

Reproductive biology and flower-visitor interactions of two bromeliad species from the Brazilian Atlantic Forest

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Background and aims – The Bromeliaceae family has great importance in the maintenance of neotropical communities. In the Brazilian Atlantic Forest, bromeliads are among the major groups responsible for maintaining the local flora and fauna and participate in important ecological interactions with insects, anurans, and hummingbirds. This work reports on aspects of the reproductive biology and the interactions between two endemic bromeliad species from the Atlantic Forest (*Aechmea bruggeri* and *Quesnelia indecora*) and their floral visitors to assess the impact of these relationships on the reproductive success and conservation of these plants.

Material and methods – Reproductive phenology, floral biology, pollination experiments, and the reproductive success of both species were investigated. To determine the floral visitors, we made direct observations on flowers and collected floral visitors that could not be identified in the field.

Key results – *Aechmea bruggeri* and *Quesnelia indecora* presented the individual and population flowering phenological pattern classified as annual with intermediate duration. The species are partially and totally self-incompatible, respectively. Both species presented a varied visitation guild, and although *Q. indecora* presented flowers with ornitophilous characteristics, no hummingbirds were recorded for this species. The hummingbird *Thalurania glaucopis* was the main visitor for *Aechmea bruggeri* and the bee *Trigona* cf. *braueri* was the main visitor for *Quesnelia indecora*. Nectar thieving by lepidopterans was observed for both species. Pollen robbing by beetles and nectar robbing by bees were registered for *Aechmea bruggeri* and *Quesnelia indecora*, respectively. Fruit and seed set of both species were highly affected by herbivory, which may negatively affect their reproductive success.

Conclusion – Our work highlights the important role of bromeliads in neotropical communities, showing how floral visitors and plants interact by participating in maintaining biological diversity in the studied forest remnant.

Keywords – *Aechmea bruggeri*; Brazil; Bromeliaceae; cloud forests; florivory; hummingbirds; pollination; *Quesnelia indecora*.

INTRODUCTION

Bromeliaceae is a neotropical family with about 3653 species (Gouda et al. continuously updated). Almost half of the bromeliad species occurs in the Brazilian territory, especially in the Atlantic Forest, which represents the main

centre of endemism and diversity (Benzing 2000; Forzza et al. 2015). The Atlantic Forest is the second largest rain forest of South America and one of the world's top biodiversity hotspots (Ribeiro et al. 2011). In many areas of the Brazilian Atlantic Forest, bromeliads offer shelter and a breeding site for several species of invertebrates, such as

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dipterans, Lepidoptera, Coleoptera, and Odonata (Marrero et al. 1996; Basílio et al. 2015), as well as some amphibians, including anuran species (Teixeira et al. 2002). Moreover, these bromeliads offer important floral resources to support pollinators, such as hummingbirds, and other occasional visitors (Rocha et al. 2004).

Pollination by hummingbirds in Bromeliaceae comprises about 60% of the genera (Givnish et al. 2014). These vertebrates are the main pollinators of bromeliad species from the Atlantic Forest (Varassin 2002). In some areas, almost half of their flowers are used as a food source for these birds (Sazima et al. 1996; Buzato et al. 2000). In the last years, many studies detailed these mutualistic interactions (Sick 1985; Sazima et al. 1996; Buzato et al. 2000; Canela & Sazima 2003a; Machado & Semir 2006; Piacentini & Varassin 2007; Magalhães et al. 2018; Kessler et al. 2020). Although some authors suggest a co-evolution between hummingbirds and bromeliads, considering the relationship between the beak morphology of these animals and the floral morphology (Benzing 2000; Givnish et al. 2014), there is still little evidence about this process. Kessler et al. (2020) highlighted that there is insufficient data on pollinators of bromeliad species, in addition to the observation that the same pollinators are shared by several bromeliads.

In addition to hummingbirds, other nectar feeding animals with a diurnal behaviour, such as butterflies and bees, also benefit from the sequential flowering and floral resources offered by bromeliad species (Varassin & Sazima 2000; Siqueira Filho & Machado 2001; Machado & Semir 2006). Bats form the second main group of vertebrates acting like bromeliad pollinators, these animals being attracted by floral scent and abundant nectar (Sazima et al. 1989; Benzing et al. 2000; Aguilar-Rodríguez et al. 2019).

Compared to the number of studies that focused on pollination biology of Bromeliaceae (e.g. Benzing et al. 2000; Kaehler et al. 2005; Carranza-Quiceno & Estévez-Varón 2008; Scrok & Varassin 2011; Schmid et al. 2011; Christianini et al. 2012; Hornung-Leoni et al. 2013; Rocca & Sazima 2013; Aguilar-Rodríguez et al. 2014a, 2016, 2019; Marques et al. 2015; Velásquez-Noriega et al. 2020; Milet-Pinheiro et al. 2021), research addressing the role of floral visitors in non-mutualistic relations with bromeliads is still scarce. Florivory has been reported for few species of Bromeliaceae (Canela & Sazima 2003b; Grohme et al. 2007; Cascante-Marín et al. 2009; Aguilar-Rodríguez et al. 2014b; Saldarriaga 2014; Palacios-Mosquera et al. 2019; Freitas et al. 2020), as well as examples of nectar robbing (González-Gómez & Valdivia 2005; Fumero-Cabán & Meléndez-Ackerman 2007, 2013).

Herbivory of fruit and/or seeds is another type of ecological interaction that can severely reduce the fitness of the species. Studies on the interactions between bromeliads and predators of fruit and seeds are also scarce (Nara & Webber 2002; Cavallari 2004; Cascante-Marín et al. 2005; Lenzi et al. 2006; Schmid et al. 2010; Filippon et al. 2012; Saldarriaga 2014; Oliveira et al. 2021), although very relevant in view of the impact on the fertility and viability of populations, which is the basis for the stability of the species in their natural habitat.

