SELBYANA
Tropical Botany and Conservation with an Emphasis on Epiphytes
Journal of MARIE SELBY BOTANICAL GARDENS

Pollinator performance of the pollination generalist *Rhytidophyllum bicolor* (Gesneriaceae) in Haiti 15 months after Hurricane Matthew

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Abstract

Pollination performance consists of the visitation rate and efficiency of animal species pollinating a given plant species, and it is central to understanding the contribution of pollinators to the evolution of species. We studied the pollination performance of different floral visitors of *Rhytidophyllum bicolor* Urb. (Gesneriaceae), a species endemic to southwest Haiti for which no pollination information exists. Although pollinator visitation rates are known for several Antillean Gesneriaceae, single visit efficiency has never been estimated and pollination performance is unknown in the group. We found that bats were more frequent and more effective pollinators than bees, and thus had a greater pollination performance even if the contribution of bees was not negligible. Hummingbird performance could not be estimated because no pollination was observed in this study although they have been observed in previous field trips. This is likely because hummingbird populations may have been strongly impacted by Hurricane Matthew that hit the region in October 2016, 15 months prior to this study. These results highlight the advantages of being a pollination generalist to ensure good reproductive success even in the absence of a pollinator, a strategy potentially important in the Caribbean islands that are frequently affected by natural disasters such as hurricanes.

Key words: Bat pollination, Gesneriaceae, Islands, Natural disasters, Pollinator efficiency, Pollinator visitation rate.

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INTRODUCTION

Without the assistance of animals to ensure their pollination, roughly 88% of angiosperms would not be able to complete their reproductive cycle (Ollerton et al., 2011). This mutualism sometimes leads to the specialization of plant species to few pollinator species, or to generalization where plants are effectively pollinated by several pollinators (Waser, 2006; Waser et al., 1996). Such ecological strategies have a strong impact on floral evolution, which is expected to be affected by the composition of pollinator guilds and, more specifically, by the relative performance of each pollinator (Aigner, 2001; Aigner, 2006). For instance, floral traits that favour one pollinator might be detrimental to another one, such as narrow corolla tubes that are thought to increase hummingbird pollination and reduce bee pollination (Castellanos et al., 2004), although empirical studies have yet to find strong support for such fitness trade-offs (Aigner, 2004; Castellanos et al., 2004; Muchhala, 2007; Sahli & Conner, 2011).

In order to better understand the reproduction of plant species and the relative importance of their different pollinators, it is important to estimate their performance (Freitas, 2013; Ne'eman et al., 2010). Pollinator performance (also called pollinator importance) consists of two main components: 1) the visitation rate or the frequency at which a pollinator makes contact with the flower reproductive organs, and 2) the pollinator efficiency, which is the capacity of a pollinator to remove pollen from the anthers (male component), transfer it to the stigma, and produce seeds (female component) following a single pollinator visit (Armbruster, 2014; Freitas, 2013; Ne'eman et al., 2010). Note that the female reproductive success (seed set produced) is sometimes estimated from the number of fertilized ovules or the number of pollen grains deposited on the stigma (Ne'eman et al., 2010). Ideally, pollinator performance for a plant would be estimated over its whole life, but this is more difficult to evaluate for perennial plants.

Many pollination studies limit their observations to visitation rates only. While this provides information about the pollinator guild of the plant, this information might not reflect the actual contribution of each pollinator towards the reproductive success of the plant. For this reason, it is important to measure pollinator performance because many studies have shown that, contrary to what was proposed by Stebbins (1970), the most frequent pollinator is not always the most effective (Fumero-Cabán & Meléndez-Ackerman, 2007; Mayfield et al., 2001; Niemirski & Zych, 2011; Sahli & Conner, 2007; Zych, 2007).

Pollination generalism, for which pollinator performance is particularly relevant because several species contribute to the reproduction of the plant, represents a common pollination strategy in angiosperms (Ollerton et al., 2007; Waser et al., 1996). There is no universal definition of a pollination generalist, but many authors agree that they describe plant species pollinated by two or more distinct functional pollinators (Gómez & Zamora, 2006; Johnson & Steiner, 2000; Ollerton et al., 2007). If pollination specialists have been widely studied (Armbruster et al., 2000; Herrera, 1996; Johnson & Steiner, 2000; Thompson, 1994), generalists have received considerably less attention despite their abundance (but see Aigner, 2004; Gómez et al., 2014; Sahli & Conner, 2007).

