Ensaios e Ciência
ISSN 1415-6938 e ISSN 2178-695X

DOI: 10.17921/1415-6938.2025v29n2p487-504

Generalization *Versus* Specialization in Plant Pollination Systems: What do Floral Visitors Tell us?

Especialização Floral *Versus* Generalização: o que os Visitantes nos Dizem a Respeito?

Leandro Pereira Polatto: Universidade Estadual Paulista, UNESP, Instituto de Biociências, Rio Claro, São Paulo, Brazil. *E-mail: lppolatto@gmail.com

Paulo Roberto de Abreu Tavares: Universidade Estadual de Mato Grosso do Sul, UEMS, Unidade Universitária de Ivinhema, Ivinhema, Mato Grosso do Sul, Brazil.

Glaucia Almeida de Morais: Universidade Estadual de Mato Grosso do Sul, UEMS, Unidade Universitária de Ivinhema, Ivinhema, Mato Grosso do Sul, Brazil.

Jessica Amaral Henrique: Universidade Federal da Grande Dourados, UFGD, Faculdade de Ciências Biológicas e Ambientais, Dourados, Mato Grosso do Sul, Brazil.

Valter Vieira Alves Junior: Universidade Federal da Grande Dourados, UFGD, Faculdade de Ciências Biológicas e Ambientais, Dourados, Mato Grosso do Sul, Brazil.

Received on: 14/02/2025
Accepted on: 03/06/2025

Abstract

Floral traits may either facilitate or constrain the gathering of food resources by certain animals. We sought to define the specialization versus generalization levels in the pollination system in plant species with high floral provision and visited by foraging insects. We therefore hypothesized that in the plant-floral visitor interaction networks there is a gradient continuum of floral specializations in a plant community, from highly generalist to fully specialized species. The species studied had eight types of flowers (dish, gullet, capitulum, dish with oil-secreting glands, dish with poricidal anthers, brush, tubular, and transition between open and deep polypetalous), and showed a continuum of pollination systems, from the more specialized levels to the most generalized. The most specialized species were visited predominantly by functional groups of efficient pollinators, whereas the most generalist species received visitors of four or five functional groups, but they did not act as efficient pollinators. In the more generalist species, it was not possible to characterize the floral visitors as pollen vectors or thieves/pillagers of resources. The parts of the insect bodies that transfer pollen to the floral stigmas can be grouped into five regions: dorsal of the thorax, ventral of the thorax and abdomen, frontal of the head, and the tibia and dorsal region of the abdomen. Plants evidencing even the highest levels of floral specialization can nonetheless be visited by floral resource thieves and/or robbers – floral specialization is not capable of eliminating floral visitors prejudicial to plant reproduction.

Keywords: Floral Shape. Foraging Behavior. Pollen Transfer. Resource Theft/Looting.

Resumo

Características florais podem facilitar ou restringir a coleta de recursos alimentares por certos animais. Buscamos definir os níveis de especialização versus generalização no sistema de polinização em espécies de plantas com elevada disposição floral e visitadas por insetos. Portanto, levantamos a hipótese que nas redes de interação planta-visitante floral há um contínuo de especializações florais em uma comunidade vegetal, de espécies altamente generalistas para espécies totalmente especializadas. As espécies estudadas tinham oito tipos de flores (disco, goela, capítulo, disco com glândulas secretoras de óleo, disco com anteras poricidas, pincel, tubulares e transição entre polipétalas abertas e profundas) e mostraram um contínuo de sistemas de polinização, dos níveis mais especializados aos mais generalizados. As espécies mais especializadas foram visitadas predominantemente por grupos funcionais de polinizadores eficientes, enquanto as espécies mais generalistas receberam visitantes de quatro ou cinco grupos funcionais, mas não agiram como polinizadores eficientes. Nas espécies mais generalistas não foi possível definir se os visitantes florais eram vetores de pólen ou furtadores/pilhadores de recursos. As partes dos corpos dos insetos que transferem pólen para os estigmas florais puderam ser agrupadas em cinco regiões: dorsal do tórax, ventral do tórax e abdômen, frontal da cabeça e a tíbia e região dorsal do abdômen. As plantas que evidenciam os níveis mais elevados de especialização floral podem, no entanto, ser visitadas por furtadores e/ou pilhadores de recursos florais – indicando que a especialização floral em si não é capaz de eliminar visitantes florais prejudiciais à reprodução das plantas.

Palavras-chave: Formato Floral. Comportamento de Forrageamento. Transferência de Pólen. Furto/Pilhagem de Recursos.

1 Introduction

The field of pollination biology recognizes interactions between plants and their pollinators as reflecting the convergence of floral attributes in response to pressure exerted by their pollinators (Fenster *et al.*, 2004; Dellinger, 2020). When considered within an evolutionary framework, floral specialization is considered to have induced the appearance of specific floral phenotypes through strong relationships with a particular functional group of pollinators (the set of visiting species that utilize the same floral resource in a similar manner) – thus generating a series of pollination syndromes (Faegri; Van der Pijl, 1979; Torezan-Silingardi; Silberbauer-Gottsberger; Gottsberger, 2021). Essentially, a specific pollination syndrome is defined as a set of floral attributes associated with the attraction and visitation of specific sets of animals as pollinators (Fenster *et al.*, 2004; Dellinger, 2020).