We focused on evaluating aspects of the reproductive biology and the flower-visitor interactions of two endemic Bromeliaceae species from a portion of the Atlantic Forest located in southeastern Brazil. Over two consecutive years of their flowering and fruiting period, we investigated the reproductive phenology, breeding systems, floral biology, reproductive success, and flower-visitor interactions. Starting from the premise that data on pollinators of bromeliads are lacking, as highlighted by Kessler et al. (2020), we aimed to improve the knowledge about these interactions through the study of species whose pollination has not been studied before. We also hypothesise that the reproductive success of these species may be affected by non-mutualistic interactions, such as pollen or nectar robbing and herbivory of fruits and seeds. Finally, considering that the studied bromeliads provide important ecosystem services, we contribute data that could support the development of strategies for the protection and conservation of endemic and/or endangered species.

MATERIAL AND METHODS

Species and study area

Our study was carried out in the Reserva Particular do Patrimônio Natural Chapadão da Serra Negra, a conservation unit located in Minas Gerais state, southeastern Brazil, with the coordinates 21°57'50"S, 43°48'1.0"W (fig. 1). The area is located in the Serra da Mantiqueira, a mountain range elected by scientists as the 8th most irreplaceable protected area on the planet and one of the ten most important locations for biodiversity conservation (Le Saout et al. 2013). Altitude in the study area ranges from 850 to 1200 m a.s.l. and the climate is Cwa (Köppen), with dry winters and wet and hot summers. The mean annual temperature is 20.6°C with a mean annual rainfall of 1376 mm. Of the forest physiognomies, dwarf cloud forests are the most common, characterised by shrubs and small trees with a 3–5 m high canopy (Oliveira-Filho et al. 2013).

We studied two Bromeliaceae species. The first one was *Aechmea bruggeri* Leme, an endemic species to the Serra da Mantiqueira forest remnants of Minas Gerais state, considered Critically Endangered in the state list of threatened flora (Drummond et al. 2005). The other one was *Quesnelia indecora* Mez, a species restricted to the Atlantic Forest domain of southeastern Brazil, with distribution in Minas Gerais and Espírito Santo states (Forzza et al. 2015). Both species have leaf rosette forming a water tank. In the study area, they occur terrestrially on leaf litter in the forest understory, forming small (*A. bruggeri*) to large (*Q. indecora*) clumps.

Reproductive phenology and floral biology

Reproductive phenophases were registered monthly from January 2019 to December 2020 in the study area, covering two consecutive flowering and fruiting periods for both species. The absence or presence of the following phenophases was recorded for 31 individuals of *A. bruggeri* and 67 individuals of *Q. indecora*: young inflorescence, floral buds, open flowers, senescent flowers, immature fruits,

and mature fruits. The classification of the phenological flowering patterns followed Gentry (1974) and Newstrom et al. (1994).

The floral biology was investigated in two individuals of *A. bruggeri* (n = 20 flowers) and two individuals of *Q. indecora* (n = 6 flowers) collected in the field and cultivated in a greenhouse. We registered data about the number of open flowers per day, length and colour of the corolla, anthesis hour, the period when flowers remained open, nectar volume, sugar concentration and mass. We measured nectar volume with a graduated microsyringe of 50 μ L (Hamilton, NV, USA) from previously bagged flowers. In each flower, we performed one measurement at the moment of flower opening and two more measurements taken every two hours from anthesis. One measurement was taken from the flowers in the senescence stage, with the petals already withered.

The nectar sugar concentration was measured at the moment of the flower opening using a hand refractometer (0–33%; Atago, Tokyo, Japan), and the total amount of sugar was calculated following Galetto & Bernardello (2005).

Pollination treatments and reproductive success

The breeding systems were investigated in four individuals of *A. bruggeri* and five of *Q. indecora* cultivated in a greenhouse. These individuals were different from those that were analyzed for floral biology. The following controlled pollination experiments were carried out: (1) hand self-pollination (n = 93 flowers of *A. bruggeri* and n = 9 flowers of *Q. indecora*), where floral buds were bagged and the flowers that opened the next day were pollinated with pollen from the same flower; (2) hand cross-pollination (n = 96 flowers of *A. bruggeri* and n = 9 flowers of *Q. indecora*), where floral buds were emasculated and pollinated the next day with pollen from other individuals of the same species. Additionally, 14 individuals (n = 2236 flowers) of *A. bruggeri* and 33 individuals of *Q. indecora* (n = 288 flowers) were randomly selected in the field for the natural (open) pollination experiments.

For each controlled pollination experiment and the open pollination experiment, fruit set was calculated as the number of formed fruits divided by the number of tested flowers.