In this study, we investigate the pollinator performance of *Rhytidophyllum bicolor* Urb. (Gesneriaceae), a species endemic to Haiti for which no published pollination information exists. According to its subcampanulate corolla (bell shape with a constriction at the base of the corolla; FIGURE 1C), we assume that *R. bicolor* is probably a pollination generalist as corolla shape is a very good predictor of pollination strategy in the group (Joly et al., 2018; Martén-Rodríguez et al., 2009). The tribe Gesneriinae, to which *R. bicolor* belongs, has indeed been the subject of several pollination studies (Martén-Rodríguez & Fenster, 2008; Martén-Rodríguez et al., 2009; Martén-Rodríguez et al., 2010; Martén-Rodríguez et al., 2015), although none have estimated pollinator efficiency. These have shown that pollination generalists in the Gesneriinae are normally pollinated by hummingbirds, bats and insects, three functionally distinct pollinators. Interestingly, pollination generalists in the New World Gesneriaceae appear to be restricted to the Antilles (Martén-Rodríguez et al., 2015) and have been shown to have evolved several times independently (Joly et al., 2018; Martén-Rodríguez et al., 2010). Generalist pollination strategies could be particularly effective on islands by providing reproductive insurance and by reducing the likelihood of local extinctions (McKinney, 1997; Raia et al., 2016). This is because islands generally have lower pollinator richness compared to nearby continents (Barrett et al., 1996; Olesen et al., 2002) and have pollinator communities that vary though time due to migrations and natural disasters such as hurricanes (Armbruster & Baldwin, 1998; Martén-Rodríguez et al., 2010). In this particular study, our investigation of pollination performance on *R. bicolor* occurred 15 months after Hurricane Matthew in October 2016.

Materials and Methods

Studied species

Rhytidophyllum bicolor. *Rhytidophyllum bicolor* is endemic to the Massif de la Hotte in South-West Haiti on the Tiburon peninsula (FIGURE 1A) where is locally abundant. It is a shrub up to 2 m tall that produces several cymose inflorescences (FIGURE 1B) throughout the year. Flowers are protogynous with temporally separated female and male stages that last one day each. The dehiscent capsules releases a few hundred seeds that drop directly on the ground.

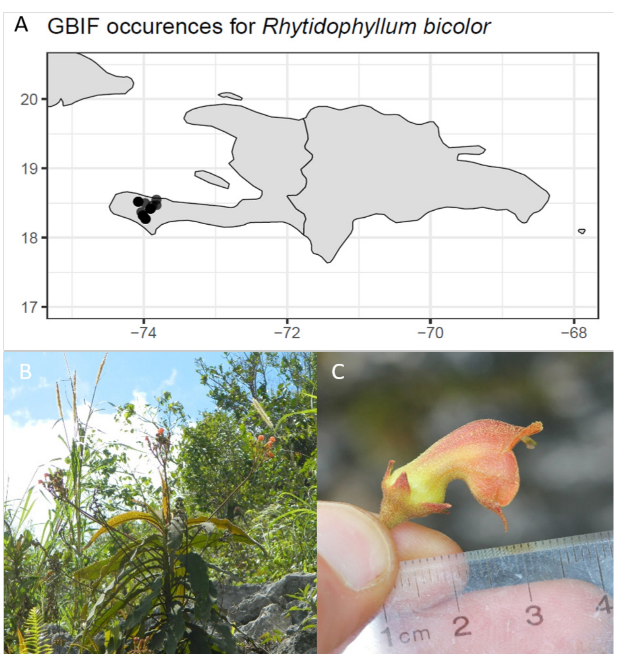

Figure 1. *Rhytidophyllum bicolor* distribution (A) estimated from georeferenced accessions obtained from GBIF (Global Biodiversity Information Facility; accessed March 30th, 2020), plant (B) and flower (C). Photo credits: J. Faure (B) and S. Joly (C).

