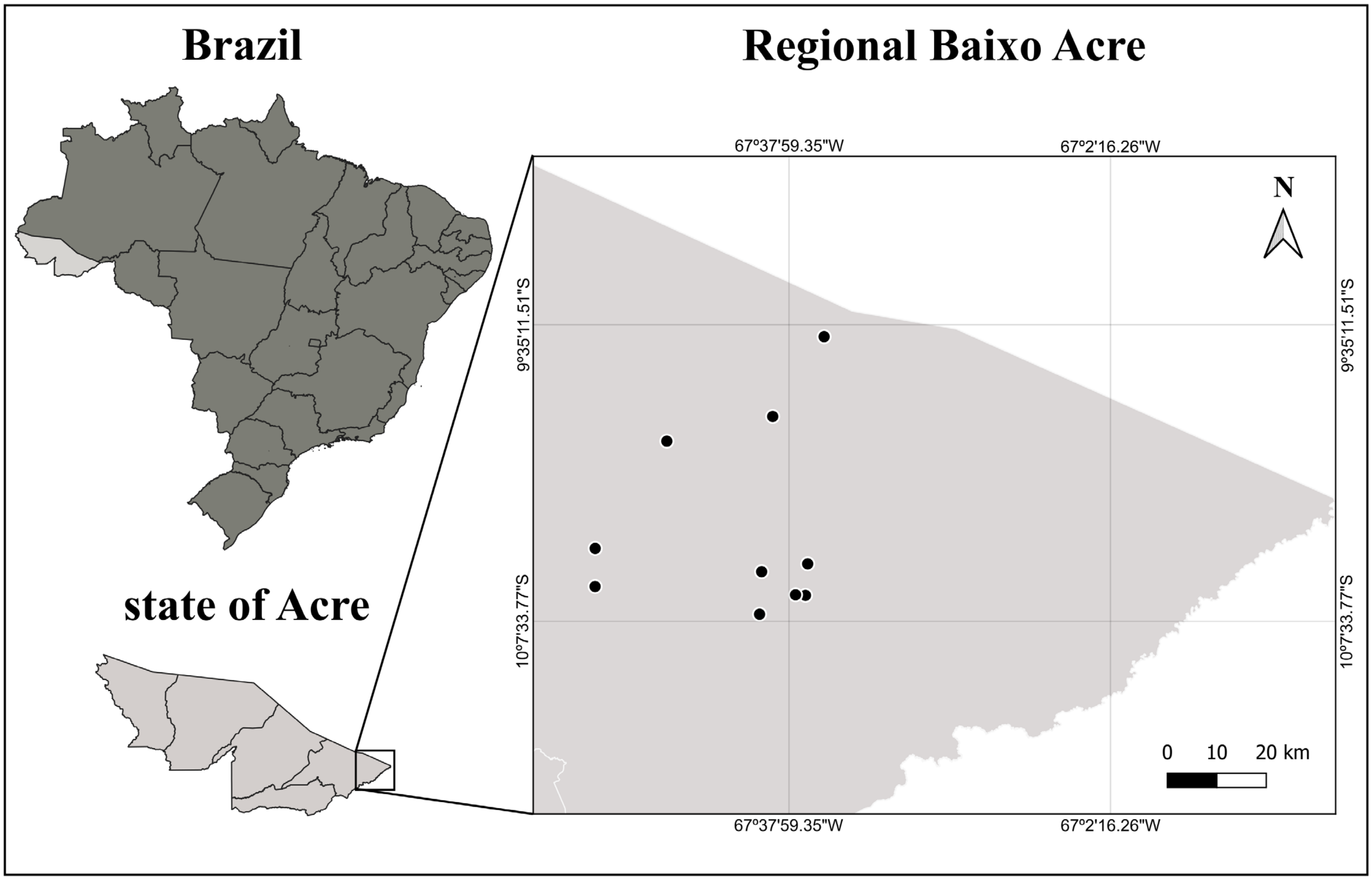

Figure 1: Location of the 10 plots used for sampling EFN-bearing plant species in the Regional Baixo Acre, state of Acre, Southwestern Brazilian Amazon.

vegetation type is open tropical rainforest (open ombrophilous forest) that can be dominated by bamboo and/or with palm trees (Silveira, 2005).

Field work

We established a plot of 6250 m^2 (250 × 25 m) in each forest fragment, with a minimum distance of 100 m from the edge, except for the smallest forest fragment, where a plot was placed at approximately 20 m from the edge. In each plot, we performed intensive field surveys to locate EFN-bearing plant species. The presence of ants feeding on EFNs helped us to locate the EFN-bearing plants within plots. We collected a plant sample from all specimens with EFNs detected in the field, for further identification and morphological characterization of these glands through a scanning electron microscopy study (see below). Plants whose EFNs were not detected in the field, but which had immobile ants with mouthparts in contact with plant tissues for several minutes, were also collected for later confirmation of the presence of EFNs through observations with a binocular stereomicroscope (Zeiss Stemi 2000, Göttingen, Germany) and a literature review. The fieldwork was carried out from June 2016 to February 2017. During this period, each plot was sampled twice, the first sampling being performed in the dry season, and the second in the rainy season, to increase the probability of detecting plants that exhibit EFNs active only in one of these seasons.

Plants were identified at species or morphospecies level through identification guides (Ribeiro et al., 1999; Pennington et al., 2004) and by comparison with specimens deposited at the Herbário da Universidade Federal do Acre (UFACPZ), Brazil. Voucher specimens of plants were deposited in this same herbarium, and the deposit numbers can be found in Supplementary Material 2. All taxa were revised by a specialist (Dr. José Eduardo Lahoz da Silva Ribeiro, Universidade Estadual de Londrina); however, as we did not have reproductive structure samples for most of the EFN-bearing plant species, it was not possible to identify all samples to species level. Considering the difficulty in identifying the botanical samples, our focus was basically to describe the morphology of some EFNs found in the Southwestern Brazilian Amazon and their distribution in terms of botanical families.

Morphological studies

We performed morphological characterization of the EFNs for 67 EFN-bearing plant species or morphospecies, which represent 47.2% of the total number of species sampled in the 10 forest fragments (n=142 plant species). These 67 species were selected to contemplate all botanical families sampled, prioritizing the most abundant species, and respecting the proportion of the number of species among families. Therefore, although the selected species constitute only 47.2% of the total number of species sampled, their total abundance (the sum of individuals for each species/morphospecies across the 10 sample plots and two sampling periods) represents approximately 80% of the total abundance calculated for the 142 EFN-bearing plant species sampled. The complete list of all species and morphospecies registered in the 10 forest fragments can be found in Supplementary Material 2.

We fixed the EFNs in FAA solution (10 ml formaldehyde + 5 ml glacial acetic acid + 50 ml ethanol + 35 ml water) (Kraus and Arduim, 1997). After a week in this solution, the EFNs were washed with water for 2 h, and then dehydrated with an ethanol solution series (30%, 50%, 70% and 100%). The samples were critical point-dried using CO_2, sputter-coated with gold-palladium and examined using a scanning electron microscope (JEOL JSM 5600LV (25 kV), Tokyo, Japan).

For the morphological characterization of the EFNs, we followed the nomenclature adapted by Marazzi et al. (2019) from Elias (1983). In the present study, we classified the morphotypes of EFNs into: (i) formless (non-structural nectaries whose nectar is secreted from tissues without structural specialization); (ii) hollow (trichomatic EFNs - structural nectaries characterized by trichomes sunk in depressions or cavities); (iii) pit (parenchymatic EFNs - structural nectaries whose glandular tissues are sunken in tissues of others organs, in depressions as large as or larger than the nectary); (iv) flattened (parenchymatic EFNs - structural nectaries whose glandular tissue is closely pressed against underlying tissue), and (v) elevated (parenchymatic EFNs - structural nectaries whose glandular tissue protruding from the organ that bears them).