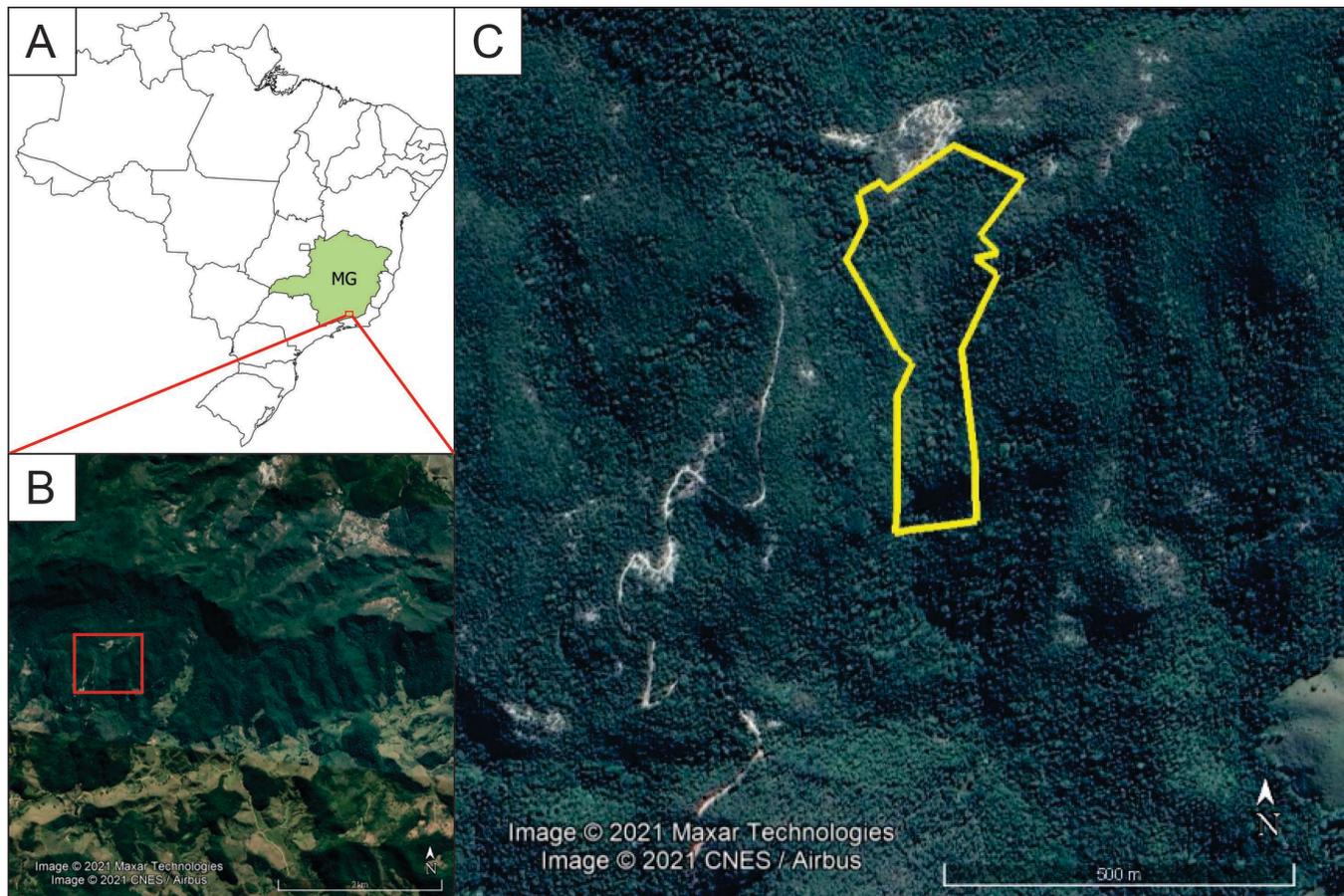


Figure 1 – Location of the study site. **A.** Portion of the Serra da Mantiqueira (indicated in red), located in the Minas Gerais state, southeastern Brazil. Map created with QGIS v.3.20.3 ‘Odense’ (QGIS Development Team 2021). **B.** Location of RPPN Chapadão da Serra Negra (red rectangle). **C.** The part of the RPPN where the reproductive studies and the floral visitor observations were done is indicated in yellow. Sources of images B and C: Google Earth. Map data ©2020 Google. Images courtesy of ©2020 CNES Airbus via Google Earth.

Furthermore, we calculated the mean seed production for each experiment. Indices of self-compatibility (SCI) were estimated for each species (Lloyd & Schoen 1992). The self-compatibility index was calculated based on the percentage of fruit set (SCI_f) or mean number of seeds per fruit (SCI_s) via hand self-pollination relative to the values from hand cross-pollination. Values close to 1 are interpreted as complete self-compatibility, and a value less than 0.75 is interpreted as being due to at least partial self-incompatibility.

Floral visitors

The observations of floral visitors were realized in 24 individuals of *A. bruggeri* and in 60 individuals of *Q. indecora*. The behaviour of floral visitors was registered at the beginning of the morning (7:00), the middle of the day (12:00), and at the end of the afternoon (16:00) to cover different periods of foraging, staying for 15 to 30 min in front of clumps of individuals of the two species. Due to difficulties in accessing the study area at night, it was not possible to observe and record nocturnal visitors. We recorded the time, frequency of visits, and the visitors' behaviour to determine their role in the interaction (e.g. pollinator, floral resource robber, herbivore). The activity of the floral visitors was recorded through photos and videos. Invertebrate visitors were collected with an entomological net, euthanised in a vial containing cotton impregnated with ether, stored in 70% alcohol, and taken to the laboratory for posterior identification by specialists. Vertebrates were recorded through photos for posterior identification.

RESULTS

Reproductive phenology and floral biology

In *Aechmea bruggeri*, the flowering period started at the end of the rainy season and extended into the dry season. There was an overlap between flowering and fruiting periods, and the mature fruits were also available during the dry season (fig. 2). According to Newstrom et al. (1994), the individual and populational flowering phenological pattern can be classified as annual (only one major cycle per year) with intermediate duration (ranging from one to five months), showing an asynchrony between the individuals. According to Gentry (1974), flowering of this species fits in the steady-

state pattern, whereby the plants produce a few flowers a day over an extended period of time (usually a month or more).

The reproductive potential of this species (total number of flowers produced per individual) was 159 ± 28 , with around 11 flowers opened per day. The inflorescences present pink-reddish peduncle bracts, brown-greenish sepals, and lilac petals, with the inflorescence about 1 m above the ground. The corolla is tubular, with a mean length of 1.37 ± 0.11 cm. The flowers open from the base to the top of the inflorescence (fig. 3). Anthesis starts around noon, and the flowers remain open and receptive for 24 h. At the moment of the flower opening, the mean volume of nectar produced per flower was 9.79 ± 3.34 μ L, with a sugar concentration ranging from 30 to 33%. The total amount of sugar found was 3.49 mg per flower (table 1). A decrease in the mean volume of nectar was observed four hours after anthesis (0.70 ± 0.75 μ L), reaching zero in senescent flowers.

Quesnelia indecora completed the flowering and fruiting cycle during the dry period of the year. Similar to *A. bruggeri*, the individual and populational flowering phenological patterns of *Q. indecora* were annual, with individuals flowering asynchronously during one to five months (fig. 2). According to Gentry (1974), flowering of this species also fits in the steady-state pattern.

