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EDITED BY
Emilio Badalamenti,
University of Palermo, Italy

REVIEWED BY
Ning Li,
Nanjing Xiaozhuang University, China
Rafael Silveira Bueno,
University of Palermo, Italy

*CORRESPONDENCE
Elena Babiychuk
✉ babiychuk.elena@gmail.com

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Conservation of animal–plant mutualistic networks is essential to prevent functional extinction of the narrow endemic morning glory *Ipomoea cavalcantei* in Amazon canga ecosystems

Elena Babiychuk^{1*}, Juliana Galaschi Teixeira¹, Lourival Tyski²,
Vera L. Imperatriz-Fonseca^{1,3} and Sergei Kushnir⁴

¹Desenvolvimento Sustentável, Instituto Tecnológico Vale, Belém, Pará, Brazil, ²Diretoria de Licenciamento Ambiental/Gerência de Estudos Técnicos de Longo Prazo, Vale S.A., Parauapebas, Pará, Brazil, ³Ecology Department, Biosciences Institute, São Paulo University, São Paulo, Brazil, ⁴Oak Park Crops Research Centre, Teagasc, Carlow, Ireland

Current studies of animal–plant mutualistic interaction networks and species climate change resilience call for redesigning biodiversity conservation management toward preventing species coextinction cascades and using interspecific hybridization as a species conservation tool. The upgrade of conservation management is urgent for narrow endemic plant species highly vulnerable to habitat destruction and defaunation. *Ipomoea cavalcantei* is a red-flowered, self-incompatible, narrow endemic morning glory confined to Amazon savanna-like ecosystems known as canga. Mining cangas reduces *I. cavalcantei* range, population sizes, and standing phenotypic variation. Here, we advance our understanding of the pollinator network that sustains *I. cavalcantei* reproductive success and interspecific gene flow. We show that ello sphinx, *Erinnyis ello*, is a new flower visitor in our model foraging nectar on *I. cavalcantei* and sister species *Ipomoea marabaensis* in cangas. We describe legitimate visiting of *I. marabaensis* flowers by the long-billed starthroat hummingbird, *Helimaster longirostris*. On artificial flower displays, hawkmoths and hummingbirds readily foraged on the magenta-colored flowers of *I. cavalcantei* × *I. marabaensis* natural hybrids. Thus, a new pollinator, the ello sphinx, and previously unknown *Ipomoea*–hummingbird interactions may sustain interspecific gene flow that could enhance the species' adaptive potential and be considered a conservation tool. Our results suggest that the overall reproductive success of *I. cavalcantei* is likely dependent on the long-billed hummingbird species. To avoid functional extinction, e.g., reduced genetic diversity due to pollinator loss, conservation must include assessing and monitoring the abundance and richness of hummingbird species at fragments of the remaining historical range and new introduction sites.

KEYWORDS

endemic, hummingbird, hybrids, *Ipomoea*, conservation, Amazon

1 Introduction

Global biodiversity is in decline (Butchart et al., 2010; Pimm et al., 2014), suggesting that the world has entered a sixth mass extinction event (Barnosky et al., 2011; Cowie et al., 2022), which represents the most serious environmental threat (Ceballos et al., 2020). Assessment of census extinctions, meaning where no individuals survive (Cronk, 2016), indicated that approximately 600 plant species have become extinct at a rate surpassing the background extinction rate (Humphreys et al., 2019). Meta-analyses estimated that extinction threatens approximately 39% of all vascular plant species (Lughadha et al., 2020), and many may be functionally extinct (Cronk, 2016). Among the drivers of species extinction, habitat destruction, particularly in humid tropical forests, is one of the primary causes (Pimm and Raven, 2000; Le Roux et al., 2019). Narrow endemic plant species are especially vulnerable to habitat destruction (Lavergne et al., 2004; Médail and Baumel, 2018).

The mutualistic interactions between plants and their animal pollinators and seed dispersers underpin much of Earth's biodiversity (Bascompte and Jordano, 2007). These interactions create complex networks with a well-defined structure that contribute to the persistence of biodiversity (Bascompte et al., 2006; Gonzalez et al., 2011). Network analysis indicates that phylogenetic effects on interaction patterns could trigger coextinction cascades among related species (Rezende et al., 2007). Coextinction cascades from plants to animals can amplify the impacts of climate change (Schleuning et al., 2016). The ability of plants to adapt to climate change through range shifts facilitated by seed dispersal is compromised by 60% due to defaunation of mammals and birds (Fricke et al., 2022). Defaunation also diminishes pollen dispersal, thereby decreasing the genetic diversity of plant populations (Wessinger, 2021). This threat is more significant in bird-pollinated plants than in those pollinated by insects (Krauss et al., 2017). Thus, shifting the focus from species census to interaction networks is necessary to achieve pressing conservation management and restoration ecology goals for conserving biodiversity (Harvey et al., 2017).

Interspecific hybridization is a natural process with contrasting roles in evolution. On the one hand, hybridization can lead to species extinction by genetic and demographic swamping (Levin et al., 1996; Todesco et al., 2016). On the other hand, hybridization can generate novel intraspecific phenotypic variation (Schmickl et al., 2017), give rise to new species (Yakimowski and Rieseberg, 2014), facilitate genetic rescue and demographic recovery (Whiteley et al., 2015), and underpin adaptive introgression (Arnold and Kunte, 2017; Schmickl et al., 2017; Bock et al., 2018; Oziolor et al., 2019). The two side effects created a controversy in setting appropriate conservation policies to treat hybridization and introgression (Allendorf et al., 2001). The current loss of biodiversity raises the question of whether organisms will adapt in time to survive the current era of rapid environmental change. Today's conservation biology, therefore, must consider hybridization as a conservation management tool that may enhance the adaptive potential and survival of the species (Chan et al., 2019; Quilodrán et al., 2020).