Pollination syndromes have been established as a way of examining patterns of convergent evolution among unrelated plants, but they are not substitutes for field observations (Johnson; Steiner, 2000; Assis, 2023), as they do not represent precise nor infallible indicators (Watts *et al.*, 2016; Wang *et al.*, 2020; Hilpman; Busch, 2021). Field studies become even more important when examining landscapes with histories of environmental degradation, such as the forest fragment used to develop this research. Under these conditions, the diversity of floral visitors and the size of their populations may change due to negative impacts to their trophic and nidification niches (among other factors) (Kearns; Inouye; Waser, 1998).

Many plants, however, do not demonstrate specific relationships with specific types of pollinators (Waser *et al.*, 1996; Ollerton *et al.*, 2009), with their interactions tending to reflect certain degrees of generalization. Those plants can be visited by various functional groups of pollinators that nonetheless promote successful reproduction (Armbruster, 2006; Waser; Ollerton, 2006). It is important to mention that the term floral generalization has several definitions, being the botanical (plant species whose flowers have floral resources that are freely accessible to any visitor) and the ecological (ability to provide pollination services with more or less equal efficiency by any floral visitor that forages its flowers) are the two most common definitions (Ollerton *et al*., 2007). Here, to define specialization versus generalization, the ecological definition is used.

Plant species evidencing generalized pollination systems are commonly observed to demonstrate high reproduction rates in degraded environments even in the absence of specific pollinator species (Bond, 1994; Ramirez, 2004). There is growing concern about the alterations humans impose on natural ecosystems, and their effects on pollination systems are generally not known (Bond, 1994; Kearns *et al.*, 1998) – although specialized plants that depend on very few specific pollinator species will almost certainly be most vulnerable. Plants with more generalized pollination systems, however, can often overcome the loss of many pollinator species (Bond, 1994; Bergamo *et al.*, 2021).

However, the floral structure for specialization versus generalization is difficult to measure experimentally, given that secondary pollinators are not excluded by pollination syndromes (Rosas-Guerrero *et al.*, 2014). What then are the factors that have influenced the evolution of floral specialization? Johnson and Steiner (2000) enumerated some of the principal mechanisms behind the evolution of floral specialization: the life histories of those plants, the occurrence of those plants in relation to the degree of environmental alteration, their abundances, and their types of reproductive system. Long-lived plants (especially perennial species or those that demonstrate vegetative reproduction) are more resistant to the risks of specialization (such as the absence of a specific pollinator for long periods of time). On the other hand, floral generalization is generally encountered among plants with short lifecycles (such as annual plants), as well as plants that depend on seeds for their continuous short-term reproduction (Waser *et al.*, 1996). Parra-Tabla and Arceo-Gómez (2021) concluded that floral generalization would be expected among invasive species, as they will flourish due to their high degree of reproductive insurance.

Flowers with specialized pollination systems tend to be pollinated by just a few efficient organisms, as compared to flowers with generalized pollination systems that normally receive larger numbers of visitors (principally low efficiency pollinators). Fenster *et al.* (2004) published a detailed review of effective pollinators, and concluded that successful pollination will depend on: (1) the proportion of visiting species that act as pollen vectors; (2) the frequency with which each of the visiting species enters into contact with the anthers and stigmas; (3) the frequency of visits that result in pollen deposition on the stigma; (4) numbers of pollen grains deposited per visit on the same flower and on the flowers that are subsequently visited (therefore favoring, or not, gene flow); (5) the quantities of pollen removed from the anthers and deposited on the stigmas; (6) fruit and seed production per visit by each of the visiting species considered; and, (7) intrinsic factors of the plant, such as pollen viability and the existence (or not) of self-compatibility.

The necessity of meticulous research must therefore be noted to be able to classify plants according to the levels of specialization of their pollination systems. Johnson and Steiner (2000) enumerated the principal criteria that should be evaluated, including: distinguishing a simple visitor from a pollen vector (an effective pollinator); quantifying the diversity of visitor species and then using the correct strategies to classify those visitors into functional groups; quantifying their different rates of visitation; and evaluating the pollination efficiency of each visiting organism. We therefore sought here to define the specialization versus generalization levels in the pollination system in plant species with high floral provision and visited by foraging insects. We hypothesized that in the plant-floral visitor interaction networks there is a gradient continuum of floral specializations in a plant community, from highly generalist to fully specialized species. To achieve the proposed objective, we attributed the levels of floral specialization to the presence or not of functional groups framed as pollinators, their proportions of visits to flowers, as well as the presence of other functional groups of floral visitors not framed as pollinators (see table 1).

2 Material and Methods

2.1 Characterizations of the study area and the plant species selected

The research presented here was undertaken within a fragment of secondary forest (covering approximately 355 hectares) located along the margins of the MS-395 highway in Mato Grosso do Sul State, Brazil, approximately 3 km from the city of Ivinhema (22°15’S, 53°48’W). Additional information concerning the area can be found in Polatto and Chaud-Netto (2013).

During the 12-month period between July/2010 and June/2011, we selected 19 plant species to study their levels of floral specialization. The choice of those plant species was based on their being susceptible to insect foraging and demonstrating high floral exposure (independent of their being pollinated by specific visitors, or not). The plant species that had a high floral exposure were those that had a high floral exhibition per plant and were represented by a high number of plants in the study area. Concomitantly, the plant species susceptible to insect foraging were those in which the ecological pressure exerted by the visitors in resource extraction was visually recorded. Collections were made of those plants and exsicates were incorporated into the herbarium at the Campus Universitário de Rio Claro (HRCB), at the Universidade Estadual Paulista – UNESP.