The species presents a mean reproductive potential of 8 ± 3 flowers per individual, with one flower opening per day. The flowers have pinkish bracts and purple sepals and petals, and the mean length of the corolla was 4.42 ± 0.2 cm, with the peduncle of the inflorescence recurved and bending down to approximately 10 cm from the ground. Anthesis occurred around 6:10, with approximately 26 h of flower availability. *Quesnelia indecora* does not show an order of flower opening along the inflorescence (fig. 4). At the moment of flower opening, the mean volume of nectar was 7.58 ± 3.96 μ L, with a sugar concentration ranging from 31 to 33%. The total amount of sugar in the nectar was 2.79 mg per flower (table 1). A decrease in the mean volume of nectar was also observed four hours after the beginning of the anthesis (1.83 ± 1.84 μ L), reaching zero in senescent flowers.

Pollination treatments and reproductive success

Aechmea bruggeri presented a higher fruit set from hand cross-pollination (88%) than the hand self-pollination

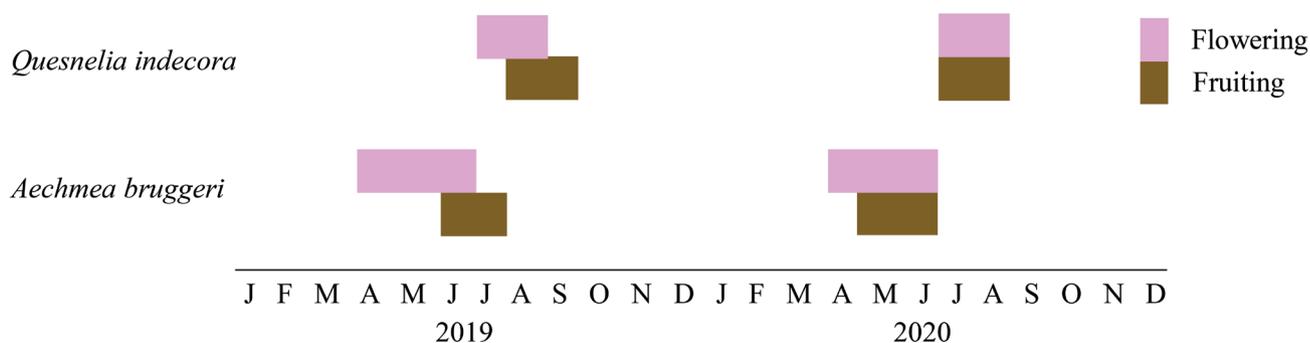


Figure 2 – Reproductive phenology of *Aechmea bruggeri* and *Quesnelia indecora* populations during the years 2019 and 2020.

Table 1 – Data on the floral biology of *Aechmea bruggeri* and *Quesnelia indecora*. X (± s) = mean (± SD); n = sample size.

	<i>A. bruggeri</i>	<i>Q. indecora</i>
Corolla colour	Lilac	Purple
Corolla length (cm)	1.37 (± 0.11) n = 10 flowers	4.42 (± 0.2) n = 3 flowers
Number of flowers per inflorescence	159 (± 28) n = 14 inflorescences	8 (± 3) n = 33 inflorescences
Number of open flowers per day	11 (± 1) n = 2 inflorescences	2 (± 0.5) n = 2 inflorescences
Floral anthesis time	12:00	06:10
Duration of anthesis	24 h	26 h
Nectar volume (µL)	9.79 (± 3.34) n = 20 flowers	7.58 (± 3.96) N = 6 flowers
Variation of sugar concentration in nectar (%)	30–33 n = 10 flowers	31–33 n = 3 flowers
Total amount of sugar (mg)	3.49	2.79

(9.6%) treatment. The mean number of seeds from hand self-pollination was 21.06 ± 2.71 , and from hand cross-pollination it was 32 ± 2.23 . The SCI_r and SCI_s indexes were 0.10 and 0.65, respectively, which indicates partial self-incompatibility. Under natural conditions, *A. bruggeri* presented a fruit set ranging from 0% (due to predation) in 2019 to 87% in 2020 (table 2). From the 14 individuals selected in the field for the open pollination treatment, four of them presented signs of fruit predation. For non-predated fruits, the mean number of seeds formed was 32 ± 3.02 (table 2).

Quesnelia indecora individuals also showed a higher fruit set from hand cross-pollination treatment (100%) than hand self-pollination (0%). The mean number of seeds from hand self-pollination was 0, and from hand cross-pollination it was 92 ± 6.21 . The SCI_r and SCI_s indexes were 0.0, which indicates total self-incompatibility for this species. Under natural conditions, the species presented a fruit set ranging

from 0% in 2019 to 100% in 2020 (table 2). *Quesnelia indecora* individuals also suffered high fruit predation. From the 33 individuals investigated, 18 presented partial or total destruction of the infructescences (fig. 5B). It was not possible to identify which visitor was responsible for the damage, and further observations are needed to verify the possible presence of nocturnal predators. For non-predated fruits, the mean number of seeds formed was 90 ± 7.91 (table 2).

Floral visitors

Eight species of floral visitors were collected, six visiting *A. bruggeri* and three visiting *Q. indecora*, with one species shared by both plants.

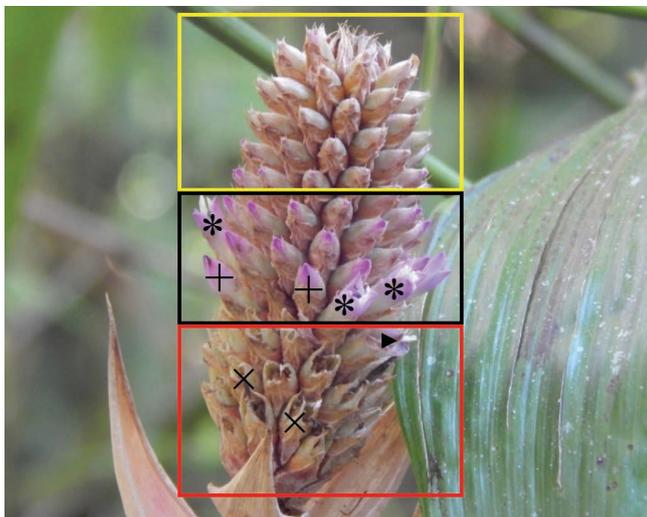


Figure 3 – *Aechmea bruggeri* inflorescence with different phenological stages. Flower buds (yellow); pre-anthesis (+) and anthesis (*) flowers (black); senescence flowers (▶) and fruits (×) (red). Photograph by Matheus Rezende e Silva.