Results

Botanical families of EFN-bearing plant species

We morphologically characterized the EFNs of 67 EFN-bearing plant species or morphospecies, distributed in 28 genera and 19 families (Table 1). We could not identify three EFN-bearing plant morphospecies at the genus level. Therefore, for these morphospecies, we left the identification at the family level (Chrysobalanaceae sp., Lecythidaceae sp., Olacaceae sp.) (Table 1). Of the 19 families sampled, Fabaceae was the most representative, with the highest number of EFN-bearing plant species (43.28% of the total plant species, n=29 plant species), followed by Bignoniaceae (13.43%, n=9) and Malpighiaceae (5.97%, n=4) (Fig. 2). Each of the families Chrysobalanaceae, Passifloraceae, Sapindaceae and Euphorbiaceae were represented by three species (4.48%, n=3) (Fig. 2). Convolvulaceae was represented by two species (2.98%), and each of the other 11 remaining botanical families were represented by only one species (1.49%, n=1) (Fig. 2). Fabaceae was also the family that presented the highest number of genera (six genera, 21.43% of the total), followed by Euphorbiaceae and Malpighiaceae, both being represented by three genera (10.71% of the total). Four botanical families were represented by only two genera (7.14% of the total) and 12 were represented by a single genus (3.57% of the total).

Life forms of EFN-bearing plant species

The life form with the greatest representation was liana (53.73% of the total plant species, n=36 species) followed by trees (43.28%, n=29). Shrubs (1.49%, n=1) and herbs (1.49%, n=1) were the life forms with a minimum number of EFN-bearing plant species (Fig. 3).

Table 1: Taxonomic distribution of EFN-bearing plant species sampled in 10 forest fragments located in the state of Acre, Brazilian Amazon. Description of the location and type of the extrafloral nectaries (EFNs) observed.

Family	Plant species	Life form	Site (location)	Type of EFN	Photo data
Bignoniaceae	*Fridericia* sp. 2	Liana	Pseudo-stipules	Flattened	Fig. 5N1-N2
	Fridericia sp. 3	Liana	Pseudo-stipules	Flattened	Fig. SM4N
	Fridericia sp. 5	Liana	Pseudo-stipules	Flattened	Fig. 5O
	Fridericia sp. 8	Liana	Inter-petiolar region	Flattened	Fig. SM4L
	Fridericia sp. 19	Liana	Pseudo-stipules	Flattened	Fig. SM4O
	Fridericia sp. 31	Liana	Inter-petiolar region	Flattened	Fig. 5M1-M2
	Fridericia sp. 35	Liana	Inter-petiolar region	Flattened	Fig. SM4M
	Memora sp. 2	Liana	Pseudo-stipules	Flattened	Fig. 5P
	Memora sp. 3	Liana	Pseudo-stipules and leaf lamina	Flattened	Fig. 6A
Chrysobalanaceae	Chrysobalanaceae sp.	Tree	Leaf margin	Elevated	Fig. SM4K
	Hirtella racemosa Lam.	Tree	Leaf lamina	Flattened	Fig. SM4P
	Hirtella sp.	Tree	Leaf lamina	Flattened	Fig. 6B1-B2
Convolvulaceae	*Ipomoea philomega* (Vell.) House	Liana	Leaf lamina	Formless	Fig. SM4S
	Ipomoea regnellii Meisn.	Liana	Leaf lamina	Formless	Fig. 6H1-H2
Costaceae	*Costus scaber* Ruiz & Pav.	Herb	Bracts	Hollow	Fig. 6N
Cucurbitaceae	*Gurania* sp.	Liana	Leaf lamina	Flattened	Fig. 6C
Euphorbiaceae	*Aparisthmium cordatum* (A. Juss.) Baill.	Tree	Leaf lamina	Flattened	Fig. SM4Q
	Dalechampia sp.	Liana	Leaf lamina	Elevated	Fig. 5F
	Omphalea diandra L.	Liana	Leaf lamina	Elevated	Fig. 5G
Fabaceae	*Bauhinia* sp. 1	Liana	Petiole and rachis	Elevated	Fig. SM3F1-F2
	Erythrina sp.	Tree	Rachis	Elevated	Fig. SM3G
	Inga acreana Harms	Tree	Rachis	Elevated	Fig. 5C
	Inga alba (Sw.) Willd.	Tree	Rachis	Elevated	Fig. SM3H
	Inga calantha Ducke	Tree	Rachis	Elevated	Fig. SM3I
	Inga capitata Desv.	Tree	Rachis	Elevated	Fig. SM3J
	Inga chartacea Poepp.	Tree	Rachis	Elevated	Fig. SM3K
	Inga densiflora Benth.	Tree	Rachis	Elevated	Fig. 5D
	Inga edulis Mart.	Tree	Rachis	Elevated	Fig. SM3L
	Inga heterophylla Willd.	Tree	Rachis	Elevated	Fig. 5B
	Inga lateriflora Miq.	Tree	Rachis	Elevated	Fig. SM3M
	Inga laurina (Sw.) Willd.	Tree	Rachis	Elevated	Fig. SM3N
	Inga microcoma Harms	Tree	Rachis	Elevated	Fig. SM3O
	Inga punctata Willd.	Tree	Rachis	Pit	Fig. 6K
	Inga sertulifera DC.	Tree	Rachis	Elevated	Fig. SM3P
	Inga suaveolens Ducke	Tree	Rachis	Elevated	Fig. SM4A
	Inga tenuistipula Ducke	Tree	Rachis	Elevated	Fig. SM4B
	Inga sp. 4	Tree	Rachis	Elevated	Fig. SM4C
	Inga sp. 5	Tree	Rachis	Elevated	Fig. SM4D
	Senegalia sp. 1	Liana	Petiole and rachis	Elevated	Fig. SM3A1-A2
	Senegalia sp. 2	Liana	Petiole and rachis	Elevated	Fig. SM3B1-B2
	Senegalia sp. 3	Liana	Petiole and rachis	Elevated	Fig. SM3C1-C2

Table 1: Continuation.

Family	Plant species	Life form	Site (location)	Type of EFN	Photo data
	Senegalia sp. 4	Liana	Petiole and rachis	Elevated	Fig. SM3D
	Senegalia sp. 7	Liana	Petiole and rachis	Elevated	Fig. SM3E
	Senegalia sp. 8	Liana	Petiole and rachis	Elevated	Fig. 5A1-A2
	Senna sp.	Shrub	Rachis	Elevated	Fig. SM4E
	Zygia sp. 1	Tree	Petiole	Elevated	Fig. 5E
	Zygia sp. 2	Tree	Petiole	Elevated	Fig. SM4F
	Zygia sp. 3	Tree	Petiole	Elevated	Fig. SM4G
Lecythidaceae	Lecythidaceae sp.	Tree	Petiole	Hollow	Fig. 6O
Malpighiaceae	*Banisteriopsis* sp. 2	Liana	Leaf lamina	Flattened	Fig. 6F
	Banisteriopsis sp. 5	Liana	Leaf lamina	Flattened	Fig. 6G
	Heteropterys sp.	Liana	Leaf lamina	Flattened	Fig. 6D1-D2
	Tetrapterys sp.	Liana	Leaf lamina	Flattened	Fig. SM4R
Malvaceae	*Byttneria benensis* Britton	Liana	Base of the mid rib	Pit	Fig. 6M
Menispermaceae	*Abuta* sp. 1	Liana	Leaf lamina	Flattened	Fig. 6E1-E2
Ochnaceae	*Ouratea* sp.	Tree	Stipules	Pit	Fig. 6L
Olacaceae	Olacaceae sp.	Tree	Leaf axils	Elevated	Fig. 5K
Passifloraceae	*Dilkea* sp.	Liana	Bracts	Formless	Fig. 6I1-I2
	Passiflora coccinea Aubl.	Liana	Leaf margin	Elevated	Fig. 5I
	Passiflora sp. 3	Liana	Bracts	Formless	Fig. SM4T
Rhamnaceae	*Gouania* sp.	Liana	Leaf margin	Elevated	Fig. 5J
Sapindaceae	*Paullinia* sp. 1	Liana	Leaf margin	Elevated	Fig. 5H
	Paullinia sp. 2	Liana	Leaf margin	Elevated	Fig. SM4H
	Paullinia sp. 6	Liana	Leaf margin	Elevated	Fig. SM4I
Solanaceae	*Solanum* sp.	Liana	Bracts	Formless	Fig. 6J
Vitaceae	*Cissus* sp.	Liana	Leaf margin	Elevated	Fig. SM4J
Vochysiaceae	*Qualea grandiflora* Mart.	Tree	Stems	Elevated	Fig. 5L1-L2