The floral shape of the plant species that was deemed essential for body adjustment to floral visitors were based on the proposals of Dafni (1992). Additional descriptions of the floral traits of the 19 plant species can be seen in Polatto *et al.* (2023).

2.2 Foraging by floral visitors

Floral visitors were observed on three plants of each of the 19 species during periods of high floral synchrony among the individuals of those populations (with from 76% to 100% of those plants flowering), following Morellato *et al.* (1990). Focal areas of from 1 to 3 m^2 having flowering branches of the selected species were chosen, and insect foraging behavior was accompanied by 20-minute intervals during each hour between 06:00 and 17:20 h for three non-consecutive days. The determination of an insect being an effective pollinator (or not), was based on the contact between insect´s body and flowers fertile parts. We simultaneously observed the intensity of foraging on the flowers per foraging flight, and if the foraging undertaken by the potential pollinator frequently involved visits to different plants of the same species – that being an important attribute for establishing the most probable pollination type (self-pollination or cross-pollination). This evaluation method, based exclusively on the flight activities of the pollinators to define pollination efficiency, is compatible with the techniques used by other researchers (Degen; Roubik, 2004; Hargreaves; Harder; Johnson, 2021; Richards, 1997; Roubik, 1989).

From 1 to 4 individuals of the different insect visitors to each plant species were captured using an insect net. Those specimens were sacrificed in a chamber containing ethyl acetate and stored in appropriately labeled 30 mL flasks. The entomological collections were subsequently sent to specialists for identification. The type of insect visitation to each flower was recorded according to the classification system proposed by Inouye (1980).

2.3 Degrees of floral specialization

The degrees of the plant species examined here were analyzed based on two attributes. The first criterium considered the numbers of functional groups of foraging insects visiting each plant species, using the classification system proposed by Robertson (1928). That author defined the following functional groups: long-tongued bees, short-tongued bees, other Hymenoptera, Diptera, Coleoptera, Lepidoptera and birds. The second criterium considered the efficiency of each functional group in pollinating the flowers of each plant species: effective pollinators, non-efficient pollinators, and non-pollinators. Among those pollinators considered effective, we considered the floral resource collected and the body region involved in pollen transfer to the stigmas of the flowers.

The definitions of the degrees of specialization of the pollination systems used here were based on the works of Faegri and Van der Pijl (1979), Waser *et al.* (1996), Aigner (2001) and Fenster *et al.* (2004) and Ollerton *et al.* (2007). The plant species were then grouped into five classes according to their degrees of floral specialization (Table 1).

1. Highly specialized. Plants whose flowers receive foraging visits of species predominately from a specific functional group. A functional visitor group was considered predominant if it represented >75% of the visitor species foraging on a specific plant species (Fenster et al., 2004). Additionally, the predominant functional group had to be composed of effective pollinators employing a specific behavioral technique to extract floral resource – that is, they had to be perfectly adequate to the floral shape. In these cases, only a specific body region of the pollinator enters into contact with the stigmas.

2. Specialized. The set of plant species pollinated by only a single functional group of effective pollinators, although those visitors were not predominant. Only a specific body region of that functional group of effective pollinators enters into contact with the stigmas of those flowers.

3. Intermediate. The set of plant species pollinated by one or more effective, but not predominant, functional pollinator groups. If there is only one functional pollinator group, it can demonstrate two or more behavioral techniques used to extract floral resources. If, on the other hand, there are two or more groups of functional pollinators, all of them will use only a single behavioral technique to extract floral resources.

4. Generalists. Plant species whose flowers are pollinated by visitors representing two or more non-predominant functional groups. All the visitors are considered non-efficient pollinators and, occasionally, some of the visits undertaken by them are considered instances of nectar theft or nectar robbing.

5. Highly generalist. Plants that produce flowers that are pollinated by organisms of any functional group with equal efficiency. It is usually impossible to determine if those visitors are pollinators or resource thieves, as their contact with the anthers and stigmas are merely casual. At least two or more functional groups of visitors would be present when foraging on the flowers of these plants.

Table 1 - Relationships between floral specialization and functional visitor groups

Characteristics of the floral Visitors	Degrees of Floral Specialization				
	Highly specialized	**Specialized**	**Intermediate**	**Generalists**	**Highly generalist**
Efficient pollinators: predominant functional group	Yes	No	No	Absent group	Absent group
Number of functional groups of efficient pollinators	1	1	1 or more	Absent group	Absent group
Number of foraging strategies of the efficient pollinator functional group	1	1	1 or more	Absent group	Absent group
Visiting pollinators also act as resource thieves and robbers	No	No	No	Yes	Yes
It is possible to characterize pollinators	Yes	Yes	Yes	Yes	No

Source: research data.

3 Results and Discussion

Five body regions of the floral visitors were identified as being involved in pollen transfer to the stigmas:

1. Dorsal region of the thorax - nototribic (Table 2, Figure 1). The gullet-shaped flowers of *Arrabidaea chica* (Bonpl.) Verl., *Arrabidaea florida* DC., *Cuspidaria convoluta* (Vell.) A.H.Gentry, and *Adenocalymma bracteatum* (Cham.) DC. (Bignoniaceae) were pollinated by pollen from this body region of the insects. For pollination to occur, the floral visitor has to be collecting nectar during legitimate floral visits (entering through the corolla mouth to gather nectar by suction) and must have sufficient body size to allow contact between the dorsal region of its thorax and the reproductive organs of the plant. To reach the nectar, the visiting insect must penetrate the corolla tube, and the dorsal region of its thorax must simultaneously touch the anthers and the stigmas. After foraging various flowers, the dorsal region of the insect's body can be seen to be stippled with pollen. The fruits of groups of plants of the same species demonstrate high proportions of seeds originating from cross-pollination, reflecting the high numbers of pollinating insects foraging on numerous different plants during a single outing. Visitors with body diameters smaller than the corolla tube opening, on the other hand, can retrieve nectar without touching the floral reproductive structures – characterizing nectar theft. Nectar robbing also frequently occurs, especially by *Oxaea flavescens* Klug (Apidae).