Pollinators. The pollinators of *Rhytidophyllum bicolor* were not known before the study, although hummingbirds were observed (S. Joly, pers. obs.). The following four species of hummingbirds present at the study site are possible pollinators: *Chlorostilbon swainsonii* (Lesson, 1829) (Trochilidae) (Peguero et al., 2006), *Mellisuga minima* (Linnaeus, 1758) (Trochilidae), *Archilochus colubris* (Linnaeus, 1758) (Trochilidae) and *Anthracothorax dominicus* (Linnaeus, 1766) (Trochilidae) (FIGURE 2 A, B, C, D). Two species of nectarivorous bats occur in the study site and are potential pollinators: *Monophyllus redmani* Leach, 1821 (Phyllostomidae) and *Phyllonycteris poeyi* Gundlach, 1861 (Phyllostomidae) (FIGURE 2 E, F). Finally, bees are known to be occasional pollinators of generalist species of Antillean Gesneriaceae (Martén-Rodríguez et al., 2015) and they could thus also pollinate *R. bicolor*.

Research site

The study was conducted in the Pic Macaya National Park in southern Haiti from January 19th to January 28th 2018. The park area is more than 8,000 hectares, where unexploited cloud forest can still be found. Elevation in the park reaches a maximum altitude of 2,347 meters above sea level at Pic Macaya. This is the most important protected area of the country and one of the largest centers of endemism in Haiti (Peguero et al., 2006). Observations were carried out around the village of Formon (latitude 18.324249, longitude -74.009565) and in Bois Formon, Bois Cavalier and Fonblé, at elevations between 900 and 1150 meters in humid karst forest and in disturbed areas where *R. bicolor* is abundant. This "buffer zone" of the park is highly disturbed and strongly affected by deforestation (Hedges et al., 2018) and farming (pers. obs.).

Pollination observations

Each observation period lasted from 1 to 4 hours and was done 2-3 meters from the plant. Every studied population had several flowers at anthesis. Daily observations were done between 6 am and 4 pm on different populations. Night observations were performed from 6:30 pm to 11 pm using red light flashlights. A camera with night vision (Sony HDR-CX550V) also was used some nights to record the contact of bats with the reproductive parts (Cárdenas et al., 2017; Muchhala & Potts, 2007). At the beginning of each observation, we noted the total