Morphotypes and location of extrafloral nectaries

In relation to the morphotypes of EFNs, we found that elevated EFNs were the most representative (58.20% of the total plant species, n=39 plant species), followed by flattened (26.87%, n=18), formless (7.46%, n=5), pit (4.48%, n=3) and hollow (2.99%, n=2) (Fig. 4). Fabaceae was the family with the highest number of species bearing elevated EFNs (28 species), followed by Sapindaceae (three species) and Euphorbiaceae (two species). Elevated EFNs were observed in the following parts of the species sampled: (I) petiole and primary rachis between the pairs of leaflets (adaxial surface) (Figs. 5A1-A2, SM3A1-A2, SM3B1-B2, SM3C1-C2, SM3D, SM3E, SM3F1-F2); (II) only primary rachis between the pairs of leaflets (adaxial surface) (Figs. 5B, 5C, 5D, SM3G, SM3H, SM3I, SM3J, SM3K, SM3L, SM3M, SM3N, SM3O, SM3P, SM4A, SM4B, SM4C, SM4D); (III) only petiole (adaxial surface) (Figs. 5E, SM4E, SM4F, SM4G); (IV) base of the leaf lamina (adaxial surface), near its junction with the petiole (Fig. 5F, 5G); (V) leaf margin (adaxial surface) (Figs. 5H, 5I, 5J, SM4H, SM4I, SM4J, SM4K); (VI) leaf axils (Fig. 5K); and (VII) stems (adaxial surface), next to the insertion of leaves (Fig. 5L1-L2).

The family with the highest number of species bearing flattened EFNs was Bignoniaceae (nine species), followed by Malpighiaceae (four species) and Chrysobalanaceae (two species). Flattened EFNs were observed in the

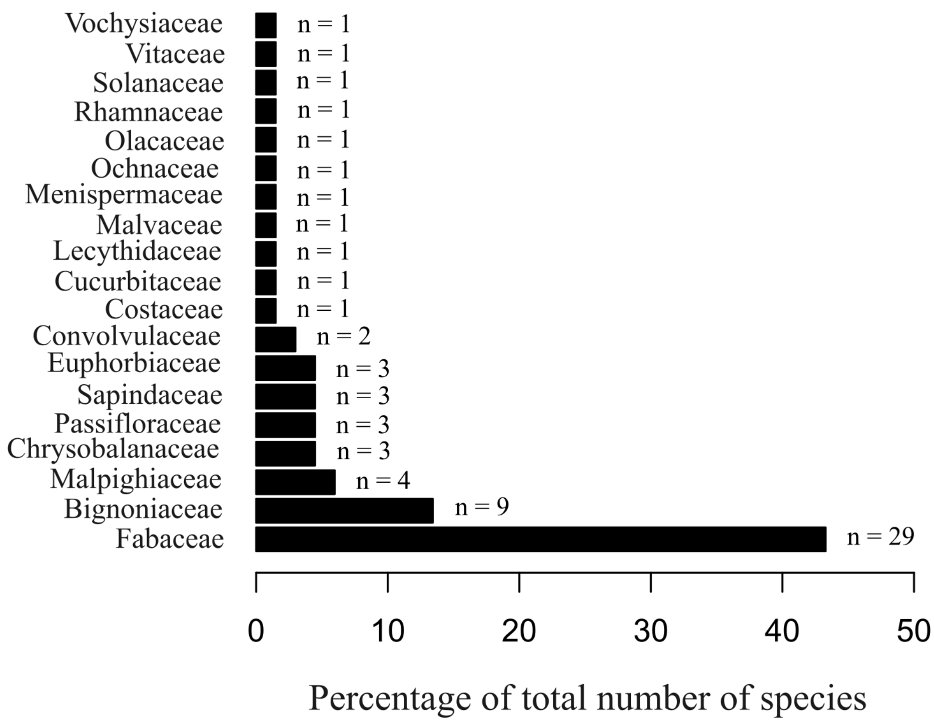

Figure 2: Taxonomical representation of EFN-bearing plant species sampled in 10 forest fragments located in the state of Acre, Brazilian Amazon.

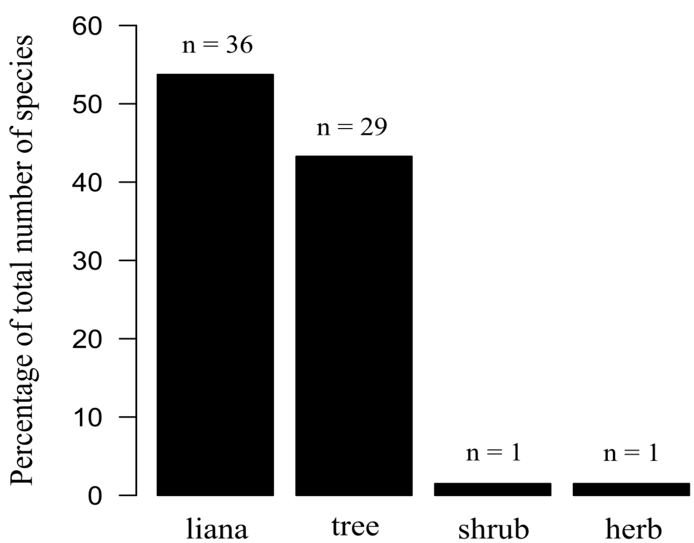

Figure 3: Life form of EFN-bearing plant species sampled in 10 forest fragments located in the state of Acre, Brazilian Amazon.

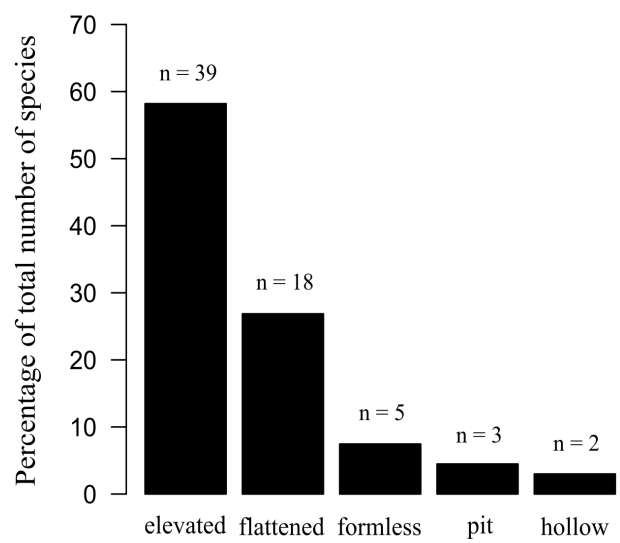

Figure 4: Morphotypes of extrafloral nectaries (EFNs) found in 10 forest fragments located in the state of Acre, Brazilian Amazon, according to Díaz-Castelazo et al. (2005). Elevated (nectaries that have glandular tissue raised above ground tissue); flattened (glandular tissue closely pressed against underlying tissue, common on leaf surfaces); formless (with no structure specialization, but may be colored in contrast to background); pit (glandular tissue sunken in the tissue of other organs, in depressions as large as or larger than the nectary); hollow (cavities in other organs with a narrow channel extending to the surface); and transformed (nectaries originated by the transformation of an organ).