Table 2 - Floral adaptations of the plant species selected here in terms of their levels of pollinator specialization. Pollen transfer behavior to the stigmas of the flowers described in the first column refers exclusively to the functional insect group most adapted to pollinating each type of flower (description in italics in the final column)

<table>
<tr><th>Reward | Regions of pollen transfer to the stigma</th><th>Floral shape</th><th>Roman numerals: degrees of floral specialization of plant</th><th>Functional groups (Number of species) | Behavior | Number of foraging</th></tr>
<tr><td>Nectar and pollen | Frontal region of the head (Casual pollinator)</td><td>Dish</td><td>I. Matayba guianensis</td><td rowspan="3">Long-tongued bees (7) | Casual pollinator | 1210
Short-tongued bees (5) | Casual pollinator | 20
Other Hymenoptera (25) | Casual pollinator | 123
Diptera (10) | Casual pollinator | 294
Lepidoptera (8) | Casual pollinator | 317
Coleoptera (7) | Casual pollinator | 15</td></tr>
<tr><td>Nectar | Frontal region of the head (Casual pollinator)</td><td>Tubular</td><td>I. Aegiphilla sellowiana</td></tr>
<tr><td>Nectar and pollen | Frontal region of the head (Casual pollinator)
Nectar and pollen | Ventral region of the thorax and abdomen (Casual pollinator)
Pollen | Tibia (Casual pollinator)</td><td>Brush</td><td>I. Senegalia polyphylla, Senegalia sp.</td></tr>
<tr><td>Nectar and pollen | Frontal region of the head (Non-efficient pollinator)</td><td>Capitula</td><td>II. Eupatorium maximalianii, Eupatorium cf. dimorpholepis</td><td>Long-tongued bees (3) | Non-efficient pollinator | 404
Short-tongued bees (2) | Non-efficient pollinator | 4
Diptera (8) | Nectar thief | 103
Lepidoptera (18) | Nectar thief | 159</td></tr>
<tr><td>Nectar (Aves) | Frontal region of the head (Efficient pollinator)
Pollen | Tibia (long-tongued bees) (Efficient pollinator)</td><td>Tubular</td><td>III. Pyrostegia venusta</td><td>Long-tongued bees (3) | Efficient pollinator | 169
Short-tongued bees (3) | Nectar and pollen thief | 10
Aves (2) | Efficient pollinator | Not quantified</td></tr>
<tr><td rowspan="2">Nectar and pollen | Frontal region of the head (Efficient pollinator)</td><td>Dish</td><td>III. Gouania cf. latifolia</td><td rowspan="2">Long-tongued bees (3) | Efficient pollinator | 1105
Short-tongued bees (3) | Efficient pollinator | 28
Other Hymenoptera (7) | Efficient pollinator | 21
Diptera (9) | Nectar thief | 317
Lepidoptera (1) | Nectar thief | 9</td></tr>
<tr><td>Dish-polypetalous</td><td>III. Serjania caracasana</td></tr>
<tr><td>Nectar | Frontal region of the head (Efficient pollinator)
Pollen | Tibia (Efficient pollinator)</td><td>Capitula</td><td>III. Trixis antimenorrhoea</td><td>Long-tongued bees (1) | Efficient pollinator | 163
Lepidoptera (1) | Non-efficient pollinator | 3</td></tr>
<tr><td>Nectar | Nototribic (Efficient pollinator)</td><td>Gullet</td><td>IV. Arrabidaea chica, Adenocalymma bracteatum, Arrabidaea florida, Cuspidaria convoluta</td><td>Long-tongued bees (16) | Efficient pollinator | 309
Short-tongued bees (11) | Nectar thief or robber | 193
Other Hymenoptera (5) | Nectar thief | 29
Diptera (3) | Nectar thief | 120
Lepidoptera (8) | Nectar thief | 43</td></tr>
<tr><td>Pollen | Dorsal region of the abdomen (Efficient pollinator)</td><td>Dish-Poricidal anthers</td><td>V. Senna obtusifolia</td><td>Long-tongued bees (3) | Efficient pollinator | 22
Short-tongued bees (1) | Pollen robber | 14</td></tr>
<tr><td>Oil | Ventral region of the thorax and abdomen (Casual pollinator) (Efficient pollinator)</td><td>Dish</td><td>V. Diplopterys pubipetala, Banisteriopsis cf. campestris, Banisteriopsis laevifolia, Byrsonima intermedia</td><td>Long-tongued bees (14) | Efficient pollinator | 511
Short-tongued bees (1) | Casual pollinator | 4</td></tr>
</table>

I. Highly generalist; II. Generalists; III. Intermediate; IV. Specialized; V. Highly specialized.
Source: research data.

Figure 1 - Flowers evidencing pollen on the stigma that was transferred from the "dorsal region of the thorax" of the pollinators during the act of nectar suction. Illustration clearly shows a pollen load adhering to the thorax of a worker bee of *Apis mellifera* Linnaeus (Apidae). Photograph *a* and *b* – *Arrabidaea florida* DC

Source: research data.