Figure 4 – *Quesnelia indecora* inflorescence with different phenological stages. Floral bud (●); anthesis flowers (*); senescence flowers (▶). Photograph by Matheus Rezende e Silva.

Table 2 – Fruit set and average number of seeds (mean \pm SD) of *Aechmea bruggeri* and *Quesnelia indecora* for controlled and natural pollination treatments carried out between 2019 and 2020. The number of plants used in each treatment is given in parentheses (n = number of individuals). The number of formed fruits and the number of tested flowers is given in parentheses (fruits/flowers). The * indicates that the result 0% are from totally predated inflorescences.

	Hand cross-pollination	Hand self-pollination	Natural (open) pollination	Mean number of seeds/fruit
<i>A. bruggeri</i>	88% (85/96) (n = 2)	9.6% (9/93) (n = 2)	0%* (2019) 87% (2020) (995/2236) (n = 14)	32 (\pm 3.02) 50 fruits
<i>Q. indecora</i>	100% (8/9) (n = 3)	0 (0/9) (n = 2)	0%* (2019) 100% (2020) (79/288) (n = 33)	90 (\pm 7.91) 50 fruits

***Aechmea bruggeri* visitors** – Visits started in the early morning, around 7:00. The only vertebrates were two hummingbird species. The violet-capped woodnymph *Thalurania glaucopis* Gmelin, 1788 (fig. 6A–B) made frequent visits after anthesis, usually between 13:00 and 16:00. We observed the presence of male and female individuals who take turns during visits that last between 3 and 5 s, with intervals of about 10 min between them. In search of nectar, they inserted their beak into the flower, removed the nectar, and consequently also the pollen. They foraged on all the open flowers of one individual and then moved to another plant.

Less frequently, the planalto hermit *Phaethornis pretrei* Lesson & Dellatre, 1839 presented the same behaviour as

T. glaucopis, but its visits had a shorter duration and longer intervals between them, since aggressive behaviour of *T. glaucopis* towards *P. pretrei* were recorded. It was often seen that *T. glaucopis* landed on branches close to *A. bruggeri* individuals, preventing other hummingbirds from visiting the flowers, as happened for *P. pretrei*. As they approached the flowers, they were attacked and chased by *T. glaucopis*, preventing them from visiting any *A. bruggeri* plants.

Concerning invertebrate visitors, in the early morning hours, the presence of a large number of male and female *Drosophila* sp. flies were observed visiting the flowers in pre-anthesis (fig. 6C–D). Curculionidae beetles were registered on the bracts of the inflorescence. Always an average of five individuals per inflorescence, the Curculionidae waited

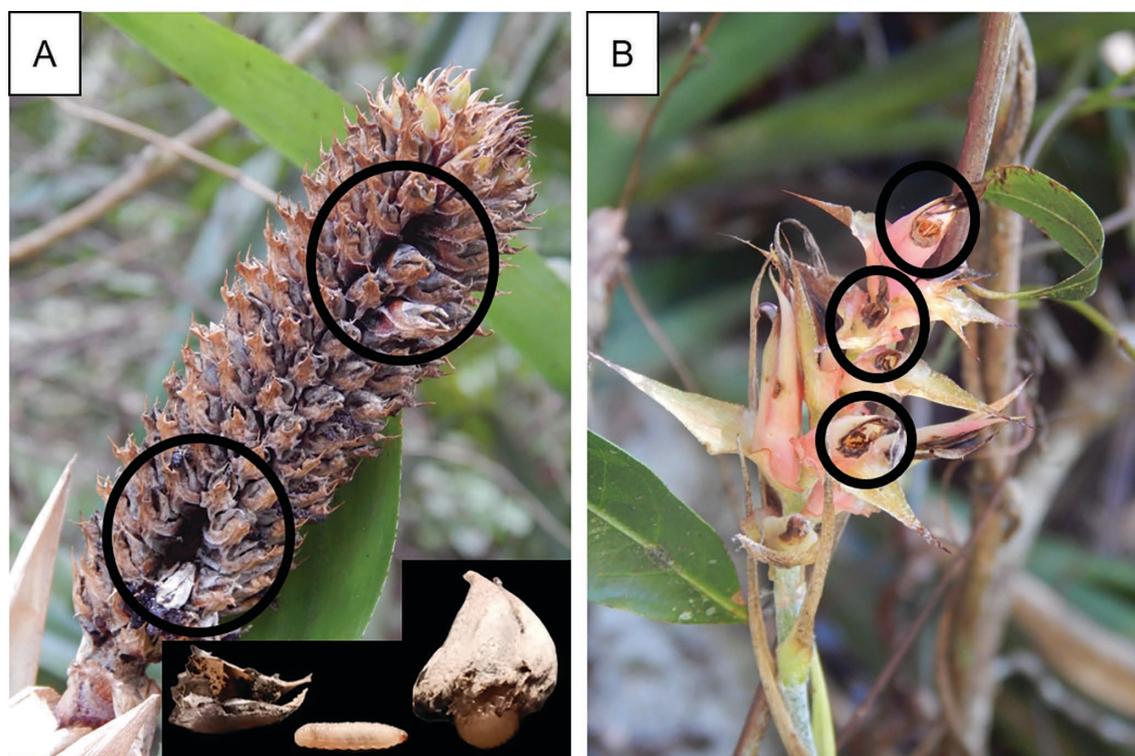


Figure 5 – Fruit predation (circles). **A.** *Aechmea bruggeri*. Curculionidae larvae feeding on the fruits. **B.** *Quesnelia indecora*. Photographs by Matheus Rezende e Silva.