The most noticeable endemic plant in the Amazon canga ecosystems is *Ipomoea cavalcantei*, which belongs to the morning glory family Convolvulaceae (Figure 1A; Austin, 1981). *I. cavalcantei* is exclusively found in Brazil's Carajás National Forest on five northern canga islands (Figure 1I; Babiychuk et al., 2017). *Ipomoea marabaensis* is a sister species inhabiting cangas with a broader distribution (Figures 1C, I; Austin and Secco, 1988). Although the two species primarily exhibit allopatric distribution, sympatry has been found in the N4 and N5 cangas (Figure 1I; Babiychuk et al., 2019). Both species display significant phenotypic variation and molecular diversity, suggesting that current populations are near the species' center of origin (Figure 1B; Babiychuk et al., 2019). The economically valuable high-grade iron ore deposits beneath cangas drive mining operations in the Carajás National Forest. On the North Ridge of the Carajás National Forest, where the N4 and N5 mines are located, 45.6% of the canga vegetation was lost between 1973 and 2016 (Souza-Filho et al., 2019), whereas the allopatric cangas N1, N2, and N3 remain intact (Figures 1H–J; Supplementary Table S1). *I. cavalcantei* and *I. marabaensis* are both self-incompatible species with flowers that provide significant rewards for pollinators, averaging 64 ± 19 and 75 ± 13 μ L of nectar, respectively. Therefore, their reproductive success and the maintenance of genetic variation depend entirely on pollen dispersal by pollinators. Additionally, *I. cavalcantei* and *I. marabaensis* readily hybridize, producing fertile F1 hybrids with magenta-colored flowers (Figure 1B). However, the pollinators of the magenta-colored hybrid flowers remain poorly understood (Babiychuk et al., 2019). Thus, canga conservation management must focus on a more thorough characterization and understanding of the plant–animal interaction network's composition and functioning, shifting toward preserving the essential network properties that underpin biodiversity persistence and climate change resilience.

Contrasting flower trait suites, such as red versus pale lavender flower color and exerted versus inserted stamens and styles, indicated that *I. cavalcantei* is an ornithophile, a species pollinated by birds, while *I. marabaensis* is bee-pollinated, known as a mellitophile (Fenster et al., 2004). The initial analysis of flower visitor assemblages showed that several native animal species accessed *I. cavalcantei* flowers legitimately, i.e., through the corolla tube opening, suggesting a potential functional role as pollinators (Babiychuk et al., 2019). Stingless *Trigona* spp. bees were common, displaying two types of behavior: nectar robbing by chewing through sepals and corolla (illegitimate visiting) and destructive behavior within the flower tube (legitimate visiting), which damaged the flower's reproductive organs, often leading to the complete absence of stamens and styles. This behavior suggested that the contribution of stingless bees to the reproductive success of *I. cavalcantei* was likely negative. Long-tongued orchid bees, *Eulaema cingulata* and *Eulaema bombiformis*, also collected nectar from *I. cavalcantei* flowers, accounting for ca. 2% of total legitimate visits when excluding *Trigona* bee visitations. Thus, preliminary data showed that several species of hummingbirds were the most frequent legitimate visitors of *I. cavalcantei*, comprising ca. 98% of visits. In this study, we aimed to better

understand which hummingbird species could be the most important for the reproductive success of *I. cavalcantei*. Additionally, the native species of flower visitors that could facilitate the formation of interspecific *I. cavalcantei* × *I. marabaensis* hybrids and the recruitment of hybrids into the interspecific gene flow remained largely unknown. A more comprehensive understanding of the *I. cavalcantei* × *I. marabaensis* hybrid flower visitor network was necessary due to its implications for the conservation management of *I. cavalcantei*. Thus, we questioned whether our model included undiscovered plant–pollinator interactions that could underpin the process of interspecific hybridization and gene flow.

2 Results

2.1 Balancing nectar robbing and legitimate foraging could influence hummingbird pollinator services

In canga ecosystems, six hummingbird species were recorded foraging for nectar on ornithophile species *I. cavalcantei*, *Cuphea annulata* (Figures 1D, E), and *Dyckia duckei* (Figures 1F, G), including black-throated mango (*Anthracothorax nigricollis*; Greeney et al., 2020); grey-breasted sabrewing (*Campylopterus largipennis*; Züchner et al., 2021); long-billed starthroat (*Heliothyrax longirostris*; Stiles and Boesman, 2020); long-tailed hermit (*Phaethornis superciliosus*; Hinkelmann et al., 2020); glittering-throated emerald (*Chionomesa fimbriata*; Weller et al., 2021); and fork-tailed woodnymph (*Thalurania furcata*; Stiles et al., 2020), see Figure 2. In our sampling, the occurrence of the hummingbird species varied between locations (Supplementary Table S2). Only glittering-throated emerald and fork-tailed woodnymph were observed in allopatric *I. marabaensis* cangas N6 and N8. Other hummingbird species were found in cangas with the presence of *I. cavalcantei*. The hummingbird species with the longest bills (ranging from 38.8 ± 2.1 to 25.5 ± 0.8 mm) exhibited legitimate feeding behavior (Supplementary Table S3) on *I. cavalcantei* flowers, which have narrow flower tubes with a mean length of 38 ± 4.2 mm (Babiychuk et al., 2019). These hummingbird species did not forage on *C. annulata* or *D. duckei*. The hummingbird species with shorter bills, namely, fork-tailed woodnymph and glittering-throated emerald, were facultative nectar robbers with 28% and 68% legitimate visits, respectively (Supplementary Table S3; Supplementary Figures S1F, G). Additionally, fork-tailed woodnymph and glittering-throated emerald legitimately foraged on *C. annulata* and *D. duckei*, accounting for 67% and 69% of combined flower visitations among the three plant species, respectively (Supplementary Table S3). During the dry season, very few plant species flower in canga. The most notable was evergreen *Norantea guianensis*, which was found in all recognized canga microhabitats, including rocky outcrops, “terra firme”, and low forests. The black-throated mango and fork-tailed woodnymph were feeding on *Norantea* flower inflorescences (Figure 2; Supplementary Table S3), indicating that these hummingbird species could be (semi)permanent canga residents.