2. Ventral region of the thorax and abdomen (Table 2, Figure 2). This type of pollination was especially observed among Malpighiaceae species (*Diplopterys pubipetala* (A.Juss.) W.R.Anderson & C.C.Davis, *Byrsonima intermedia* A.Juss., *Banisteriopsis cf. campestris* (A.Juss.) Little, and *Banisteriopsis laevifolia* (A.Juss.) B.Gates), as they evidenced typically open floral forms; it was also seen in species with brush -shaped flowers [*Senegalia polyphylla* (DC.) Britton & Rose and *Senegalia* sp. (Fabaceae)]. The ventral surfaces of the thoraxes and abdomens of the bees will be strongly pressed against the anthers and stigmas of Malpighiaceae species as they attempt to extract oils with their anterior and median legs. As the stigmas are located very near the anthers, pollen is frequently deposited on the bees during foraging. Cross pollination is therefore very common in those species, as insect pollinators were observed visiting numerous different plants before completing their oil caches and returning to their nests. Among plants that produce brush-shaped flowers, on the other hand, the simple contact of the ventral portions of the thorax or abdomen with the anthers and stigmas and can result in successful pollination. The production of large numbers of flowers by those two species will tend to favor endogamic pollination.

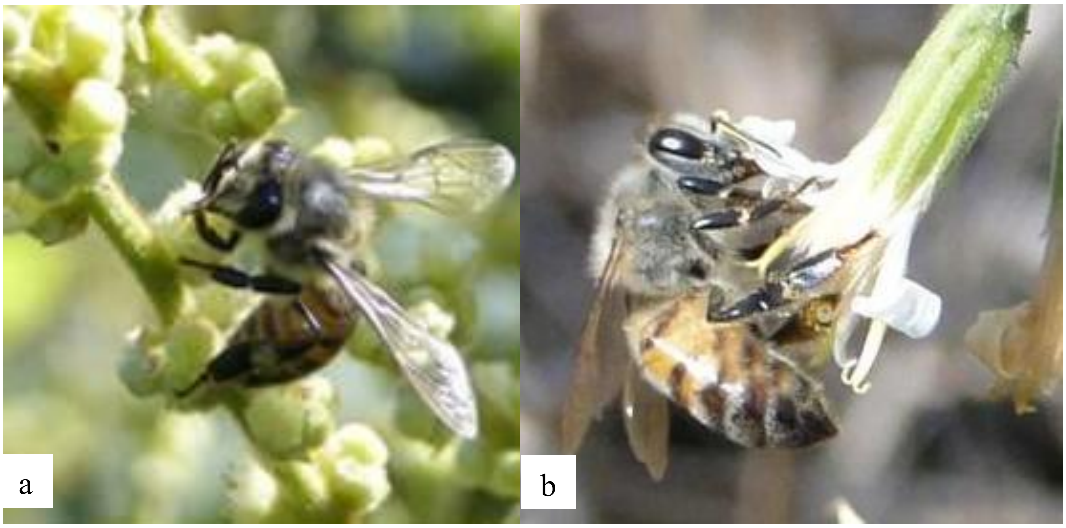
Figure 2 - Flowers evidencing pollen on the stigma that was transferred from the "ventral regions of the thorax and abdomen" of the pollinators during the act of collecting oil, pollen, or nectar. Photograph *a* – *Byrsonima intermedia* A.Juss. (Malpighiaceae) and *b* – *Senegalia* sp. (Fabaceae)

Source: research data.

3. Frontal region of the head (Table 2, Figure 3). We did not observe a basic pattern of floral shape associated with pollination effected by visitors that use their mouthpieces to extract floral resources. Pollination occurs in this way in open, brush-shaped, tubular, polypetalous, and capitular-type flowers. When the resource collected is nectar (Online Resource – Fig. 3), the frontal portion of the pollinators' heads constantly enter contact with the anthers, and pollen grains will adhere to that part of their bodies. While foraging on different flowers, the pollen-impregnated body structures of those insects will enter into contact with the stigma and deposit part of the pollen load onto those reproductive organs, thus affecting pollination. If the resource collected is pollen (Online Resource – Fig. 4), the pollen-impregnated heads of those bees will enter direct contact with the stigmas of the flowers. That type of pollination is possible because some pollen collection techniques using mouth parts can deposit material onto other body parts (such as the tibias of their hind legs), and the quantities of pollen transported in these cases will be related to the size of those agents. Large bees tend to forage on two or more plants to complete their pollen loads – thus promoting cross-pollination. Small bees and other functional pollinator groups, however, carry lesser volumes of resources and their foraging is usually limited to a single plant.

4. Tibia (Table 2, Figure 4). This type of pollination has exclusively been developed by bees of the Apidae family that deposit the collected pollen in corbicula (scopa). There is therefore no requirement for the anthers and/or stigmas to be located near each other, because large quantities of pollen are naturally deposited on the stigma as those bees scramble over the reproductive organs while transporting their pollen loads.

Figure 3 - Flowers evidencing pollen on the stigma that was transferred from the "frontal region of the head" of the pollinators during the act of nectar suction. Photograph *a* – *Gouania* cf. *latifolia* Reissek (Rhamnaceae) and *b* – *Trixis antimenorrhoea* (Schrank) Kuntze (Asteraceae)



Source: research data.