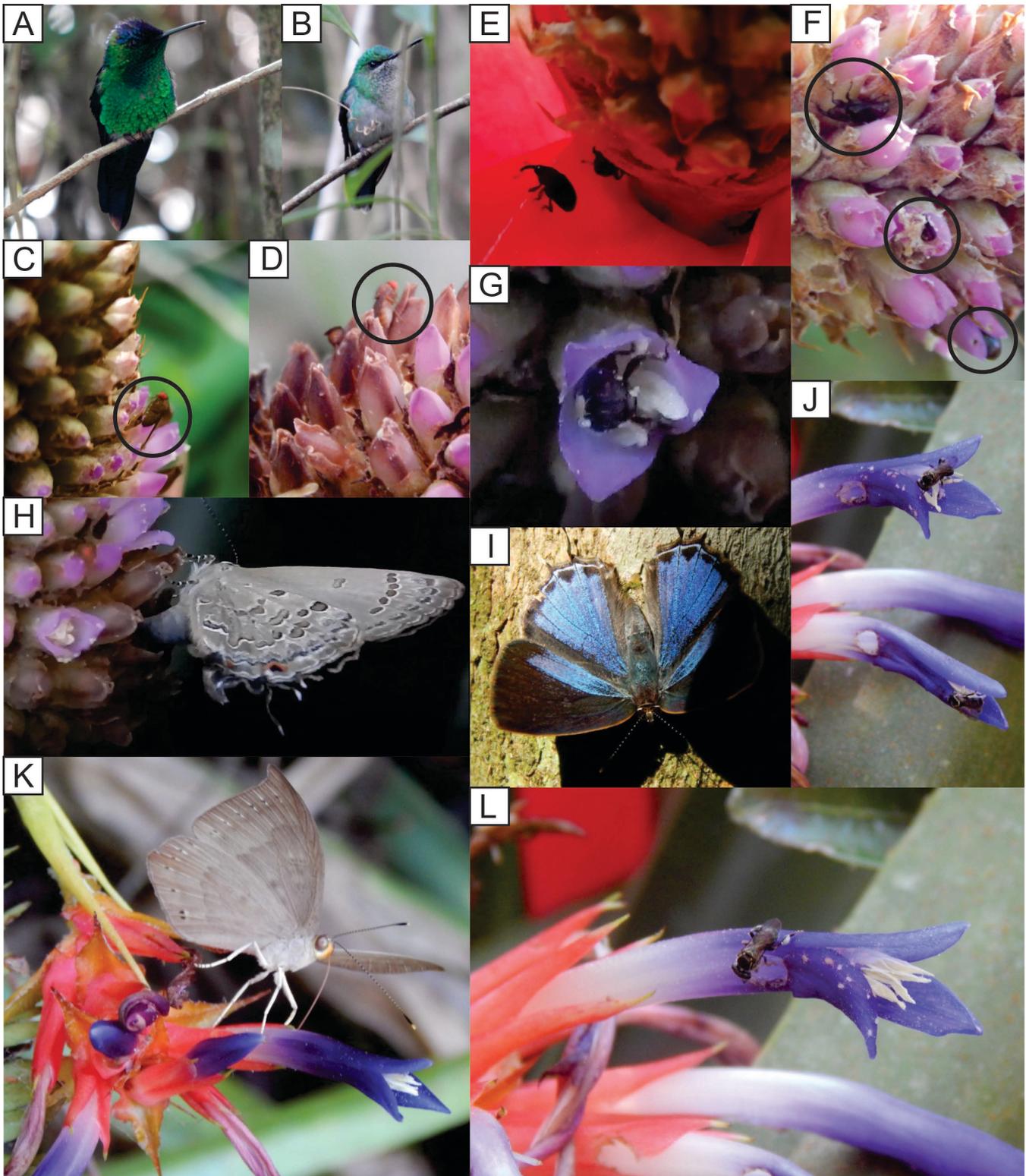


Figure 6 – *Aechmea bruggeri* and *Quesnelia indecora* visitors. **A.** Male *Thalurania glaucopsis*. **B.** Female *T. glaucopsis*. **C–D.** Individuals of *Drosophila* sp. **E–G.** Individuals of Curculionidae. **H–I.** *Strymon oreala*. **J, L.** *Trigona* cf. *braueri*. **K.** *Eurybia pergea*. All photographs by Matheus Rezende e Silva.

for anthesis so that they could feed on the pollen (fig. 6E–G). For this, they used their legs to scrape the anthers to remove pollen and discard them after feeding on the grains. Larvae were also found in the fruits, causing partial or total destruction (fig. 5A).

The butterfly *Strymon oreala* Hewitson, 1868 was registered only twice, flying around the inflorescence. They landed on flowers and inserted their proboscis into them to collect nectar (fig. 6H–I). The records were made in the middle of the afternoon, between 13:00 and 16:00. The stingless bee *Trigona* cf. *braueri* Friese, 1900 was registered visiting only three times. This species foraged on the flower in search of nectar located at the end of the corolla tube. Because it is a small flower, the bee touched the anthers and released the pollen, causing pollen transfer among individuals.

Based on these behaviour patterns, it was possible to classify *Drosophila* sp. and *S. oreala* as nectar thieving, since they used the flowers without necessarily transferring pollen to other plants and without causing damage to floral structures (Inouye 1980; Freitas 2018). The Curculionidae beetles, which caused damage to the floral structures in search of pollen, can be considered as pollen robbers. The hummingbirds *T. glaucopsis* and *P. pretrei* were considered as pollinators since, to access the available resource, they end up releasing pollen and transferring it to other plants. *Trigona* cf. *braueri* showed both thieving and pollinator behaviour.

***Quesnelia indecora* visitors** – For this species, three floral visitors were registered: *Trigona* cf. *braueri*, *Plebeia* sp., and *Eurybia pergaea* Geyer, 1832.

Trigona cf. *braueri* (fig. 6J, L) was the most frequent, with 23 visits. It was possible to register that, in addition to accessing the nectar at the end of the tube through the corolla entrance (consequently causing the transfer of pollen grains to other individuals), this bee also damaged the base of the flower to access the nectar resource (fig. 3L). The same was observed for the stingless bee *Plebeia* sp. The butterfly *E. pergaea* showed similar behaviour to *S. oreala*, using their proboscis to access the nectar from the opened corolla (fig. 6K). The difference is that this species does not follow a flower visitation pattern, as recorded for *S. oreala*.