Hummingbirds can be primary or secondary nectar robbers (Irwin et al., 2010). Within three distinct components of flower function, i.e., attraction, reward, and filtering mechanisms, the nectar chamber likely plays a role in filtering among flower visitors and is typically associated with hummingbird pollination (Stiles, 1981; Gill, 1987; Gonzalez et al., 2021). The nectar produced by *I. cavalcantei* and *I. marabaensis* flowers was primarily contained in the nectar chamber (Supplementary Figures S1A–D). The centrally located style and the abundant epidermal hairs on the stamens, particularly in *I. cavalcantei* (Supplementary Figure S1C), obstruct access to the nectar chamber through five narrow passages. In cangas, nectar robbing by large carpenter bees, *Xylocopa* spp., and stingless *Trigona* spp. bees was prevalent (Babiychuk et al., 2019). Unable to enter the narrow flower tubes of *I. cavalcantei*, carpenter bees use their maxillae to make slits in the flower corollas (Supplementary Figure S1E). We examined 47 flowers from three *I. cavalcantei* individuals in canga N1 to capture a $\geq 95\%$ confidence interval in a nectar-robbing pattern. All flower corollas exhibited slit-like perforations. The examination of flowers robbed by glittering-throated emerald and fork-tailed woodnymph revealed longitudinal slit perforations, a typical feature of carpenter bee robbing. This observation indicates that those hummingbirds may be secondary nectar robbers utilizing the flower tube perforations created by carpenter bees. In an *ex situ* collection, the black-eared fairy hummingbird (*Heliothyrax auritus*; Schuchmann et al., 2020) was identified as a primary, likely obligatory nectar robber on both *I. cavalcantei* and *I. marabaensis* (Supplementary Tables S3, Supplementary Figures S1H, I). Unlike carpenter bees, the hummingbird created puncture-like perforations in the sepal-covered proximal corolla tube section, accessing the nectar chamber directly (Supplementary Figures S1J, K).

2.2 Long-billed starthroat hummingbird was a legitimate visitor of *I. marabaensis* flowers

Previously, we did not obtain evidence of hummingbirds foraging for nectar on *I. marabaensis* (Babiychuk et al., 2019). This result was surprising because i) the flowers of this species produced more nectar than those of *I. cavalcantei*; ii) the passage to the nectar chamber appeared less restrictive (Supplementary Figure S1B versus S1C); and iii) mean nectar offer is thought to be the only parameter related to hummingbird visitation frequency, regardless of flower color or pollination syndrome (Waser et al., 1996; Maruyama et al., 2013). However, while monitoring plants in an *ex situ* collection that simulated sympatry, i.e., the co-occurrence of two *Ipomoea* species, we documented five instances of legitimate visits to *I. marabaensis* flowers by the long-billed starthroat (Figure 2). To validate this observation in canga settings and to characterize the flower visitors of the *I. cavalcantei* × *I. marabaensis* hybrids, we presented hummingbirds with artificial flower displays prepared as described in the Materials and Methods. We tested 52 displays, one per day per location, at six sites: cangas N1, N2, N3, N4, N8, and an *ex situ* collection (Supplementary Table S4).



FIGURE 1

Plant species structuring plant–hummingbird interaction networks in canga and *Ipomoea calycanthoides* range. The red-colored *I. calycanthoides* (A) and pale lavender-colored *Ipomoea marabaensis* (C) are predominant flower types in canga ecosystems. (B) The flowers were harvested from plants rescued for *ex situ* collection that comprised white, pink, purple, and magenta colors, with the last flower type from natural interspecies hybrids. *Cuphea annulata* is a densely branched perennial shrub (D) that produces large masses of red-orange-colored, tubular flowers (E). A bromelia *Dyckia dyckii* developed orange-colored inflorescence stalks (F) bearing orange-red tubular flowers (G). (I) The map illustrates the study locations. Dark green color is due to the rain forest that covers eroding Carajás Mountain range, the part of which is preserved within the Carajás National Forest. Canga savannas evolved on iron lateritic rocks of the mountain plateaus that are false-colored in Adobe Photoshop CS6 to emphasize the morning glory species distribution. The allopatric *I. calycanthoides* populations are found in cangas N1, N2, and N3, which are in red, according to the predominant flower color of the species. Lavender-colored cangas N6 to N9, Morro 1 (M1) and Morro 2 (M2), Tarzan (T), and S11 plateau (S11) host *I. marabaensis* allopatric populations. Magenta color of the cangas N4 and N5 fragments signifies species co-occurrence, i.e., sympatric cangas. Sossego (SO) is a granitic inselberg populated by *I. marabaensis*, where the species grows along the boundaries of exposed granitic bedrocks and the forest. The yellow dot corresponds to the location of the *ex situ* collection. Cangas are named in accordance with the geological survey maps. The geographic map was generated using the software QGIS version 2.18 (<http://qgis.org>) based on satellite imagery source (<https://mt1.google.com/vt/lyrs%3Ds%26x%3D%7Bx%7D%26y%3D%7By%7D%26z%3D%7Bz%7D&zmax=20&zmin=0>) from Google (Google Maps satellite Carajás, Pará, Brazil; retrieved December 16, 2018). (H, J) Close-up satellite images downloaded from Google Earth Pro to compare mining exploration of cangas N4 and N5 in 1985 and 2024, respectively. The red bar is 1 km.

Hummingbirds did not visit displays in cangas N1 (10 displays, 35 videos each with a 20-minute duration), N2 (four displays, 12 videos), and N3 (15 displays, 34 videos). At the boundary with the forest in the canga N4 fragment 1 (Supplementary Table S1), two hummingbird species, the long-billed starthroat and the long-tailed

hermit, visited three and four displays out of the 11 presented, respectively (Supplementary Figure S2; Supplementary Table S5). Out of 10 displays at the *ex situ* collection, the long-billed starthroat also foraged on three displays, and additionally, the black-eared fairy robbed nectar from both *Ipomoea* species and their hybrids on