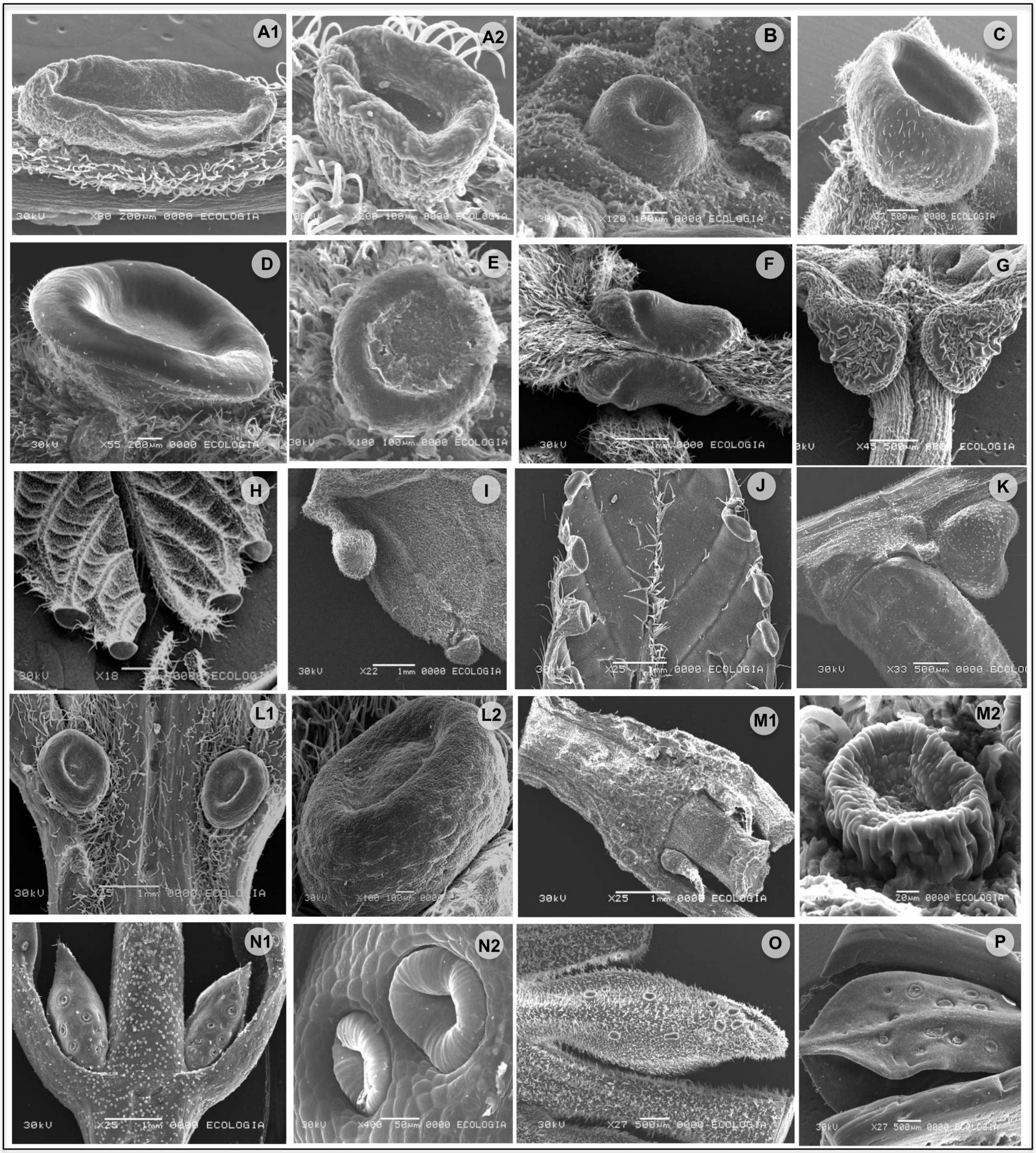

Figure 5: Elevated extrafloral nectaries (EFNs): A1-A2. *Senegalia* sp. 8 (Fabaceae); B. *Inga heterophylla* Willd. (Fabaceae); C. *Inga acreana* Harms (Fabaceae); D. *Inga densiflora* Benth. (Fabaceae); E. *Zygia* sp. 1 (Fabaceae); F. *Dalechampia* sp. (Euphorbiaceae); G. *Omphalea diandra* L. (Euphorbiaceae); H. *Paullinia* sp. 1 (Sapindaceae); I. *Passiflora coccinea* Aubl. (Passifloraceae); J. *Gouania* sp. (Rhamnaceae); K. Olacaceae sp. (Olacaceae); L1-L2. *Qualea grandiflora* Mart. (Vochysiaceae). Flattened extrafloral nectaries (EFNs): M1-M2. *Fridericia* sp. 31 (Bignoniaceae); N1-N2. *Fridericia* sp. 2 (Bignoniaceae); O. *Fridericia* sp. 5; P. *Memora* sp. 2 (5P).

following parts of the plant species sampled: (I) inter-petiolar regions (adaxial surface), mainly of young branches (Figs. 5M1-M2, SM4L, SM4M); (II) pseudo-stipules (adaxial surface), which are more evident in the inter-petiolar regions of young branches (Figs. 5N1-N2, 5O, 5P, SM4N, SM4O); (III) pseudo-stipules and leaf lamina (Fig. 6A); (IV) leaf lamina (adaxial surface), at the apex and base of the leaves (Figs. 6B1-B2, SM4P), or only at the base of the leaves (adaxial surface) (Fig. 6C); and (V) leaf lamina (abaxial surface), at the base of the leaves, with two EFNs separated from each other by the primary vein (Figs. 6D1-D2, 6E1-E2, 6F, 6G, SM4Q, SM4R).

Both families Convolvulaceae and Passifloraceae were represented by two species bearing formless EFNs. This EFN morphotype was observed in the following parts of the plant species sampled: (I) leaf lamina (abaxial surface), with two secretory fields of these glands on opposite sides of the petiole, near its junction with the leaf lamina (Figs. 6H1-H2, SM4S); and (II) bracts (Figs. 6I1-I2, 6J, SM4T).

Three families (Fabaceae, Malvaceae and Ochnaceae) had one species bearing pit EFNs, located in: (I) primary rachis between the pairs of leaflets (Fig. 6K); (II) base of stipules (abaxial surface) (Fig. 6L); and (III) base of the mid rib (adaxial surface) (Fig. 6M). Finally, two families (Costaceae and Lecythidaceae) had one species bearing hollow EFNs, located in: (I) central part of the bracts that cover the flowers (Fig. 6N); and (II) petiole (adaxial surface) (Fig. 6O).

Discussion

We observed that Fabaceae was the family with greatest representation, accounting for 43.28% of the EFN-bearing plant species analyzed, followed by Bignoniaceae (13.43%) and Malpighiaceae (5.97%). In general, 20% of the EFN-bearing plant genera belong to Fabaceae (Marazzi et al., 2019). A greater abundance and diversity of EFN-bearing plant species from this family was also detected in other studies. Machado et al. (2008) reported a higher representation of Fabaceae in the Brazilian Cerrado, a markedly seasonal environment, comprising 26.3% of the total EFN-bearing plant species recorded. However, only studies carried out in tropical rainforests found such a high representation of this family as in our study, equivalent to more than 40% of the total number of species (Morellato and Oliveira, 1991; Díaz-Castelazo et al., 2005; Aguirre et al., 2013). The dominance observed for Fabaceae is possibly related to the evolution of reproductive structures of the species belonging to the former subfamily Mimosoideae and to the subfamily Caesalpinioideae (Polhill et al., 1981). Most of the EFN-bearing plant species of Fabaceae are distributed in these two subfamilies (Elias, 1983; Judd et al., 1999; Melo et al., 2010), which present flowers whose reproductive organs are highly exposed and susceptible to environmental aggression (Polhill et al., 1981). In this context, the defense system provided by the association with ants (Rico-Gray and Oliveira, 2007) may have favored the wide distribution of EFNs in Fabaceae, considering that, according to Polhill et al. (1981), the co-evolution involving plants and animals as a function of defense possibly led to the appearance of these glands. Just like ours, other studies carried out in tropical regions of the American continent also observed a relatively high representation of the Bignoniaceae and Malpighiaceae families (Díaz-Castelazo et al., 2005; Machado et al., 2008; Aguirre et al., 2013; Dáttilo and Dyer, 2014), indicating a probable pattern for the tropical region of this continent.