Due to these behaviour patterns, *E. pergaea* was classified as a nectar thieving, without transferring pollen to other plants. *Trigona* cf. *braueri* and *Plebeia* sp. exhibited behaviours of nectar robbers (causing damage to flower structure) and occasionally behaved as pollinators, when accessing nectar through the corolla opening.

DISCUSSION

There was no variation in the flowering and fruiting seasons for both species over the two consecutive reproductive cycles. The continuous or steady-state phenology registered for *A. bruggeri* and *Q. indecora* points out that these bromeliads are an important food source for pollinators in the study area. The steady-state flowering pattern is often related to plants visited by trapline foraging pollinators, such as hummingbirds and many tropical bees, which are characterised by having a repeated and fixed visitation route

capable of covering long distances (Janzen 1971; Gentry 1974; Tello-Ramos et al. 2015). Visits by trapliners are common in Bromeliaceae (Canela & Sazima 2003a; Kessler et al. 2020) and have been reported for other species of *Aechmea* (Canela & Sazima 2003a; Lenzi et al. 2006; Kamke et al. 2011; Scrok & Varassin 2011; Pool-Chalé et al. 2018).

Aechmea bruggeri presented many of the floral traits for ornithophily: scentless flowers, tubular corolla, pink-reddish inflorescence peduncle bracts, and nectar secretion during the whole diurnal anthesis (Faegri & van der Pijl 1979). However, the nectar sugar concentration is higher and more related to butterfly and/or moth pollination (Krömer et al. 2008). Many bromeliad species are still little known with respect to their insect pollinators (Krömer et al. 2008). Although the lepidopteran *S. oreala* proved to be a nectar thieving, a wide variety of other insects visited *A. bruggeri*. Our results suggest that *A. bruggeri* is a generalist plant, however, further analyses including observations of nocturnal visitors will be important to elucidate the type of pollination system of this species.

The individuals of *A. bruggeri* produced their largest nectar volume at flower opening, and sugar concentration did not change during anthesis. This dynamic of producing a greater volume of nectar at the beginning of anthesis is common among species of Bromeliaceae (Canela & Sazima 2003a; Machado & Semir 2006; Schmid et al. 2011; Aguilar-Rodríguez et al. 2016). Nectar with high sugar concentrations tends to attract and hold the attention of the plant visitor and, when presented in small but sufficient quantities, as observed in *A. bruggeri*, it forces the animal to visit a maximum number of flowers, which may increase cross-pollination rates (Baker 1975).

The average production of nectar by *A. bruggeri* (9.79 μ L) is considered low, compared to other ornithophilous species from the same genus with longer corolla tubes, such as *A. beeriana* L.B.Sm. & M.A.Spencer (37 μ L; Nara & Webber 2002) and *A. pectinata* Baker (79.5 μ L; Canela & Sazima 2003a), besides bromeliads from other genera, such as *Billbergia horrida* Regel and *Tillandsia polystachia* (L.) L. (64.1 μ L and 43.7 μ L, respectively; Tagliati et al. 2018). Low nectar volumes similar to those found in *A. bruggeri* were observed for the short-corolla species *A. caudata* Lindm. (15.5 μ L; Kamke et al. 2011), where bees were registered as an important visitor for pollination success, and *A. bracteata* (Sw.) Griseb. (4.64 μ L; Pool-Chalé et al. 2018), whose low nectar production was directly related to the small size of the corolla. Insects, mainly bees, are frequent flower visitors in many short-corolla bromeliads with ornithophilous features (Nara & Webber 2002; Araujo et al. 2004; Lenzi et al. 2006) and might also have an important role in the pollination system of these species due to their high frequency at the flowers. As bees were not observed visiting *A. bruggeri* frequently, whose pollination was carried out mainly by hummingbirds, the low nectar volume production for this species is probably associated with its short corolla length.

Thalurania glaucopsis was an effective pollinator of *A. bruggeri*, corroborating the close mutualistic relationship of this group of plants with hummingbirds of the Trochilidae family (Sick 1985). *Thalurania glaucopsis* was the main

pollinator for other *Aechmea* species, such as *A. pectinata* (Canela & Sazima 2003a), *A. lindenii* (Lenzi et al. 2006), and *A. nudicaulis* (Schmid et al. 2011), as well as for several other genera of Bromeliaceae (Kessler et al. 2020). Its territorial and agonistic behaviour towards other species of hummingbirds was also reported by Canela & Sazima (2003a) for *A. pectinata*. Although *P. pretrei* is considered the most effective hummingbird pollinator for many other Bromeliaceae species, such as *A. constantinii* (Mez) L.B.Sm. (Rios et al. 2010), *Alcantarea turgida* (Versieux & Wanderley 2007), *Tillandsia geminiflora* Brogn., *T. polystachia* (L.) L., and *T. stricta* Sol. (Tagliati et al. 2018), the frequency of visits of the *A. bruggeri* flowers, and consequently, its importance in the total pollination success of this species is diminished by the agonistic behaviour of *T. glaucopsis*.