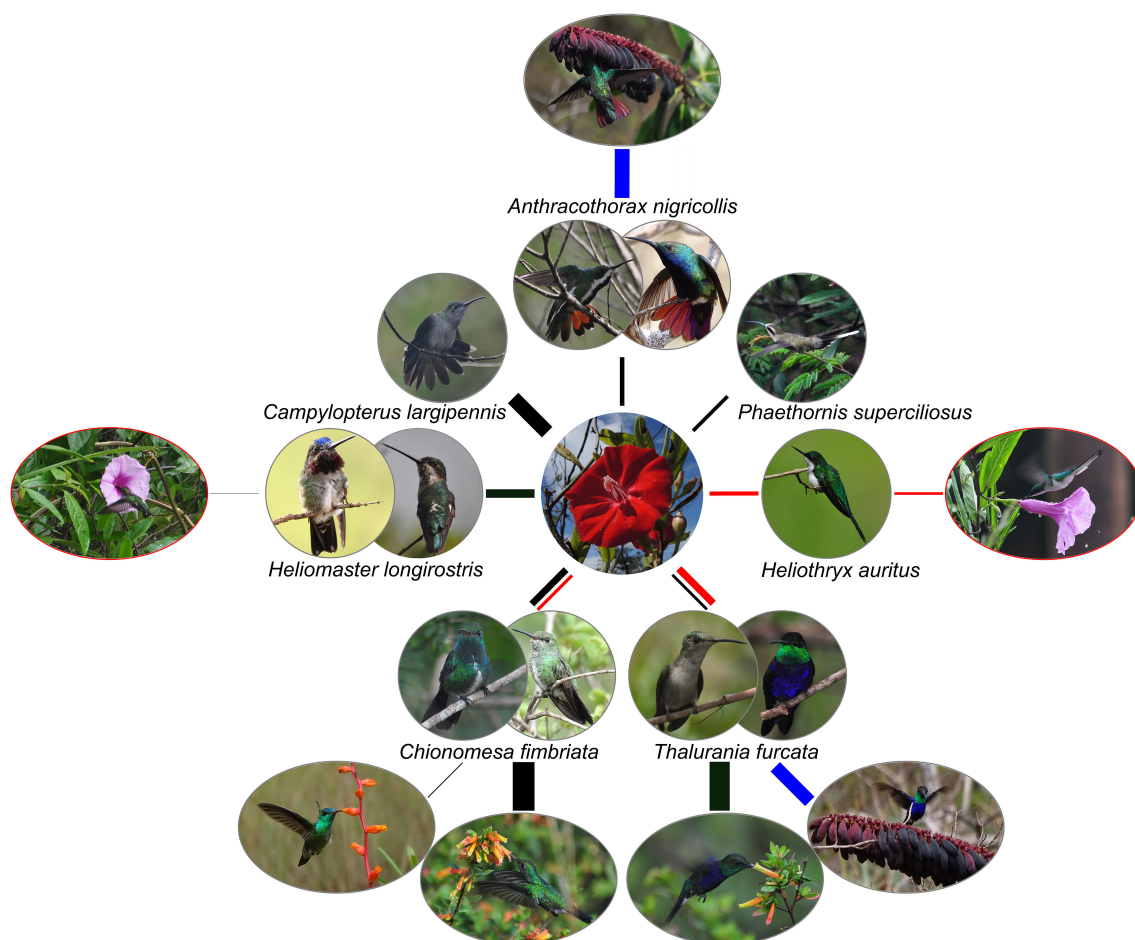


FIGURE 2

Summary of hummingbird species foraging on canga plant species. The plant–hummingbird interaction network is centered on the red-colored *Ipomoea cavalcantei* flower. Other plant species are represented by the lavender-colored *Ipomoea marabaensis*, orange flowers of *Cuphea annulata* and *Dyckia duckei*, and purple extrafloral cup-shaped nectaries of *Norantea guianensis*. Hummingbird species are identified by their Latin names. Sexual dimorphism is illustrated, permitting image availability. Flower visitations of canga plant species are indicated by the connecting lines (edges). The thickness of the edge reflects bird–plant interaction frequencies; see [Supplementary Table S3](#) for observed interactions. Legitimate nectar feeding and nectar robbing behaviors are shown by the edge color, black and red, respectively. Connectors to *N. guianensis* that flower during the dry season are colored in blue. Images encircled by red lines are illustrations of a hummingbird foraging on *I. marabaensis* flowers as observed in *ex situ* collection.

four different displays in which flowers were not placed in water-filled plastic tubes ([Supplementary Table S5](#); [Supplementary Figure S2](#)). The Kruskal–Wallis tests revealed significant differences in visitation rates among flower types for the long-billed starthroat: $H(6) = 74.0$, $p < 0.0001$, and the long-tailed hermit: $H(5) = 29.0$, $p < 0.0001$. Post-hoc pairwise Dunn’s tests with Bonferroni correction identified specific differences among flower colors. *H. longirostris* showed highly significant differences in visitation among flower types on artificial displays ([Figure 3A](#)). For example, there were notable contrasts between magenta and red ($p = 1.1 \times 10^{-4}$), pink and purple ($p = 5.2 \times 10^{-5}$), and lavender and white ($p = 0.0188$). This species clearly distinguishes between different flower types and may prefer certain color groups, such as frequently visiting lavender and magenta-colored flowers. Despite this biological difference, the rank-based Dunn’s test did not find substantial differences between some groups. This could be due to the many tied ranks and the similarly low visitation numbers among certain floral types. The

long-tailed hermit, *P. superciliosus*, showed fewer meaningful differences in flower visitation ([Figure 3B](#)). Notably, lavender vs. red ($p = 0.00025$) and pink vs. red ($p = 0.0043$) were significant, indicating a preference for red flowers over paler colors like lavender and pink. The nectar robber black-eared fairy foraged on floral displays at the *ex situ* site, showing differences in visitation rates in the Kruskal–Wallis test $H(3) = 31.0$, $p < 0.0001$. Dunn’s tests revealed that the species robbed lavender flowers significantly more than red ($p = 9.0 \times 10^{-7}$) and magenta ($p = 0.0146$), indicating a tendency to forage more on pale morphs ([Figure 3C](#)). Analysis of the video footage also highlighted the noteworthy features of *I. marabaensis* visitation by the long-billed starthroat. In six of the nine recorded visits, hummingbirds grasped the limb of the *I. marabaensis* flower while feeding ([Supplementary Figure S2D](#)). Additionally, the corolla limbs of *I. marabaensis* began to flutter upon the bird’s close approach. The corolla limbs sometimes flipped upward, enfolding the bird and touching its wings.