In our study, lianas were the life form with the greatest number of EFN-bearing plant species, followed by trees, shrubs, and herbs. Schupp and Feener (1991), sampling EFN-bearing plants in Barro Colorado Island (Panama), also observed a larger number of liana species in their samples. In contrast, Aguirre et al. (2013), in a tropical forest located in the Los Tuxtlas Biological Field Station (Mexico), found a greater number of tree species with EFNs, when compared to other life forms. The different patterns observed by us and by Aguirre et al. (2013) are possibly related to structural differences in the forests studied (e.g. tree and shrub density, canopy cover and litter depth), mainly due to the presence of bamboo in the forests of our work. The presence of bamboo promotes an increase in light into the understory (Griscom and Ashton, 2003; Silveira, 2005), which tends to favor the presence of lianas, since these plants are well adapted to this condition (Putz, 1984; Laurance et al., 2001). Furthermore, we cannot fail to mention that

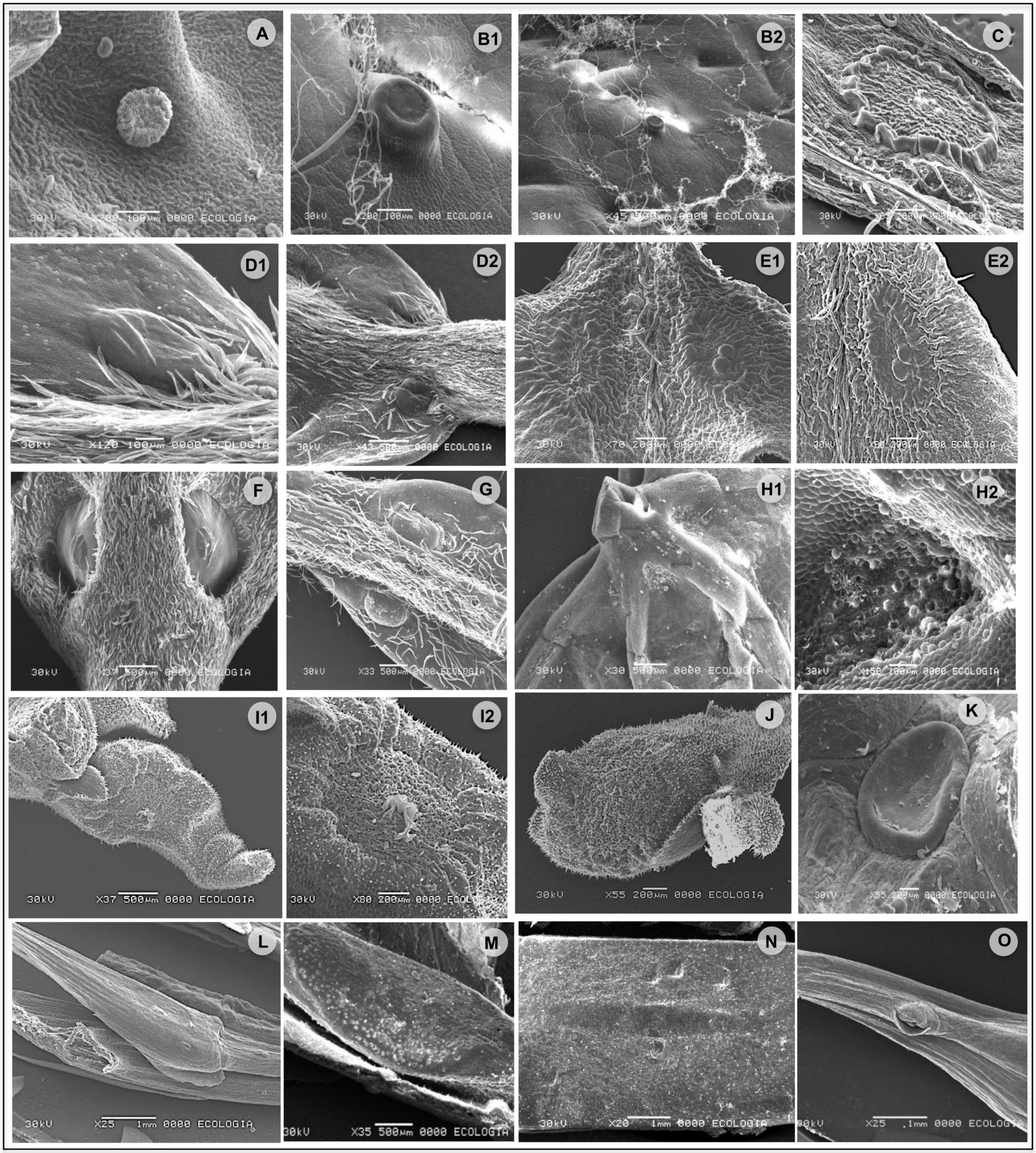

Figure 6: Flattened extrafloral nectaries (EFNs): A. *Memora* sp. 3 (Bignoniaceae); B1-B2. *Hirtella* sp. (Chrysobalanaceae); C. *Gurania* sp. (Cucurbitaceae); D1-D2. *Heteropterys* sp. (Malpighiaceae); E1-E2. *Abuta* sp. 1 (Menispermaceae); F. *Banisteriopsis* sp. 2 (Malpighiaceae); G. *Banisteriopsis* sp. 5 (Malpighiaceae). Formless extrafloral nectaries (EFNs): H1-H2. *Ipomoea regnellii* Meisn. (Convolvulaceae); I1-I2. *Dilkea* sp. (Passifloraceae); J. *Solanum* sp. (Solanaceae). Pit extrafloral nectaries (EFNs): K. *Inga punctata* Willd. (Fabaceae); L. *Ouratea* sp. (Ochnaceae); M. *Byttneria benensis* Britton (Malvaceae). Hollow extrafloral nectaries (EFNs): N. *Costus scaber* Ruiz & Pav. (Costaceae); O. Lecythidaceae sp.

this greater representation of lianas could also be related to the conservation status of the forest fragments considered, since they have all already undergone anthropogenic actions, mainly the removal of wood.

Based on scanning electron microscopy images, we observed that elevated EFNs were the most representative, followed by flattened EFNs. The highest number of plant species with elevated EFNs is directly associated to the dominance of the Fabaceae, since almost all species of this family presented this morphotype of EFN. Machado et al. (2008) and Aguirre et al. (2013) also found a greater number of plant species with elevated EFNs because of the prevalence of this family in their samples. In our study, elevated EFNs occurred mostly on the leaf rachis, which is the main location of these glands in EFN-bearing plant species of Fabaceae (Pascal et al., 2000; Marazzi et al., 2013). It is important to emphasize that elevated EFNs, because they are relatively larger and secrete a larger nectar volume than smaller and non-vascularized glands (Díaz-Castelazo et al., 2005), are more frequently visited by ants (Blüthgen et al., 2000). Therefore, the large number of EFN-bearing plant species with the elevated morphotype in our study indicates that the ant defense system is an important strategy against herbivory in the Brazilian Amazonian rainforest.