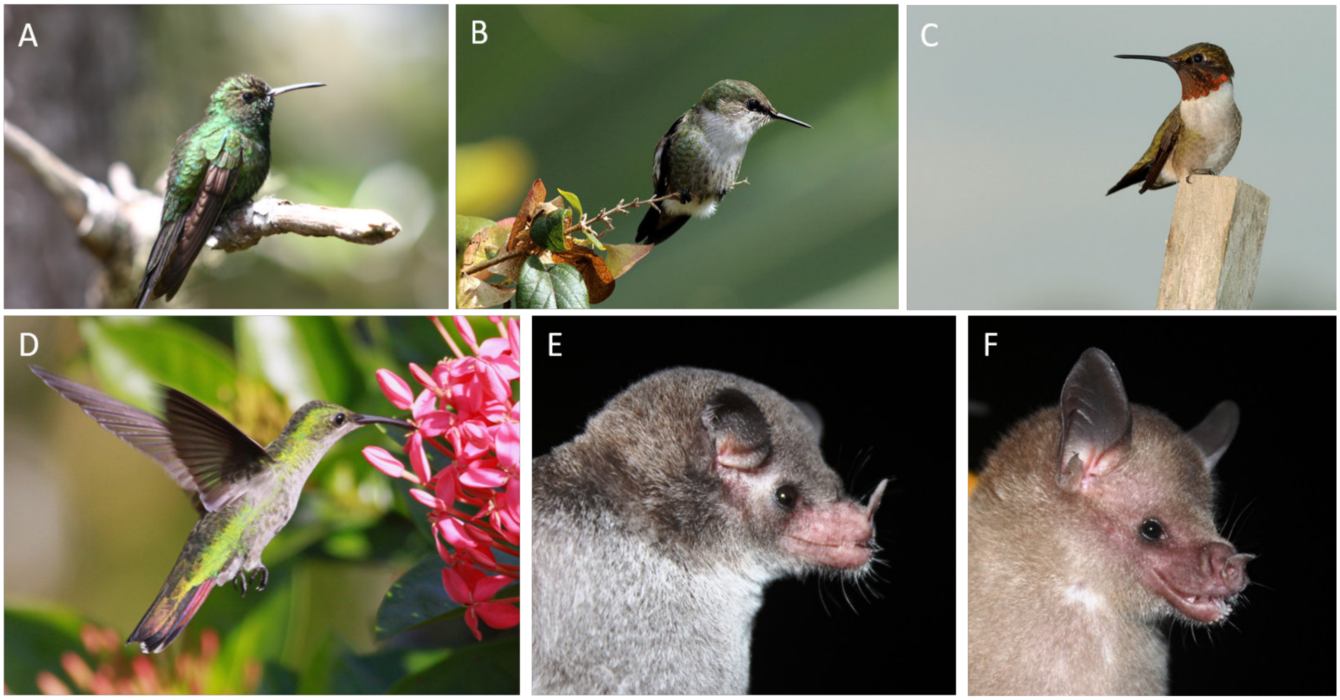

Figure 2. Pictures of putative pollinators of R. bicolor: A) *Chlorostilbon swainsonii* © Silvana Marten-Rodriguez, B) *Mellisuga minima* © Charles J. Sharp (CC BY-SA 4.0), C) *Archilochus colubris* © Joe Schneid (CC BY 3.0), D) *Anthracothorax Dominicus* © zankaM (CC BY-SA 3.0), E) *Monophyllus redmani* © Joaquín Ugarte (CC BY-NC 4.0)(CC BY-NC 4.0) and F) *Phyllonycteris poeyi* © Joaquín Ugarte, some rights reserved (CC BY-NC).

number of flowers available, the number of flowers in female phase and thus with receptive stigma, and we removed the stigmas of flowers that had already received pollen (determined visually).

Pollinator performance

We followed Freitas (2013) and estimated the pollinator performance (called pollinator effectiveness by Freitas) as the visitation rate multiplied by the single visit efficiency (i.e. pollinator efficiency). Visitation rate is the number of times a pollinator contacts the reproductive organs of one specific flower per hour on average. As the visitation rate often conforms to a Poisson distribution, a 95% confidence interval was calculated with the exact method because of our small sample sizes (Ulm, 1990). The pollinator efficiency was estimated by the mean number of pollen grains deposited on the stigma after a single pollinator visit (Olsen, 1996; Park et al., 2016; Rogers et al., 2013; Thomson & Goodell, 2001).

To count the number of pollen grains deposited on the stigma after a single pollinator visit, stigmas were removed from the flower immediately following the visit and placed in a tube containing 70% isopropyl alcohol and brought back to the laboratory. In the laboratory, the tube was vortexed for 30 seconds to remove all the pollen from the stigma. The stigma was then removed and the tube was weighed to calculate the total volume of alcohol in the tube using the volumetric mass of 70% isopropyl alcohol. The number of pollen grains in 2 µL of solution was counted using an haemocytometer from ten replicates per tube of alcohol, with five replicates pipetted from the top of the tube and five from the bottom immediately after vortexing. The total number of pollen grains in each tube was then estimated by multiplying the mean number of pollen grains in 2 µL by the dilution ratio. A Mann-Whitney-Wilcoxon test was performed to compare the mean pollen deposited by each pollinator.

Results

We performed 23 hours of day observations and 18 hours of night observations throughout ten days of field work, from January 19th to January 28th 2018. Nine populations were studied and the number of receptive flowers in each populations varied between 3 to 17 (SUPPLEMENTARY MATERIAL TABLE 1). Bee pollination came from two distinct populations while all bat pollinations were observed in a single population. Consequently, we could not properly assess the variation amongst populations. Bats were the most abundant pollinators with a visitation rate of 0.121 with 95% confidence interval (CI) [0.0739, 0.182] visits per hour per flower (TABLE 1), however, species identification could not be confirmed with the video camera. Bee pollination of *R*. *bicolor* was rarer, with a visitation rate of 0.0176 95% CI [0.0048, 0.045] visits per hour per flower. We were not able to photograph or capture bees, so their identification is tentative. Bees appeared to represent members of the genus *Anthophora* based on the color and shape of the head, thorax and abdomen, and their size.

No hummingbird was observed pollinating *R*. *bicolor,* which results in a visitation rate of 0. However, hummingbirds were virtually absent from the park. Only 4 individuals (three *Mellisuga minima* and one *Archilochus colubris*) were observed during our ten days of field work in the park. Hummingbirds were observed to be abundant in the park during a previous research expedition (S. Joly, pers. obs., 2014). Drastic changes in the decline of hummingbird populations is also supported by the testimony of four park guides hired during our research expedition.

Three types of pollen were observed on the slides. Gesneriaceae pollen is easily recognised by its small, pale, oval-shaped tricolporate pollen with three prominent colpi. Two other types of pollen were also observed but could not be identified. One was large, dark and circular (henceforth called unknown pollen 1) and the other had a triangular shape and ornamentations (unknown pollen 2). The pollen of different Gesneriaceae species is difficult to distinguish under a microscope (Beaufort-Murphy, 1983), but other species were relatively rare in the park and were not present within 500 m of the studied plants.