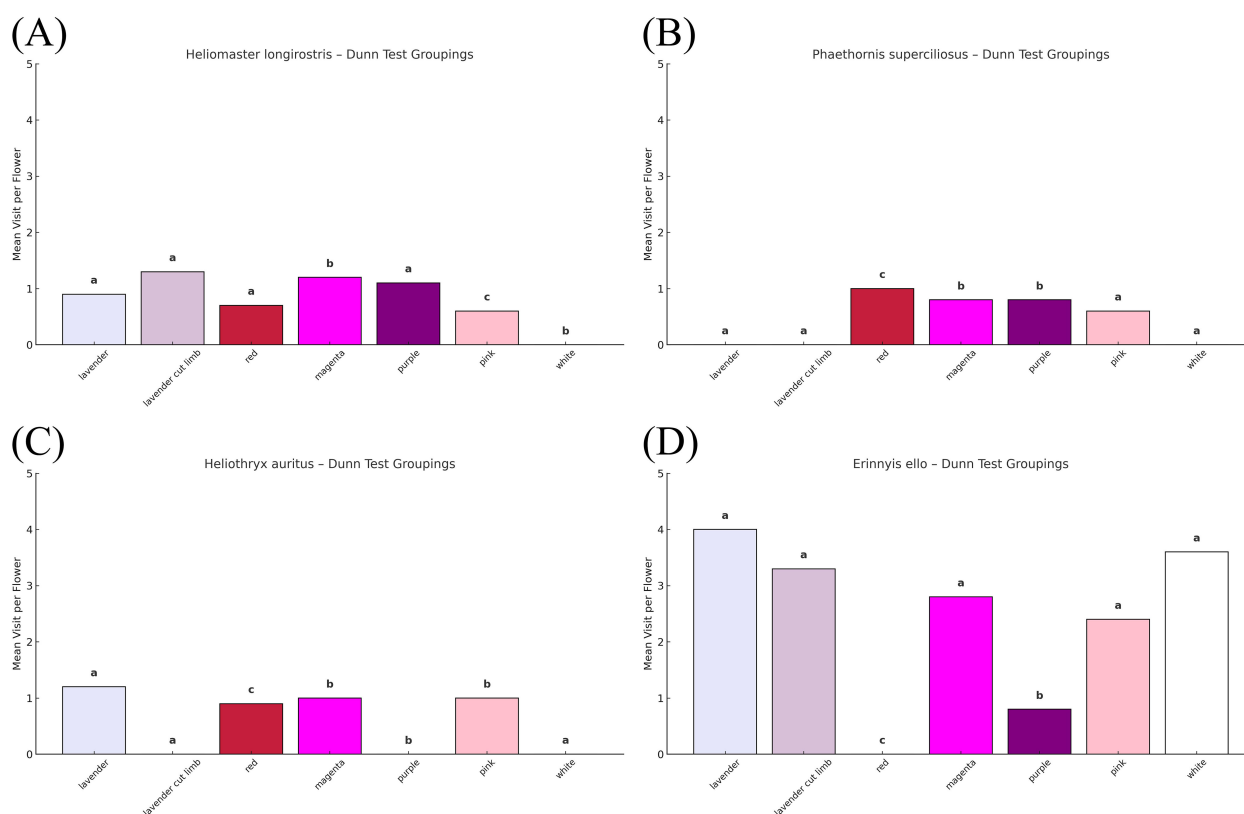


FIGURE 3

Flower visitor preferences on artificial floral displays. Bar plots show mean visitation rates per flower for each floral type. Bars are colored to match natural flower coloration. Letters above bars indicate statistical groupings based on pairwise post-hoc Dunn's tests with Bonferroni correction ($p < 0.05$). Latin names of visitor species are at the bar plot titles: (A) *Heliomaster longirostris*, the long-billed starthroat; (B) *Phaethornis superciliosus*, the long-tailed hermit; (C) *Heliophryx auritus*, the black-eared fairy; and (D) *Erinnyis ello*, the ello sphinx.

2.3 Hawkmoth foraged on *I. cavalcantei* and *I. marabaensis* flowers

To determine whether other groups of plant pollinators were also visiting morning glory flowers, we began fieldwork in 2020 at the start of the *Ipomoea* flowering period. We found that on each day between February 20 and 28, individuals of a single hawkmoth species were foraging for nectar on both *I. marabaensis* and *I. cavalcantei*, at sympatric canga N4; allopatric cangas N1, N2, and N3 (*I. cavalcantei*); and allopatric cangas N6 and N8 (*I. marabaensis*) (Figures 4A, B). We recorded 86 visitations of *I. cavalcantei* and 81 visitations of *I. marabaensis*. The earliest hawkmoth visitations occurred at 8:46 am and the latest at 1:36 pm. In addition to morning glory flower visitations, we noted 110 instances of ello sphinxes foraging on the flowers of *Bauhinia longicuspis* from the Fabaceae family (Figure 4C), indicating generalist behavior. Hawkmoths disappeared abruptly and were not seen again until the end of the field trip, from March 1 to 11. Identification from the acquired digital imagery strongly suggested that the hawkmoth species was ello sphinx, *Erinnyis ello*. As shown in Figure 4B, ello sphinxes landed on the corolla limbs and were able to enter the flower tubes of *I. marabaensis*, which were broad enough to accommodate the large insect's body. The flower tubes of

I. cavalcantei were too narrow for ello sphinxes to enter. These animals landed on the flower limbs such that the hawkmoth's head was near the exerted anthers of *I. cavalcantei* (Figure 4A). Ello sphinxes also foraged on floral displays in allopatric canga N3 and a remaining fragment of sympatric canga N4 (Figures 4D–F; Supplementary Tables S4, S5). The Kruskal–Wallis test revealed significant differences in ello sphinx visitation rates among flower types on artificial floral displays: $H(6) = 33.0$, $p < 0.0001$. Dunn's tests revealed significant pairwise differences, such as lavender vs. purple ($p = 0.0118$), lavender vs. red ($p = 0.0001$), and red vs. white ($p = 0.0008$), indicating that the moth preferred pale-colored flowers like lavender and white and avoided red flowers (Figures 3D, 4D, E). Ello sphinx foraged on magenta hybrid flowers at frequencies not significantly different from lavender or white flowers (Figure 4F).