The flattened EFN was the morphotype with the second highest number of EFN-bearing plant species, and this result can also be attributed to the relatively great representation of the Bignoniaceae and Malpighiaceae families in our samples, considering that all species which belong to these families presented flattened EFNs. Concerning gland location on the plant body, in Malpighiaceae and in the less represented family Chrysobalanaceae, flattened EFNs occurred on the leaf lamina, according to the usual pattern observed for the respective gland morphotype (Koptur, 1992). However, for the Bignoniaceae, these EFNs occurred on the pseudo-stipules and in the inter-petiolar region, which is a typical region of secretory gland occurrence in the family (Ribeiro et al., 1999; Gonzalez, 2011). In general, flattened EFNs are smaller than elevated EFNs, and consequently tend to produce a smaller nectar volume (Díaz-Castelazo et al., 2005), which represents a disadvantage in terms of attractive potential. However, flattened EFNs usually occur in a large number in the same region (e.g. leaf lamina or pseudo-stipules), unlike elevated EFNs that usually occur in isolation or in a small number in the same region (Koptur, 1992). According to Elias and Gelband (1976), the occurrence of many EFNs in the same region represents an excellent advantage since damage to one or more glands does not eliminate the attractive potential total of the region.

Formless, pit, and hollow were the morphotypes of EFNs with a smaller number of EFN-bearing plant species. Similar results were observed in other localities for formless and pit EFNs, such as in a mesophyll vine forest in Australia (Blüthgen and Reifenrath, 2003), in a Brazilian Cerrado region (Machado et al., 2008) and in a tropical rainforest in Mexico (Aguirre et al., 2013). Unlike us, Aguirre et al. (2013) sampled a greater number of EFN-bearing plant species with hollow EFNs than with flattened ones. This difference is related to the high number of liana species with flattened EFNs in our samples, mainly of the Bignoniaceae and Malpighiaceae. Again, this pattern is possibly a reflection of the bamboo influence on the forest structure. We sampled only two plant species with hollow EFNs, one of them being *Costus scaber* Ruiz & Pav. (Costaceae), also recorded by Aguirre et al. (2013), and recently documented with more morphological and anatomical detail by Rodríguez-Morales et al. (2016).

In summary, we collected a greater number of EFN-bearing plant species belonging to Fabaceae, followed by Bignoniaceae and Malpighiaceae, which, in general, corresponds to the results of studies carried out in other localities. Liana was the life form with the highest number of EFN-bearing plant species, followed by trees, shrubs, and herbs. We believe that the pattern found is related to the presence of bamboo and the conservation status of the forest fragments studied (i.e., forest altered mainly by removal of wood), since both conditions tend to increase the light into the understory, favoring the liana growth. We also observed that elevated and flattened EFNs were the most representative morphotypes. The dominance of the elevated EFNs is directly associated with the dominance of Fabaceae, considering that almost all EFN-bearing plant species of this family presented this gland morphotype. Similarly, the relatively greater representation of flattened EFNs is also associated with the high number of liana species belonging to the Bignoniaceae and Malpighiaceae which presented, without exception, this gland morphotype. It is also important to emphasize that elevated and flattened EFNs have advantages in relation to the attraction potential of ants, the first ones because they secrete a larger nectar volume due to their larger sizes (Díaz-Castelazo et al., 2005), and the latter because they occurred, at least in most of the species sampled, in a greater number in a same region, which in turn ensures the attraction potential of the region even if one or more glands are damaged (Elias and Gelband, 1976). Therefore, the high frequency of these two advantageous morphotypes of EFNs in our samples evidences the importance of the ant defense system against herbivory in these Brazilian Amazonian rainforests (Elias and Gelband, 1976; Blüthgen et al., 2000). Finally, our results point to the existence of a high diversity of EFN-bearing plant species in the Brazilian Amazon, which in turn constitutes a large study area to be considered in future research.

Author contributions

PN and WD conceived and designed the study. PN and IB made the fieldwork. IB and JE made the species identification. PN, AA and WD made the morphological studies. PN and WD wrote the manuscript with the assistance of JE, AA and IB.

Funding

This work was supported by the Instituto Federal do Acre, and partially funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior by a doctoral fellowship received during the period in which PN stayed at the Instituto de Ecología, A.C. (INECOL), analyzing the dataset of the present study.

Acknowledgements

The authors thank Tiburcio Laez Aponte (Instituto de Ecología, A.C.) for his help with the scanning electron microscope images; and the Herbarium of the Federal University of Acre (UFACPZ), Jhonatan Sena Lopes, and Celeste Magalí Caruso for their assistance in depositing the EFN-bearing plant specimens.

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Supplementary material 1: Location of the 10 forest fragments sampled in the state of Acre, Brazilian Amazon.

Fragment	Site	Geographic coordinates	Area (ha)
1	Senador Guiomard private fragment	10°3'59.16''S 67°34'51.90''W	5.26
2	Senador Guiomard private fragment	10°4'52.34''S 67°36'2.64''W	27.82
3	Senador Guiomard private fragment	10°6'58.02''S 67°41'6.90''W	123.16
4	Forestry School	9°59'48.12''S 67°59'20.12''W	332.15
5	Projeto de Assentamento Walter Arce	9°48'0.46''S 67°51'26.95''W	681.05
6	Porto Acre private fragment	9°36'28.60''S 67°34'6.15''W	1072.34
7	Catuaba Experimental Farm	10°4'48.9''S 67°37'8.6''W	1282.42
8	Embrapa Acre	10°2'17.64''S 67°40'54.24''W	1871.17
9	Senador Guiomard private fragment	10°1'24.66''S 67°35'48.66''W	2894.77
10	Humaitá Reserve	9°45'15.2''S 67°39'44.9''W	3042.02

Supplementary material 2: Total abundance of EFN-bearing plant species and morphospecies registered in 10 forest fragments located in the state of Acre, Brazilian Amazon, between June 2016 and February 2017. The deposit number refers to the the voucher specimens that were deposited at the Herbário da Universidade Federal do Acre (UFACPZ).

Family	Plant species	Abundance	Deposit number	Species analyzed in this study
Bignoniaceae	*Fridericia* sp. 1	1	A29360	-
	Fridericia sp. 2	20	A29479	X
	Fridericia sp. 3	7	A29478	X
	Fridericia sp. 4	2	A29338	-
	Fridericia sp. 5	10	A29477	X
	Fridericia sp. 6	5	A29372	-
	Fridericia sp. 7	4	A29353	-
	Fridericia sp. 8	30	A29476	X
	Fridericia sp. 9	4	A29389	-
	Fridericia sp. 10	1	A29388	-
	Fridericia sp. 11	3	A29396	-
	Fridericia sp. 12	3	A29352	-
	Fridericia sp. 13	6	A29409	-
	Fridericia sp. 14	2	A29387	-
	Fridericia sp. 15	2	A29395	-
	Fridericia sp. 16	4	A29351	-
	Fridericia sp. 17	2	A29397	-
	Fridericia sp. 18	1	A29394	-
	Fridericia sp. 19	8	A29475	X
	Fridericia sp. 20	2	A29408	-
	Fridericia sp. 21	3	A29375	-
	Fridericia sp. 22	1	A29366	-
	Fridericia sp. 23	1	A29344	-
	Fridericia sp. 24	2	A29345	-
	Fridericia sp. 25	1	A29374	-
	Fridericia sp. 26	4	A29407	-
	Fridericia sp. 27	1	A29373	-
	Fridericia sp. 28	1	A29406	-
	Fridericia sp. 29	1	A29343	-
	Fridericia sp. 30	1	A29337	-
	Fridericia sp. 31	3	A29474	X
	Fridericia sp. 32	3	A29371	-
	Fridericia sp. 33	1	A29380	-
	Fridericia sp. 34	1	A29342	-
	Fridericia sp. 35	6	A29473	X
	Memora sp. 1	1	A29386	-
	Memora sp. 2	6	A29472	X
	Memora sp. 3	1	A29471	X
Chrysobalanaceae	Chrysobalanaceae sp.	1	A29468	X
	Hirtella racemosa Lam.	16	A29469	X
	Hirtella sp.	2	A29470	X

Supplementary material 2: Continuation.