Figure 4- Flowers evidencing pollen on the stigma that was transferred from the "tibias" of pollinators during pollen collection. Photograph *a* – *Trixis antimenorrhoea* (Schrank) Kuntze (Asteraceae) (Asteraceae) and *b* – *Senegalia* sp. (Fabaceae)

Source: research data.

5. Dorsal region of the abdomen (Table 2, Figure 5). Bees with the ability to buzz the floral anthers have their entire bodies covered with pollen grains – a method of pollen extraction that was only observed here with *Senna obtusifolia* (L.) H.S.Irwin & Barneby (Fabaceae). The upper region of the abdomen of those bees then generally come into contact with the stigma of the flower.

Figure 5 - Pollen on the stigma that was transferred from the "dorsal region of the abdomen" during pollen collection from poricidal anthers. Photograph – *Senna obtusifolia* (L.) H.S.Irwin & Barneby (Fabaceae)

Source: research data.

As those plants produce few flowers, and in light of the elevated demand for that resource (as those bees are quite large – especially the genera *Bombus* and *Xylocopa*, with total lengths >14 mm and thorax diameters of 6 mm [Roubik, 1989]), cross-pollination probably occurs much more frequently in *S. obtusifolia* than in any other plant species examined in the present study.

Among the various insect functional groups examined here, the largest number of foraging events were carried out by long-tongued bees. That same functional group was also responsible for the greatest success of pollen transport to the floral stigmas. The other foraging behaviors were characterized as robbing or theft of floral resources (nectar, pollen, or oils) (Table 2).

Four floral specialization levels were observed among most of the plant species classified as evidencing highly specialized pollination; generalist systems were observed in only two plant species (Table 2).

The flowers of generalist and highly generalist plants were pollinated by four or five functional insect groups considered casual or inefficient pollinators (Table 2). The plant species *Matayba guianensis* Aubl. (Sapindaceae), for example, was foraged on by 28 different visitor species (five functional groups), with all of them being classified as casual pollen vectors.

Only small quantities of pollen remained adhered to their bodies, and when they perchance contacted the floral stigmas, only very reduced volumes of pollen grains became deposited. Although generalist flowers evidence low levels of pollination efficiency, it was generally possible to characterize an insect as a pollinating species, even though they did not demonstrate any notable efficiency at transferring pollen to the stigmas (Table 2).

Specialist and highly specialized plant species, on the other hand, evidenced visitation by only a few pollinators that shared very similar body shapes. The efficient deposition of pollen grains on the stigmas of Malpighiaceae species and on *S. obtusifolia* flowers involved only one type of pollinator and has established as a single unique behavioral technique (Table 2). The flowers of *B. laevifolia*, for example, were only pollinated by four bee species of the Centridini and Tapinotaspidini tribes. Visitors to those flowers were bees belonging to the Centridini, Tapinotaspidini, and Tetrapediini tribes.

Floral specialization generally requires the effective pollinator to develop predominant stereotyped behavior to obtain the floral resource produced (Waddington, 1983). There is a greater possibility of a plant demonstrating floral specialization when there is a strong difference in the reward received by an effective pollinator as opposed to a non-efficient or casual pollinator. Although there is little information available concerning how non-efficient pollinators effect the reproductive capacities of plants with specialized flowers, it is generally assumed that those interactions produce negative effects (Thomson; Thomson, 1992). Intense visitation by non-efficient foragers (those that extract large quantities of pollen, but only deposit small quantities of the same on the plant stigmas) reduce potential rewards to effective pollinators (those that extract large quantities of pollen but deposit large quantities of xenogamic pollen on the stigmas) as pollen is a limited resource (Aigner, 2001; Hargreaves; Harder; Johnson, 2009). In those situations, floral visitors that are not effective pollinators can provoke more negative than beneficial effects (Ashman *et al.*, 2004).

Plants do not always evidence floral specialization for a given type of pollinator, however (Aigner, 2001). Generalist flowers are frequently visited by casual pollinators belonging to various functional groups, each of which demonstrates, or not, specific foraging and pollen deposition behaviors on the floral stigma (Gomez, 2002). The quantities of the pollen deposited on the stigmas by casual pollinator appear low, however, due to the lack of adjustment between those vectors and the flower. That situation therefore probably requires greater numbers of visits to assure an adequate deposition of pollen on the stigmas for fruit formation.

There are a number of additional behavioral techniques demonstrated by floral visitors that generally do not benefit flowers through pollination, although they are not considered cases of floral resource thieving or robbing (see Inouye, 1980). A floral visitor that engages in the theft of floral resources will enter through the same access point as a legitimate pollinator, but the incompatibility between the morphological structures of that visitor and the flower itself will frequently frustrate the possibility of pollination (Inouye, 1980). That same author reported that a resource thief visitor might accidentally pollinate a flower if any part of its body carrying pollen contacts the floral stigma. Among plant species with highly generalist flowers, essentially all of its visitors could be considered resource thieves in light of the arguments presented by Hargreaves *et al.* (2009) and Polatto *et al.* (2012). Resource thieves represent the most inefficient animals for assuring cross-pollination, although they can occasionally deposit small pollen loads on the stigmas of flowers of other plants of the same species (and consequently effect pollination). As such, it has been suggested that casual pollen vectors should be considered apart, as they may act as pollinators or resource thieves depending on their position within the flower during resource collection.