3 Discussion

Here, we demonstrate that at least two species of hummingbirds foraged nectar from the pale lavender-colored flowers of *I. marabaensis*, which exhibit characteristics of melittophily, or pollination by bees. The long-billed starthroat, *H. longirostris*, and

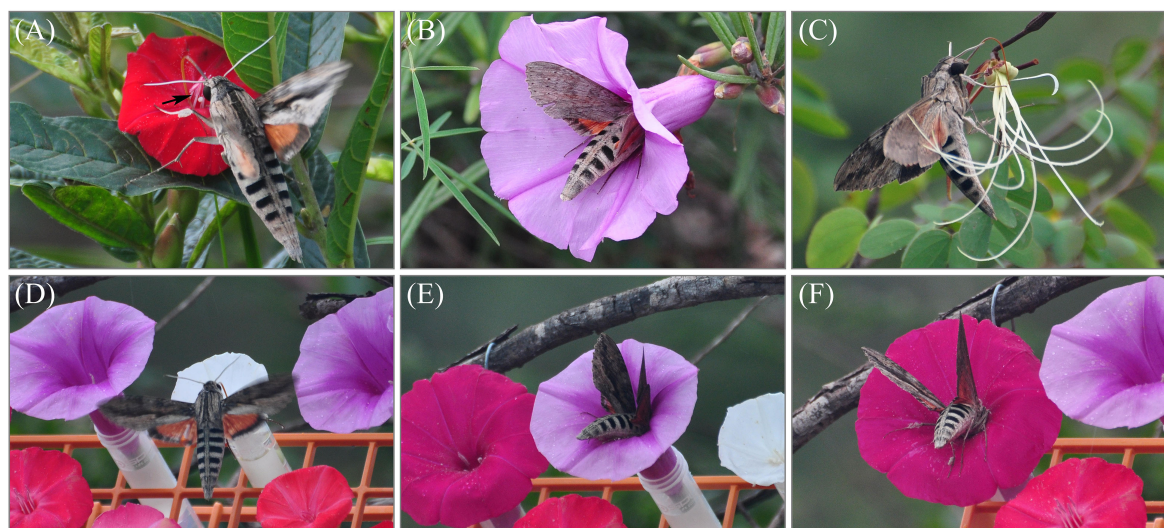


FIGURE 4

Ello sphinx flower visitation in the wild and on artificial floral displays. In canga, *Erinnyis ello* was feeding on flowers of *Ipomoea cavalcantei* (A), *Ipomoea marabaensis* (B), and *Bauhinia pulchella* (C). The hawkmoth foraging on flower displays, white *I. cavalcantei* flowers (D), flower limb trimmed *I. marabaensis* (E), and magenta-colored interspecies hybrids (F). The black arrow in panel (A) indicates the exerted anthers of the *I. cavalcantei* flower.

the black-eared fairy, *H. auritus*, were identified as new potential pollinator and nectar robber of *I. marabaensis*, respectively. Hummingbird foraging behaviors on artificial floral displays indicated contrasting preferences by the long-billed starthroat and the long-tailed hermit, *P. superciliosus*, which are legitimate visitors. The long-tailed hermit favored *I. cavalcantei* and the magenta-colored *I. cavalcantei* × *I. marabaensis* hybrids but did not visit *I. marabaensis* lavender flowers. It is well known that hummingbirds visit different plant species at varying rates (Colwell, 1973; Feinsinger, 1976). Five community roles linking hummingbird foraging strategies to the spatial distribution and defensibility of nectar-bearing floral resources were proposed (Feinsinger and Colwell, 1978; Leimberger et al., 2022). In this classification, both the hermit *P. superciliosus* and the non-hermit *H. longirostris* are considered as high-reward trapliners that repeatedly visit a sequence of spatially dispersed, nectar-rich flowers (Feinsinger and Colwell, 1978). The long-tailed hermit has a longer bill than the long-billed starthroat, measuring 38.8 ± 2.1 compared to 35.0 ± 2.8 mm, which argues against the trait-matching hypothesis as an explanation for the differing visitation rates to *I. marabaensis* flowers. We also report on the movement of *I. marabaensis* flower limbs during hummingbird visits. The biomechanical properties of flowers may influence hummingbird foraging preferences.

We found that the short-billed species, glittering-throated emerald, *C. fimbriata*, and fork-tailed woodnymph, *T. furcata*, were legitimate nectar foragers on ornithophiles with short corolla tubes, facultative nectar robbers on *I. cavalcantei*, and, as previously tested (Babiychuk et al., 2019), were not attracted to nectar-rich *I. marabaensis* tubular flowers. This structuring of pairwise interactions in canga aligns with the known roles of trait-matching and spatiotemporal co-occurrence of interaction partners as primary reasons why hummingbirds visit some plants

more frequently than others (Dalsgaard et al., 2021). However, unlike black-eared fairy, short-billed hummingbirds did not rob *I. marabaensis*, although carpenter bees robbed many flowers in allopatric cangas N6 and N8, which created flower tube perforations that hummingbirds can use to access the nectar chamber, as observed in canga N1 on *I. cavalcantei* flowers. The results suggest that the primary nectar larceny of *I. cavalcantei* by carpenter bees positively correlates with the secondary nectar robber behavior of the short-billed species, reducing the role of glittering-throated emerald and the fork-tailed woodnymph hummingbirds in *I. cavalcantei* reproductive success despite their relatively high abundance in wild canga ecosystems, accounting for 32% and 34% of all plant species visits, respectively (Supplementary Table S3). The absence of the single visit pollination effectiveness (SVE) data is a significant limitation of our work (Page et al., 2021). However, pollination effectiveness and visitation frequencies are often correlated (Page et al., 2021). Additionally, hummingbirds could be more effective pollinators than insects (Leimberger et al., 2022). Current data suggest that in our model, the long-billed hummingbird species, which account for 76% of total legitimate visits, are likely primary pollinators, largely determining *I. cavalcantei* reproductive success in canga.