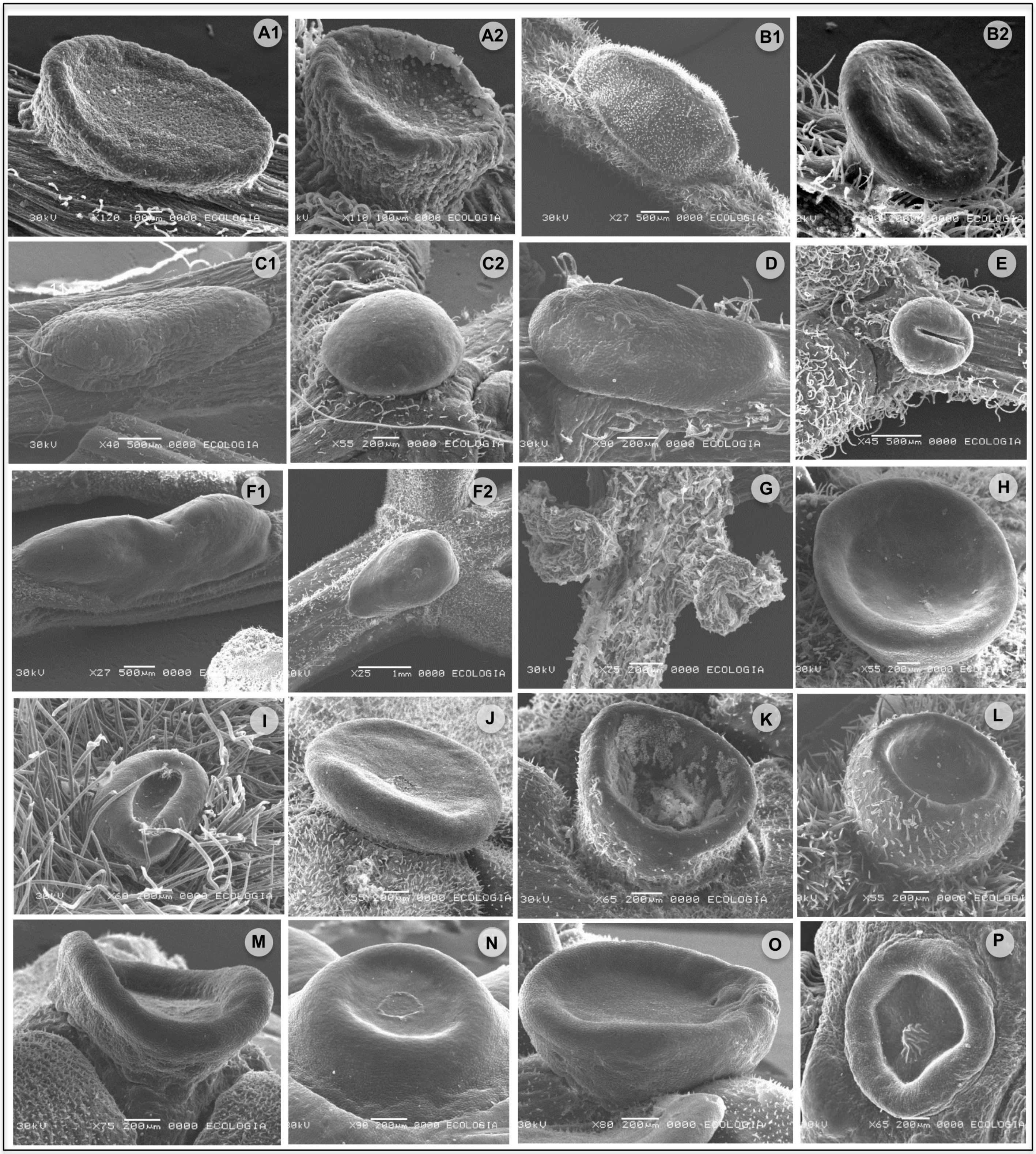
Family	Plant species	Abundance	Deposit number	Species analyzed in this study
Convolvulaceae	*Ipomoea philomega* (Vell.) House	1	A29467	X
	Ipomoea regnellii Meisn.	1	A29466	X
Costaceae	*Costus scaber* Ruiz & Pav.	6	A29465	X
Cucurbitaceae	Cucurbitaceae sp.	1	A29411	-
	Gurania sp.	2	A29464	X
Euphorbiaceae	*Acalypha* sp.	4	A29354	-
	Aparisthmium cordatum (A. Juss.) Baill.	10	A29463	X
	Dalechampia sp.	1	A29462	X
	Omphalea diandra L.	6	A29461	X
Fabaceae	*Bauhinia* sp. 1	99	A29460	X
	Bauhinia sp. 2	1	A29367	-
	Bauhinia sp. 3	1	A29398	-
	Bauhinia sp. 4	3	A29368	-
	Bauhinia sp. 5	1	A29376	-
	Bauhinia sp. 6	2	A29399	-
	Centrosema sp. 1	3	A29362	-
	Centrosema sp. 2	2	A29361	-
	Centrosema sp. 3	2	A29412	-
	Erythrina sp.	3	A29459	X
	Fabaceae sp.	4	A29410	-
	Inga acreana Harms	2	A29458	X
	Inga alba (Sw.) Willd.	6	A29457	X
	Inga calantha Ducke	2	A29456	X
	Inga capitata Desv.	4	A29455	X
	Inga chartacea Poepp.	3	A29454	X
	Inga densiflora Benth.	6	A29453	X
	Inga edulis Mart.	6	A29452	X
	Inga heterophylla Willd.	1	A29451	X
	Inga lateriflora Miq.	10	A29450	X
	Inga laurina (Sw.) Willd.	18	A29449	X
	Inga microcoma Harms	1	A29448	X
	Inga punctata Willd.	6	A29447	X
	Inga sertulifera DC.	8	A29446	X
	Inga suaveolens Ducke	1	A29445	X
	Inga tenuistipula Ducke	7	A29444	X
	Inga sp. 1	1	A29391	-
	Inga sp. 2	2	A29349	-
	Inga sp. 3	3	A29359	-
	Inga sp. 4	5	A29443	X
	Inga sp. 5	15	A29442	X
	Inga sp. 6	1	A29336	-

Supplementary material 2: Continuation.