The hypothesis therefore arises that plant species with specialized flowers and with effective pollinators present in their habitats, would experience more negative impacts due to the foraging of non-efficient or casual pollinators. When efficient pollinators (medium or large sized bees) forage on flowers that were previously visited by non-efficient or casual pollinators, the presumed pollination efficiencies of those large bees would be drastically reduced as a result of the limited pollen loads attached to their thoraxes. It seems that *C. convoluta*, however, depends on non-efficient pollinators to fecundate their flowers – as they demonstrate very little apparent selectivity for efficient pollinators. That fact may explain the low natural fruiting rate observed in *C. convoluta* as compared to other plants with gullet-shaped flowers (Polatto, 2020). Even though the widely observed diversity of flower shapes is usually explained through traditional hypotheses related to co-evolutionary relationships between angiosperms and their pollinators [from Darwin (1862) to recent times (Dellinger, 2020)], it is clear that a wide range of floral visitors are not especially adapted to pollinating specific angiosperms (Maloof; Inouye, 2000; Dedej; Delaplane, 2004).

4 Conclusion

Descriptive evaluations of floral attributes and the foraging techniques used by floral visitors were sufficient to define the specialization levels of the flowers examined here. Plants with highly specialized flowers are forged principally by effective pollinators that use only a single resource collection technique. On the other hand, all of the floral visitors that forage on highly generalist flowers can act as occasional pollinators during some of their visits – but as resource thieves during subsequent visits – as there are no adequate adjustments between the bodies of those animals and the reproductive organs of those plants. Plants evidencing even the highest levels of floral specialization can nonetheless be visited by floral resource thieves and/or robbers – indicating that floral specialization in itself is not capable of eliminating floral visitors prejudicial to plant reproduction.

Acknowledgments
Authors wish to express their sincere thanks to the technician Daniela de Oliveira Dinato and Prof. Dr. Júlio Antonio Lombardi, both from Botany Department of the Institute of Biosciences of Rio Claro/UNESP, for identifying the plant species and preparing the exsiccates for deposit into the Herbarium of Rio Claro.

References

AIGNER, P.A. Optimality modeling and fitness trade-offs: when should plants become pollinator specialists? Oikos, v.95, n.1, p.177-184, 2001. doi: https://doi.org/10.1034/j.1600-0706.2001.950121.x

ARMBRUSTER, W.S. Evolutionary and ecological aspects of specialized pollination: views from the Arctic to the Tropics. In: WASER, N.M.; OLLERTON, J. (Ed.). Plant-pollinator interactions: from specialization to generalization. Chicago: University of Chicago Press, 2006. p.260-282.

ASHMAN, T.L. et al. Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. Ecology, v.85, n.9, p.2408-2421, 2004. doi: https://doi.org/10.1890/03-8024

ASSIS, L. C. S. Pollination syndromes and the origins of floral traits. Ann. Bot., 147, 2023. doi: https://doi.org/10.1093/aob/mcad147

BERGAMO, P.J. et al. Pollination generalization and reproductive assurance by selfing in a tropical montane ecosystem. Sci. Nat., v.108, n.50, 2021. doi: https://doi.org/10.6084/m9.figshare.16777729

BOND, W. J. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philos. Trans. Royal Soc. London. v.344, n.1307, p.83-90, 1994. doi: https://doi.org/10.1098/rstb.1994.0055

DAFNI, A. Pollination ecology: a practical approach. Oxford: Oxford University Press, 1992.

DARWIN, C. On the various contrivances by which British and foreign orchids are fertilized by insects. London: John Murray, 1862.

DEDEJ, S.; DELAPLANE, K.S. Nectar-robbing carpenter bees reduce seed-setting capability of honey bees (Hymenoptera: Apidae) in rabbiteye blueberry, *Vaccinium ashei*,'climax'. Environ. Entomol., v.33, n.1, p.100-106, 2004. doi: https://doi.org/10.1603/0046-225X-33.1.100

DEGEN, B.; ROUBIK, D.W. Effects of animal pollination on pollen dispersal, selfing, and effective population size of tropical trees: a simulation study. Biotropica, v.36, n.2, p.165-179, 2004. doi: https://doi.org/10.1111/j.1744-7429.2004.tb00309.x

DELLINGER, A.S. Pollination syndromes in the 21 st century: where do we stand and where may we go? New Phytol., v. 228, n. 4, p. 1193-1213, 2020. doi: https://doi.org/10.1111/nph.16793

FAEGRI, K.; VAN DER PIJL, L. The principles of pollination ecology. London: Pergamon Press, 1979.

FENSTER, C.B. et al. Pollination syndromes and floral specialization. Ann. Rev Ecol. Evol. Syst., v.35, p.375-403, 2004. doi: https://doi.org/10.1146/annurev.ecolsys.34.011802.132347

GOMEZ J. M. Generalizations in the interactions between plants and pollinators. Rev Chilena Hist. Nat., v.75, n.1, p.105-116, 2002.

HARGREAVES, A.L.; HARDER, L.D.; JOHNSON, S.D. Consumptive emasculation: the ecological and evolutionary consequences of pollen theft. Biol. Rev, v.84, n.2, p.259-276, 2009. doi: https://doi.org/10.1111/j.1469-185X.2008.00074.x

HASEGAWA, T.M.; MAKINO, T.T.; SAKAI, S. Optimal pollen stickiness to pollinators for maximizing paternal fitness: increased number of recipient flowers or increased pollen deposition on recipient flowers? J. Theor. Biol., v.524, 2021. doi: https://doi.org/10.1016/j.jtbi.2021.110731

HILPMAN, E.T.; BUSCH, J.W. Floral traits differentiate pollination syndromes and species but fail to predict the identity of floral visitors to *Castilleja*. Am. J. Bot., v.108, n.11, p.2150-2161, 2021. doi: https://doi.org/10.1002/ajb2.1784

INOUYE, D.W. The terminology of floral larceny. Ecology, v.61, n.5, p.1251-1253, 1980. doi: https://doi.org/10.2307/1936841

JOHNSON, S.D.; STEINER, K.E. Generalization versus specialization in plant pollination systems. Trends Ecol. Evol., v.15, n.4, p.140-143, 2000. doi: https://doi.org/10.1016/S0169-5347(99)01811-X

KEARNS, C.A.; INOUYE, D.W.; WASER, N.M. Endangered mutualisms: the conservation of plant-pollinator interactions. Ann. Rev Ecol. Syst., v.29, p.83-112, 1998.