We show that the long-billed starthroat, *H. longirostris*, hummingbird and ello sphinx hawkmoth, *E. ello*, foraged on both *I. cavalcantei* and *I. marabaensis* flowers. Thus, in addition to the native orchid bees, *Eulaema* spp., and the alien honeybees, *Apis mellifera* (Babiychuk et al., 2019), species from two other distinct pollinator groups could mediate the natural formation of the *I. cavalcantei* × *I. marabaensis* F1 hybrids. The ello sphinx appeared as an ephemeral pollinator and abruptly disappeared by the end of February; thus, their role in the overall reproductive success of morning glories during the flowering period lasting until May needs

to be assessed more thoroughly. Furthermore, in the Amazon regions, the peak of ello sphinx activity was reported to occur at 5–6 am, i.e., before local sunrise. By that time, *I. cavalcantei* and *I. marabaensis* flowers are open, as found in this study, suggesting that reported visitation frequencies are underestimated because fieldwork started at 8 am at the earliest. On floral displays, ello sphinxes favored the pale lavender-colored flowers of *I. marabaensis* and the white flowers of *I. cavalcantei*. *E. ello* is thought to be a nocturnal or crepuscular, short-tongued hawkmoth (Amorim et al., 2013). Many nocturnal hawkmoth-pollinated flowers are white or cream-colored, which offers a contrast to the surrounding environment. Differences in flower visibility between *I. cavalcantei* flower color variants could explain the observed high visitation rates of the white flowers on artificial flower displays. In contrast to data on foraging in natural settings, we did not detect a single feeding attempt on six tested, red-colored *I. cavalcantei* flowers on artificial flower displays. The discrepancy between visitation differences on natural displays of flowers in canga versus artificial flower displays indicated that in distinct plant communities, i.e., *I. cavalcantei* allopatric cangas N1, N2, and N3, the ello sphinx showed the so-called reward economics behavior, e.g., nectar quantity/quality trade-offs influencing pollinator foraging choices. We also need to consider methodological biases caused by limitations of artificial flower displays, such as the absence of scent, foliage cues, and the rigid angle at which flowers are held in tubes, which may skew pollinator preferences.

We demonstrate that the long-billed starthroat, long-tailed hermit, and ello sphinx legitimately foraged on magenta-colored *I. cavalcantei* × *I. marabaensis* flowers. The evolutionary significance of interspecific hybridization relies on hybrid fertility. Our prior manual pollination experiments at *ex situ* collection indicated that *I. cavalcantei* × *I. marabaensis* hybrids were both male and female fertile. In the wild, all examined magenta-flowered hybrids in N4 and N5 canga fragments produced seeds that germinated into fully viable F2 progeny plants, confirming natural female fertility (Babiychuk et al., 2019). The hybrid fertility in our model can support interspecific gene flow, generating phenotypic variation for natural selection. For instance, variation at the *Intensity* locus *I/i*, which encodes the R2R3-Myb protein in *Phlox drummondii*, results in the co-occurrence of plants with light red, dark red, light blue, and dark blue flowers, influencing visitation frequencies by pollinators (Hopkins and Rausher, 2011). A similar intensity locus may determine the intense red, dominant *I* allele, and pale lavender, recessive *i*, in the common flower color types of *I. cavalcantei* and *I. marabaensis*, respectively. Such genetic control could account for pink flowers in sympatric cangas and *I. marabaensis* individuals with intensely colored flowers in canga N6 (Babiychuk et al., 2017). A limitation of our study is that we infer hybrid and color variant flower visitation frequencies from artificial flower displays. Several constraints influenced the use of an artificial flower display experimental design. At the beginning of our studies, we observed hummingbirds foraging on hybrids and color variants found in fragments of cangas N4 and N5. However, the plants of interest

were growing far apart, which made direct comparisons difficult, and only a few hours of fieldwork at those sites were feasible. In the following years, we were unable to access intensely mined sympatric sites. Growing plants with contrasting flower phenotypes adjacent to each other is a common approach reported in several comparative studies of plant–pollinator interactions. Rescuing unique genotypes from the mining-driven local extinction and recreating a sympatry site where all color variants grow together, enabling further experimental work, were key objectives in establishing the *ex situ* collection. However, the pollinator species composition at the *ex situ* site differed from that of the cangas; for example, we have not sighted black-throated mango, grey-breasted sabrewing, long-tailed hermit, glittering-throated emerald, or ello sphinx hawkmoth at the *ex situ* site indicated by a yellow dot in Figure 11. Nevertheless, tracking animal visitors through direct observation in the *ex situ* collection demonstrated that orchid bees (data not shown) and long-billed starthroat hummingbirds foraged on hybrid plants with magenta flowers. Our data suggest that native species of hummingbirds, hawkmoths, and orchid bees are likely candidates for mediating interspecific hybridization and gene flow, resulting in both F1 and F2 progeny in the wild.

Human civilization needs iron. In the coming years, the range of *I. cavalcantei* could be further diminished (Figure 1; Supplementary Table S1). The species persistence can only be ensured at protected fragments of the historical range, the so-called refugees, or through an introduction to new habitats, which are not a guarantee against functional extinction and genetic bottlenecks (Cronk, 2016). Our previous and new results show that to avoid functional extinction, to preserve the species' adaptability, and to avoid genetic bottlenecks, it will be critical to conserve standing phenotypic diversity by systematic collection of seeds from as many individuals as feasible and through the entire remaining species range, followed by seed stock deposition in curated seed banks with seed long-term storage capabilities. At the expanding iron ore mines' edges, an additional rescue effort must be carried out by replanting living plants for *ex situ* collection and/or refugees, focusing on phenotypic variants. Interspecies hybrids were common in sympatry on cangas N4 and N5 (Babiychuk et al., 2019). The evolutionary role of interspecific hybrids can have different consequences. As a positive effect, it can facilitate genetic rescue and demographic recovery (Whiteley et al., 2015) or underpin the introgression of favorable traits, the so-called adaptive introgression, which explains recent adaptations to the changing environment (Arnold and Kunte, 2017). The downside of interspecific hybridization is a risk of species extinction by genetic and demographic swamping, for example, of a rare *Eucalyptus tetrapleura* (Rutherford et al., 2019; reviewed Allendorf et al., 2001; Todesco et al., 2016). We do not know if sympatry existed before iron ore mining at Carajás was initiated in the 1980s. The identification of the *I. cavalcantei* individual, a likely migrant, in canga N8, can be due to a geological exploration road connecting N4 to N8 through the surrounding rainforest (Babiychuk et al., 2019), suggesting that mining-associated traffic may have altered historical species distribution, creating new sympatry zones. Interspecific hybrids are often limited to disturbed sites,