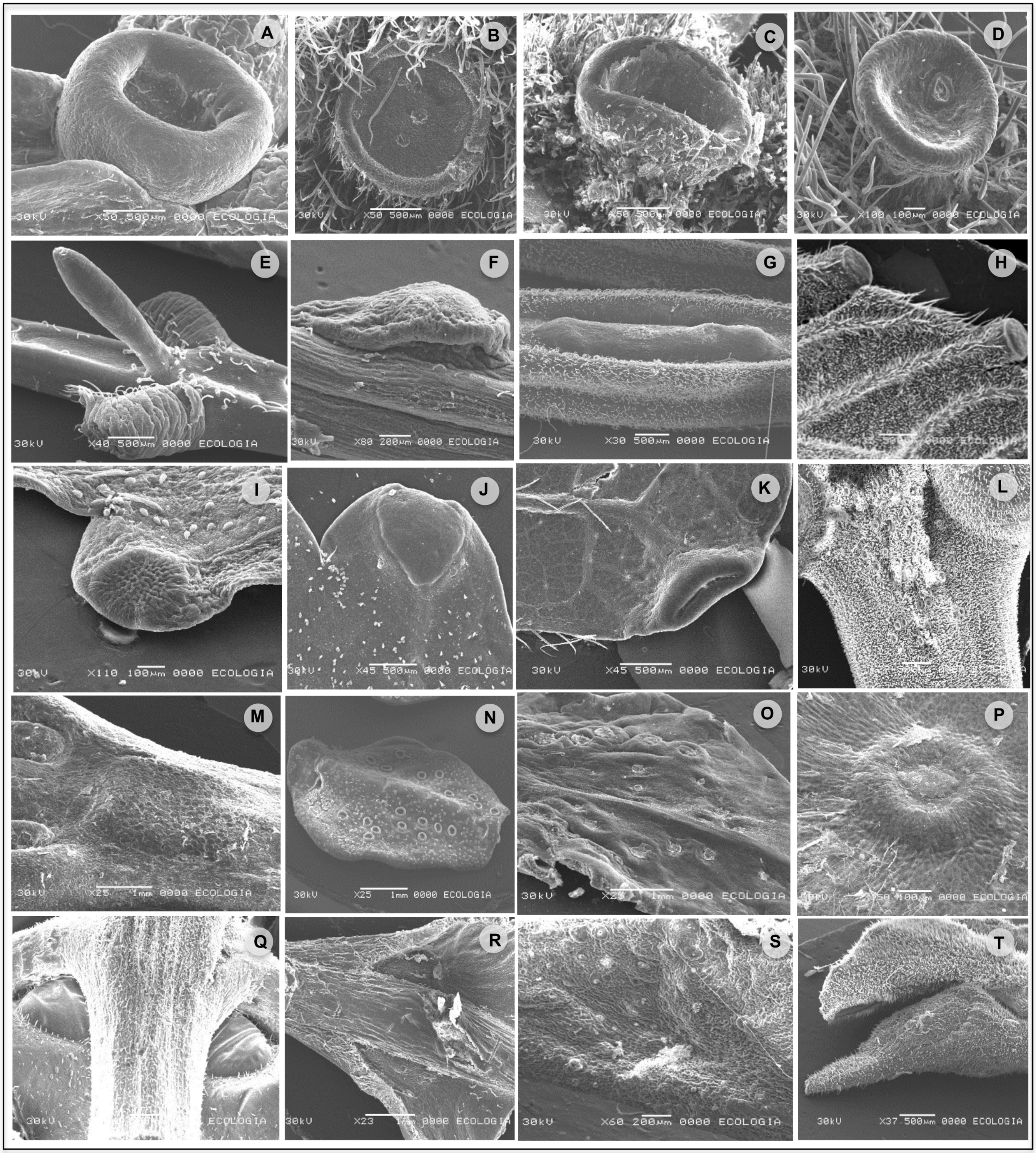
Family	Plant species	Abundance	Deposit number	Species analyzed in this study
Fabaceae	*Inga* sp. 7	3	A29403	-
	Inga sp. 9	3	A29350	-
	Inga sp. 10	2	A29370	-
	Inga sp. 12	2	A29365	-
	Inga sp. 13	2	A29364	-
	Inga sp. 14	3	A29405	-
	Inga sp. 15	1	A29379	-
	Inga sp. 16	3	A29404	-
	Inga sp. 18	1	A29393	-
	Inga sp. 20	1	A29392	-
	Senegalia sp. 1	16	A29441	X
	Senegalia sp. 2	41	A29440	X
	Senegalia sp. 3	21	A29439	X
	Senegalia sp. 4	16	A29438	X
	Senegalia sp. 5	1	A29355	-
	Senegalia sp. 6	1	A29348	-
	Senegalia sp. 7	7	A29437	X
	Senegalia sp. 8	15	A29436	X
	Senegalia sp. 9	1	A29382	-
	Senna sp.	1	A29435	X
	Zygia sp. 1	6	A29434	X
	Zygia sp. 2	3	A29433	X
	Zygia sp. 3	1	A29432	X
	Zygia sp. 4	1	A29378	-
Lecythidaceae	*Gustavia augusta* L.	4	A29341	-
	Lecythidaceae sp.	3	A29431	X
Malpighiaceae	*Banisteriopsis* sp. 1	4	A29401	-
	Banisteriopsis sp. 2	95	A29430	X
	Banisteriopsis sp. 3	4	A29400	-
	Banisteriopsis sp. 4	2	A29381	-
	Banisteriopsis sp. 5	10	A29429	X
	Banisteriopsis sp. 6	3	A29347	-
	Banisteriopsis sp. 7	1	A29346	-
	Banisteriopsis sp. 8	1	A29339	-
	Heteropterys sp.	3	A29428	X
	Tetrapterys sp.	7	A29427	X
Malvaceae	*Byttneria benensis* Britton	6	A29426	X
Menispermaceae	*Abuta* sp. 1	1	A29425	X
	Abuta sp. 2	1	A29377	-
Ochnaceae	*Ouratea* sp.	5	A29424	X
Olacaceae	*Olacaceae* sp.	7	A29423	X
Passifloraceae	*Dilkea* sp.	1	A29422	X
	Passiflora coccinea Aubl.	3	A29421	X

Supplementary material 2: Continuation.

Family	Plant species	Abundance	Deposit number	Species analyzed in this study
Passifloraceae	*Passiflora* sp. 1	1	A29385	-
	Passiflora sp. 2	1	A29358	-
	Passiflora sp. 3	1	A29420	X
	Passiflora sp. 4	1	A29369	-
Rhamnaceae	*Gouania* sp.	1	A29419	X
Rubiaceae	*Tocoyena* sp.	1	A29402	-
	Palicourea sp.	26	A29335	-
Sapindaceae	*Paullinia* sp. 1	3	A29418	X
	Paullinia sp. 2	6	A29417	X
	Paullinia sp. 3	3	A29384	-
	Paullinia sp. 5	1	A29383	-
	Paullinia sp. 6	1	A29416	X
	Serjania clematidea Triana & Plach.	4	A29333	-
Solanaceae	*Solanum* sp.	1	A29415	X
Vitaceae	*Cissus* sp.	1	A29414	X
Vochysiaceae	*Qualea grandiflora* Mart.	4	A29413	X
	Volchysia sp.	1	A29390	-



Supplementary material 3: Elevated extrafloral nectaries (EFNs): A1-A2. *Senegalia* sp. 1; B1-B2. *Senegalia* sp. 2; C1-C2. *Senegalia* sp. 3; D. *Senegalia* sp. 4; E. *Senegalia* sp. 7; F1-F2. *Bauhinia* sp. 1; G. *Erythrina* sp.; H. *Inga alba* (Sw.) Willd.; I. *Inga calantha* Ducke; J. *Inga capitata* Desv.; K. *Inga chartacea* Poepp.; L. *Inga edulis* Mart.; M. *Inga lateriflora* Miq.; N. *Inga laurina* (Sw.) Willd.; O. *Inga microcoma* Harms; P. *Inga sertulifera* DC.



Supplementary material 4: Elevated extrafloral nectaries (EFNs): A. *Inga suaveolens* Ducke; B. *Inga tenuistipula* Ducke; C. *Inga* sp. 4; D. *Inga* sp. 5; E. *Senna* sp.; F. *Zygia* sp. 2; G. *Zygia* sp. 3; H. *Paullinia* sp. 2; I. *Paullinia* sp. 6; J. *Cissus* sp.; K. Chrysobalanaceae sp. Flattened extrafloral nectaries (EFNs): L. *Fridericia* sp. 8; M. *Fridericia* sp. 35; N. *Fridericia* sp. 3; O. *Fridericia* sp. 19; P. *Hirtella racemosa* Lam. (SM4P); Q. *Aparisthmium cordatum* (A. Juss.) Baill.; R. *Tetrapterys* sp. Formless extrafloral nectaries (EFNs): S. *Ipomoea philomega* (Vell.) House; T. *Passiflora* sp. 3.