MALOOF, J.E.; INOUYE, D.W. Are nectar robbers cheaters or mutualists? Ecology, v. 81, n. 10, p. 2651-2661, 2000. doi: https://doi.org/10.1890/0012-9658(2000)081[2651:ANRCOM]2.0.CO;2

MORELLATO, L.P.C. et al. Estratégias fenológicas de espécies arbóreas em floresta de altitude na Serra do Japi, Jundiaí São Paulo. Rev. Bras. Biol., v.50, n.1, p.149-162, 1990.

OLLERTON, J. et al. The openness of a flower and its number of flower-visitor species. Taxon, v.56, n.3, p.717-728, 2007. doi: https://doi.org/10.2307/25065856

OLLERTON, J. et al. A global test of the pollination syndrome hypothesis. Ann. Bot., v.103, n.9, p.1471-1480, 2009. doi: https://doi.org/10.1093/aob/mcp031

PARRA-TABLA, V.; ARCEO-GÓMEZ, G. Impacts of plant invasions in native plant-pollinator networks. New Phytol., v.230, n.6, p.2117-2128, 2021. doi: https://doi.org/10.1111/nph.17339

POLATTO, L.P. Reprodução de plantas em um ecótono floresta Atlântica-Cerradão: dependência de agentes polinizadores. Biodiversidade, v.19, n.1, p.17-27, 2020.

POLATTO, L.P.; CHAUD-NETTO, J. Influence of *Apis mellifera* L. (Hymenoptera: Apidae) on the use of the most abundant and attractive floral resources in a plant community. Neotrop. Entomol., v.42, n.6, p.576-587, 2013. doi: https://doi.org/10.1007/s13744-013-0165-x

POLATTO, L.P. et al. Exploitation of floral resources on *Sparattosperma leucanthum* (Bignoniaceae): foraging activity of the pollinators and the nectar and pollen thieves. Acta Ethol., v.15, n.1, p.119-126, 2012. doi: https://doi.org/10.1007/s10211-011-0116-7

POLATTO, L.P. et al. Plantas intensamente forrageadas por abelhas em uma floresta estacional semidecidual: caracterização dos atributos florais. Acta Biol. Catarinense, v.10, n.4, p.69-81, 2023.

RAMIREZ, N. Pollination specialization and time of pollination on a tropical Venezuelan plain: variations in time and space. Bot. J. Linnean Soc., v.145, n.1, p.1-16, 2004. doi: https://doi.org/10.1111/j.1095-8339.2004.00181.x

RICHARDS, A.J. Plant breeding systems. London: Taylor & Francis, 1997.

ROBERTSON, C. Flowers and insects: lists of visitors of four hundred and fifty-three flowers. Carlinville: Charles Robertson, 1928.

ROSAS-GUERRERO, V. et al. A quantitative review of pollination syndromes: do floral traits predict effective pollinators? Ecol. Letters, v.17, n.17, p.388-400, 2014. doi: https://doi.org/10.1111/ele.12224

ROUBIK, D.W. Ecology and natural history of tropical bees. Cambridge: Cambridge University Press, 1989.

THOMSON, J.D.; THOMSON, B.A. Pollen presentation and viability schedules in animal-pollinated plants: consequences for reproductive success. In: WYATT, R. Ecology and evolution of plant reproduction. New York: Chapman & Hall, 1992. p.1-24.

TOREZAN-SILINGARDI, H.M.; SILBERBAUER-GOTTSBERGER, I.; GOTTSBERGER, G. Ecologia da Polinização: história natural, perspectivas e direções futuras. In: DEL-CLARO, K.; TOREZAN-SILINGARDI, H.M. Interações planta-animal. Springer, Cham, 2021. p.119-174. doi: https://doi.org/10.1007/978-3-030-66877-8_6

WADDINGTON, K.D. Foraging behavior of pollinators. In: REAL, L. Pollination biology. Orlando: Academic Press, 1983. p.213-239.

WANG, X. et al. Plants are visited by more pollinator species than pollination syndromes predicted in an oceanic island community. Sci. Rep., v.10, n.1, 13918, 2020. doi: https://doi.org/10.1038/s41598-020-70954-7

WASER, N.M. et al. Generalization in pollination systems, and why it matters. Ecology, v.77, n.4, p.1043-1060, 1996. doi: https://doi.org/10.2307/2265575

WASER, N.M.; OLLERTON, J. Plant-pollinator interactions: from specialization to generalization. Chicago: University of Chicago Press, 2006.

WATTS, S. et al. The influence of floral traits on specialization and modularity of plant-pollinator networks in a biodiversity hotspot in the Peruvian Andes. Anna. Bot., v.118, n.3, p.415-429, 2016. doi: https://doi.org/10.1093/aob/mcw114