Of the three types of pollen observed, the Gesneriaceae pollen was the most abundant (FIGURE 3). The maximum number of pollen grain deposited for the unknown pollen 1 and 2 was 9.2 (standard error (se) = 2.05) and 35 (se = 35.19) respectively, but they were often completely absent on sampled stigmas. Pollen of *R*. *bicolor* was deposited by both bats and bees, while the two other types of pollen were only deposited by bats (FIGURE 3). The Gesneriaceae pollen laid on the stigma by bats per visit (mean = 21868, se = 4648, min = 4675, max = 44945) was more abundant than the pollen deposited by bees (mean = 4813, se = 2592 min = 1945, max = 12572; Mann-Whitney-Wilcoxon test, p=0.04176). For both pollinators, the amount of pollen deposited varied strongly between visits.

The pollinator performance of bats was 2646 pollen grains deposited per flower per hour on average, versus 84 pollen grains deposited per flower per hour for bees (TABLE 1). For hummingbirds, pollinator performance could not be measured as we did not observe any hummingbird pollination or hummingbird visits.

Table 1. Pollinator mean visitation rate, mean single visit efficiency and overall pollinator performance. Sample sizes are indicated for visitation rates (number of visits) and single visit efficiency (number of pollinations). The 95% confidence intervals are indicated and estimated from the expectation from a Poisson distribution for the visitation rate and from standard errors for the single visit efficiency.

Pollinator	**Bats**	**N (bats)**	**Bees**	**N (bees)**
Visitation rate *Mean pollinator visits per flower per hour*	0.121, 95% CI [0.0739, 0.182]	21 visits	0.0176, 95% CI [0.0048, 0.045]	4 visits
Single visit efficiency *Mean number of pollen grains deposited on the stigma per visit*	21868, 95% CI [12758, 30978]	12 pollinations	4813, 95% CI [0, 9893]	4 pollinations
Pollinator performance *Mean number of pollen grains deposited per flower per hour*	2646	n.a.	84.71	n.a.

Pollinator behaviour

Bats first started to be seen around *R. bicolor* after sunset, between 7pm and 8pm. At first, the bats were only observed flying around the plant before starting to pollinate them. Visitation sometimes occurred repeatedly on the same flower (flowers not receptive anymore of with the stigma removed still offer nectar), sometimes within a short time lapse. The bat contacted the flower in a fraction of a second for each visit and then left without visiting another flower from the same population. In contrast, bees tended to stay a relatively long time (ca. one minute) on a flower collecting pollen, and generally passed to a neighbouring flower. We know from previous observation-based studies (S. Joly pers. obs., 2014) that hummingbirds also pass from one flower to another of the same population (not always from the same plant) when they pollinate.

DISCUSSION

We studied the pollination biology of *Rhytidophyllum bicolor*, a species endemic to Haiti for which no pollination data was previously available. Combined with previous partial observation data, observations have shown that *R. bicolor* is pollinated by bats, hummingbirds and bees. Given that *R. bicolor* is visited and likely pollinated by functionally distinct pollinators, it can be considered a generalist. Yet, because of the small number of species