Although hummingbird pollination has been reported for some terrestrial species of *Quesnelia*, such as *Q. arvensis* (Vell.) Mez, *Q. humilis* Mez, and *Q. lateralis* Wawra (Kessler et al. 2020), in our study, *Q. indecora* was not visited by this group of birds, even though it presented some floral traits characteristic for ornithophily, such as tubular corolla, pink-reddish inflorescence peduncle and bracts, and high sugar concentration (Hainsworth & Wolf 1976; Faegri & van der Pijl 1979). One explanation for the absence of hummingbird visits in this species would be related to its flower display. During the inflorescence development, the peduncle tends to bend down and stay close to the ground, hiding the flowers in the understory vegetation and positioning them out of the hummingbird's visual field. Blem et al. (1997) reported that the hummingbird *Selasphorus rufus* Gmelin showed a preference for sucrose sources ranging from 3 to 25 m in height, and this behaviour was interpreted to avoid predation. In addition, they point out that taller flowers are more visible in the animal's field of view. Henderson et al. (2001) demonstrated that not only this same hummingbird species but also others have the cognitive ability to remember the location of a certain flower, showing a preference for those that are located higher. Since in *Q. indecora*, the inflorescences were approximately 10 cm from the ground, this may explain the non-visitation by hummingbirds. The colour attraction for each group of visitors can also be taken into account. While bees and butterflies prefer colours of the yellow-pink-violet-blue and yellow-blue-red-orange spectrum (Faegri & van der Pijl 1979; Westerkamp 1997; Weiss 2009), respectively, birds tend to be attracted to colours of the red spectrum (Varassin & Amaral-Neto 2014), which even when present in the bracts of *Q. indecora*, are blending into the foliage.

Pollination by dipterans is widely distributed among the basal angiosperms, being found in Cabombaceae, all families of Austrobaileyales, some Annonaceae, Monimiaceae, Lauraceae, Winteraceae, Saururaceae, Piperaceae, and Aristolochiaceae (Endress 2010). The flowers pollinated by this group are usually hermaphrodite and protogynous, with odour production and temperature regulation (thermogenesis). Nectar production is not common and other floral resources are available, such as pollen, heat, shelter, and places for reproduction (Larson et al. 2001; Endress 2010). The interactions between bromeliads and flies have been scarcely investigated, with records only

for the genus *Aechmea* (Dejean & Olmsted 1997). Schmid et al. (2011) observed the presence of dipterans of the suborder Brachycera visiting *A. nudicaulis*, removing nectar from extrafloral nectaries present in the sepals. Dejean & Olmsted (1997) observed a large diversity of dipteran larvae inhabiting the phytotelm of *A. bracteata*. For *A. bruggeri*, the *Drosophila* individuals do not act as pollinators but rather as nectar thieving.

The beetles of the family Curculionidae caused serious damage to the inflorescences of *A. bruggeri*. In addition to feeding on the pollen and damaging the anthers, numerous larvae were found in the fruits, directly interfering with the plant's reproductive success since they prevent the full development of fruits and seeds. Previous studies already indicated that Curculionidae adults and larvae feed on various reproductive and vegetative plant structures, causing serious losses in bromeliad populations (Frank 1999). Albertoni et al. (2016) listed 18 species of beetles associated with *Hohenbergia augusta* (Vell.) E.Morren and *Vriesea friburguensis* Mez, being the first list of beetles associated with bromeliad species.

Schmid et al. (2010) recorded the predation of bromeliad inflorescences by Lepidoptera larvae of the genus *Strymon*, among them, *S. oreala*, which fed on the developing fruits of *A. caudata* and *A. lindenii*. After feeding, the larvae went to the rosette of the species to start their pupal stage. These authors also highlighted the importance of the Bromeliaceae family in maintaining the lepidopteran fauna in the Atlantic Forest. Although we only recorded *S. oreala* feeding on *A. bruggeri* nectar, further observations are necessary to confirm whether the species also uses *A. bruggeri* during its larval development.

The interactions between organisms are not fixed but changeable according to the circumstances of the environment (Zhang et al. 2015). Some visitors of the same species can play a dual role, with mutualistic and antagonistic behaviours. In this work, the stingless bees *Trigona* cf. *braueri* and *Plebeia* sp. are both pollinators and robbers, with this last behaviour frequently observed in *Q. indecora*, where they feed on the nectar by damaging the base of the flowers.

Nectar robbers may have direct and indirect effects on plant reproductive success, from damaging reproductive organs to removing floral rewards without the benefit of pollination (Irwin et al. 2010). However, the presence of nectar robbing is not proof of negative fitness effects (Fumero-Cabán & Meléndez-Ackerman 2013). Some studies, for example, have found that flowers with less nectar can have increased cross-pollination (Lasso & Naranjo 2003; Irwin et al. 2010; Pelayo et al. 2011; Rojas-Nossa et al. 2015; Hazlehurst & Karubian 2016). Considering that *Q. indecora* is totally dependent on pollinators for fruit and seed set, our data on the reproductive success suggest that the costs of loss of floral rewards by nectar robbing can vary from maximum to minimum, given the fruit set under natural conditions. While the antagonistic behaviour of the bees can lead to the total absence of fruit set in certain periods of the reproductive phenology of this plant, these visitors also play a fundamental role as pollinators, allowing 100% fruit set

in other periods. For *A. bruggeri*, the foraging behaviour of *T. cf. braueri* does not seem to affect hummingbirds as the effective pollinators of this species. As Aguilar-Rodríguez et al. (2016) stated, the secondary pollinators may be important as a 'fail-safe' system by which to guarantee the pollination of some species.

Other plant-animal interactions such as herbivory, can negatively affect the reproductive success of the species, interfering in important processes (e.g. seed dispersal) for the establishment of new individuals in their natural habit. In the study area, seed dispersal of *A. bruggeri* is severely affected by the predation of fruits by Curculionidae beetles. Fruit and seed herbivory negatively affecting the reproductive success have also been registered for other bromeliad species, such as *A. beeriana* Smith & Spencer (Nara & Webber 2002), *A. lindenii* (Lenzi et al. 2006), *A. nudicaulis* (L.) Griseb. (Schmid et al. 2010), and *Puya nitida* Mez (Saldarriaga 2014). Failures in seed production and dispersal can bring great risks to endangered species, especially for those which have restricted distributions and high habitat specificity, such as *A. bruggeri*.

Conservation efforts for the studied species should focus primarily on habitat preservation and their pollinators. Future studies involving observations of nocturnal visitors and pollinator exclusion experiments will be important to deepen the knowledge about the pollination ecology of these species. However, considering the ecological importance of the Bromeliaceae family in the Atlantic Forest, this work reinforces how the interactions between animals and bromeliads are important to sustain the biological diversity of these forest remnants.

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