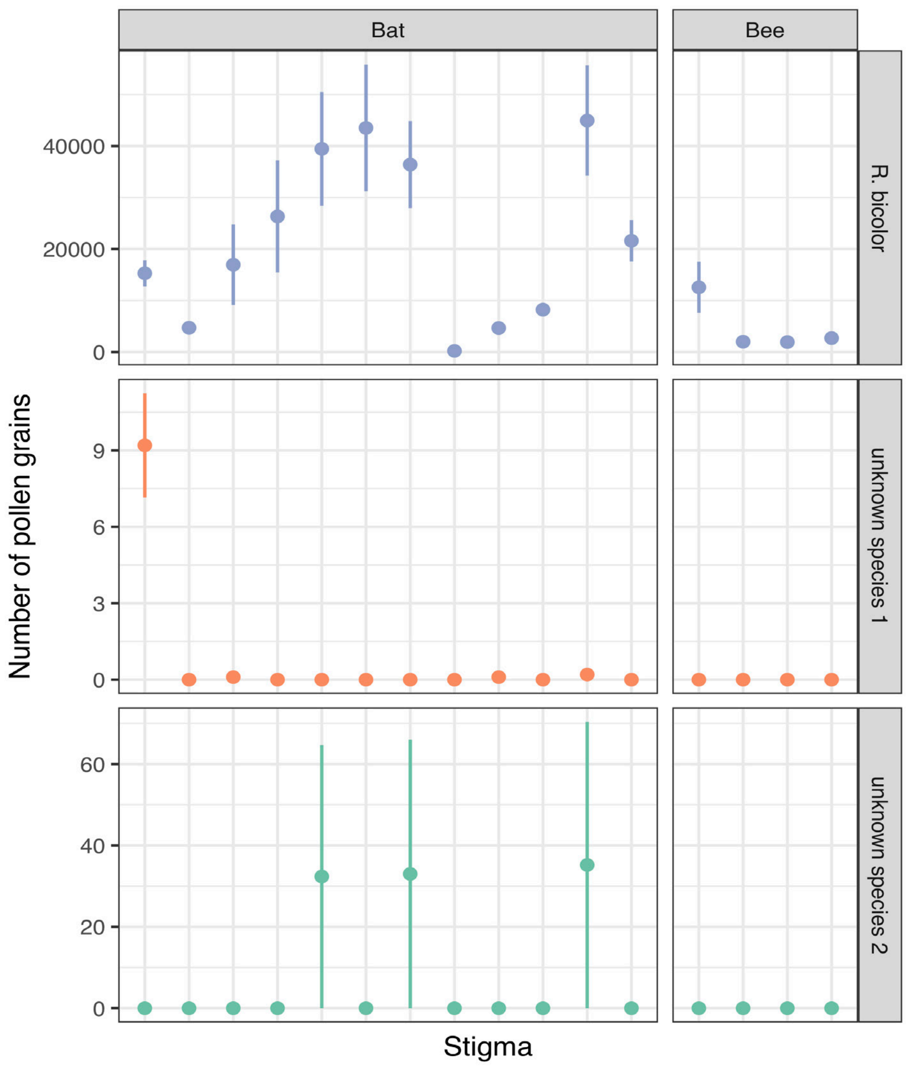

FIGURE 3. Estimates of pollen grains of *R. bicolor* and two unknown pollens deposited during a single visit by each type of pollinator. Each point column in the graph represents a different stigma. Errors bars represent the standard errors of the technical replicates.

involved, this strategy is sometimes called mixed-pollination or multimodal (e.g., bimodal) pollination (Gómez & Zamora, 2006; Herrera, 2005; Niemirski & Zych, 2011; Ollerton et al., 2007). This mixed-pollination strategy with hummingbirds, bats and bees is frequent in Antillean Gesneriaceae (Martén-Rodríguez & Fenster, 2008; Martén-Rodríguez et al., 2009; Martén-Rodríguez et al., 2015) and has been shown to have evolved several times independently (Joly et al., 2018; Martén-Rodríguez et al., 2010).

Our study is the first in Antillean Gesneriaceae to quantify single visit efficiency of pollinators and calculate pollinator performance. This information is important to understand the role that different pollinators can play on the evolution of flowers in a species (Armbruster, 2014; Freitas, 2013; Ne'eman et al., 2010). Unfortunately, we were not able to estimate single visit efficiency for hummingbirds. We did, however, find that bats were more efficient than bees for depositing pollen on the stigma of *R. bicolor*. In terms of overall pollinator performance, bats were better than bees with both a higher visitation rate and higher pollinator performance. Nectarivorous bats are important pollinators in the tropics and have been shown to be effective pollinators on generalist species (Aguilar-Rodríguez et al., 2016; Nassar et al., 1997), sometimes more than hummingbirds (Muchhala, 2003; Muchhala & Thomson, 2010; Queiroz et al., 2016) even if they are less frequent visitors (Law & Lean, 1999). We note, however, that single-visit efficiency of bees is not negligible for *R. bicolor*, as is the case for other pollination generalists (Aguilar-Rodríguez et al., 2016; Nassar et al., 1997). Indeed, even if visits of bees are rare, the pollen deposited in a single visit has the potential of fertilizing a good fraction of the thousands of ovules present in the ovary of each flower and do contribute to the reproduction of *R. bicolor*. Although the number of ovules per flower is not known for *R. bicolor*, it varies between 1700 and 3000 for two new world Gesneriaceae investigated, *Besleria trifolia* and *Drimonia rubra* (Feinsinger et al., 1986). If these numbers are indicative of ovule numbers in *R. bicolor*, the number of pollen grains deposited by bees could well exceed the number of ovules per flower in most visits. Note, however, that the amount of deposited pollen represents the female function of the flower. Because bees collect important amounts of pollen grains for consumption they could have a negative impact on the male flower function and further reduce their importance as pollinators compared to hummingbirds.

Unfortunately, we were unable to estimate the single visit efficiency and the pollinator performance of hummingbirds because they did not pollinate *R. bicolor* during our study. This is clearly a consequence of the low population densities of hummingbirds at the time of the study, which were likely the result of the passage of Hurricane Matthew through the Pic Macaya Park on October 4th, 2016, with winds over 240 km/h. Based on previous pollination studies of Antillean Gesneriaceae, we could have expected hummingbirds to have visitation rates very similar to that of bats (Martén-Rodríguez & Fenster, 2008; Martén-Rodríguez et al., 2009; Martén-Rodríguez et al., 2015), but further studies when the hummingbird populations have recovered will be needed to properly estimate the pollination performance of hummingbirds for *R. bicolor*.

Many studies have proposed that the higher preponderance of generalist pollination strategies on islands compared to the continent could be at least partially explained by the temporal variation of pollinator populations (Armbruster & Baldwin, 1998; Gómez & Zamora, 2006; Martén-Rodríguez et al., 2009; Waser et al., 1996; Wiley & Wunderle, 1993). Indeed, Caribbean islands are known to be subjected to frequent natural catastrophes (Wiley & Wunderle, 1993). Our study is a good example; Hurricane Matthew had a strong impact on hummingbirds populations, likely through direct mortality as well as indirect mortality due to depleting part of their food sources via the loss of flowers (Donihue et al., 2018; Spiller et al., 1998; Wiley & Wunderle, 1993; Willig et al., 2010). By measuring the presence of pollinators, their efficiency and their visitation rate, the recovery of pollinator populations could be better understood, as was done by Wiley and Wunderle (1993). Unfortunately, there was no quantification of the hummingbirds population before Hurricane Matthew, but personal observations (S. Joly, 2014) and testimonies by park rangers confirmed a huge drop in hummingbird abundance. It is in such situations where a generalist pollination strategy becomes advantageous. Indeed, even if the hummingbird populations in the park Pic Macaya were almost completely depleted by Hurricane Matthew, *R. bicolor* could still rely on its other pollinators for its reproduction. The bat populations were also strongly affected by the Hurricane when compared to their abundance in 2014 (S. Joly, unquantified pers. obs.), and as such visitation rates might be affected. But bats were still sufficiently abundant in 2018 to pollinate *R. bicolor* and consequently ensure its reproduction. Although pollination generalist strategies are frequent in Antillean Gesneriaceae, none have yet to be reported from the continent (Martén-Rodríguez et al., 2015). These observations could be potentially linked to the fact that ecological generalists tend to have lower extinction rates in general (McKinney, 1997; Raia et al., 2016).

Further studies are needed to measure the performance of pollinators in specialist and generalist plant species and to better understand their role in the evolution of species at both microevolutionary and macroevolutionary levels. The Antillean Gesneriaceae represents an ideal group for such studies because it allows for comparison of pollinator efficiencies among pollination strategies, between species with a given strategy, and on different islands. Additionally, as hummingbird and bat populations are likely to eventually return to pre-hurricane levels, future pollination studies of *R. bicolor* could contribute to better understand the fluctuation of hummingbird and bat populations in the Antilles and their impact on the reproductive strategy of *R. bicolor*.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found at *Selbyana* online.

SUPPLEMENTARY TABLE 1. Field notes collected during the pollination observations on *Rhytidophyllum bicolor*.

ACKNOWLEDGEMENTS

The authors thank Gonzalo Bilbao for field assistance, William Cinea, Sadgina Laguerre and Adrien for field trip logistics, and our field guides Pierre Honnête, Franklin, Hectnor and Bel Jean. We thank the associated editor, John L. Clark, and an anonymous reviewer for their constructive comments on a previous version of this manuscript. This study was supported by a Jacques Rousseau grant from the Institut de recherche en biologie végétale to JF and by a Discovery grant from the Natural Sciences and Engineering Research Council of Canada to SJ (402363-2011).

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