endangering rare plant species, for example, *Eucalyptus benthamii* trees (Butcher et al., 2005) and the endemic shrub *Kunzea sinclairii* (de Lange and Norton, 2004). Given the uncertainty about the history of sympatric zones and the possibility of local population extinctions through genetic and demographic swamping, i) *I. cavalcantei* refuge sites must be controlled against *I. marabaensis* migrants, and ii) the new introduction sites must be differentiated as sites with and without *I. marabaensis*. The interspecies hybridization zone, as we knew it in cangas N4 and N5, can be reconstructed in *I. marabaensis*-populated cangas outside of the protected Carajás National Forest. Other introduction sites must be i) *I. marabaensis*-free; ii) at several kilometers from *I. marabaensis* populations, considering the foraging ranges of described pollinators; iii) controlled by genetic monitoring every 5 years; and iv) sun-exposed but near the forest. Most hummingbird species prefer forest habitats (Leimberger et al., 2022). In fragmented tropical forest landscapes, hummingbird visitation rates showed significant and substantial decay with increasing distance to the forest of 10–40 m (Kormann et al., 2016). In the Carajás geographic area, the boundaries between native forest and agricultural land resulting from deforestation appear to be appropriate sites for *I. cavalcantei* introduction. Using *I. cavalcantei* in such natural biodiversity management borders on farms could also enhance hummingbird species abundance, hummingbird species richness and potentially benefit the yields of crops that depend on effective pollinators, e.g., coffee plantations. At public and private parks and gardens, the design and establishment of “hummingbird gardens” using local, native ornithophiles, such as *I. cavalcantei*, *C. annulata*, and *D. duckei*, is strongly recommended.

4 Materials and methods

4.1 Study sites

Fieldwork was carried out in the Carajás National Forest (Pará, Brazil), which comprises 13 Canga islands (Babiychuk et al., 2019). Amazon savanna-like ecosystems known as cangas evolved on iron laterite rock outcrops at similar elevations of ca. 700 m above sea level in the Carajás Mountain range. A mountainous rainforest encircles cangas, indicating the insular type of geographic isolation (Babiychuk et al., 2017). Canga soils are shallow and edaphically restrictive (Schaefer et al., 2016). Dry–wet seasons are partitioned by rain precipitation that varies between <60 and 1,900 mm/month; thus, most canga plants flower during periods of the wet season, November–May. The openness, heat, low nutrients, drought susceptibility, and toxic metal-rich conditions in combination with the insular isolation resulted in highly specialized canga plant communities composed of more than 800 plant species (Mota et al., 2018). The focus species *I. cavalcantei* was restricted to the Northern cangas N1, N2, N3, N4, and N5. Sister species *I. marabaensis* was common in N6, N7, N8, N9, Morro 1, Morro 2, S11 plateau, and Tarzan and had localized occurrence in N4 and N5. Therefore, we distinguished cangas N4 and N5 as “sympatric”; other cangas were designated as “allopatric”. The areas of cangas

and canga fragments, as shown in Supplementary Table S1, were measured using the polygon tool in Google Earth Pro. Work was carried out with permissions per authorization #48272–3 and #63324–1 by the SISBIO (<https://www.gov.br/icmbio/pt-br>), Chico Mendes Institute for Biodiversity Conservation (ICMBio), and Brazilian Ministry of Environment (MMA). The Supplementary Table S1 footnotes detail the additional authorizations and accessibility limitations for work at study sites.

4.2 Morning glory anthesis and field work time frames

To characterize morning glory flower anthesis, we set a Bushnell camera to acquire images every 5 minutes at the *ex situ* collection. Time-lapse tracking of 15 pre-anthesis flower buds showed that *I. cavalcantei* flowers began to open between 2:45 and 3:15 am and were fully expanded at 5:30–5:40 am, i.e., just before sunrise. *I. marabaensis* flowers (n = 45) began to unfold at 2:50–3:30 am and were fully open at 5:30–6:15 am. Morning glory flowers were short-lived and began to show senescence at midday and late afternoon among *I. marabaensis* and *I. cavalcantei* individuals, respectively. As explained in the Supplementary Table S1 footnotes, we were only able to observe the activity of diurnal animal species in the field starting at 8 am at the earliest and ending at 5 pm at the latest, a time frame that excluded nocturnal pollinator groups such as nectarivorous bats and species-rich moths. At the *ex situ* collection, the pollinator visitation of morning glory individuals in BioParque Vale Amazônia (<https://vale.com/pt/bioparque-vale-amazonia>) could be followed at dawn, approximately 5–6 am, or after 5 pm. In the wild, we conducted 64 days of observation, spanning the wet season months of January through May and during the dry season in August. We conducted daily surveys between 8 am and 5 pm when visiting cangas N1, N2, and N3. Data collection time was limited to 3–4 hours when visiting more difficult-to-access cangas N4, N5, N6, and N8, which depended on unpredictable waiting time for scout cars mandatory for a passage through mining areas and, occasionally, longer driving time when the geological survey dirt track road required machete clearing of the fallen trees.

4.3 Canga ornithophile plant species, flower visitation tracking, and species identification

In addition to *I. cavalcantei*, two canga co-flowering plant species had conspicuous hummingbird pollination flower trait suites: *C. annulata*, family Lythraceae (Cavalcanti et al., 2016), and *D. duckei*, family Bromeliaceae (Monteiro and Forzza, 2016). *C. annulata* plants grew as densely branched perennial shrubs that were 30–150 cm tall. Plants produced large masses of long-lived, red-orange-colored, 15–21-mm-long– tubular flowers (Figures 1D, E). *C. annulata* was common in most cangas. In some parts of cangas N1, N3, N4, N5, and N8, the species were very abundant,

covering the ground. The bromeliad with rosette growth habit, *D. duckei*, is a succulent that mainly grows on open rocky outcrops. Plants developed 30–55-cm-long, orange-colored inflorescence stalks bearing orange-red tubular flowers measuring 10–13 mm in length (Figures 1F, G). We dedicated approximately 250 person-hours of field studies to observations of hummingbirds foraging on *I. cavalcantei*, *I. marabaensis*, *C. annulata*, and *D. duckei* and the acquisition of still images and digital video recordings. We found that the videos recorded from a stationary camera had limited usefulness because i) hummingbirds would forage on several nearby plants of *I. cavalcantei*, *D. duckei*, and *C. annulata*; thus, the birds were often out of the camera frame. ii) In addition, the orientation of flowers in relation to the camera made it difficult to distinguish between legitimate and illegitimate foraging. Still images were less sensitive to the shortcomings of the video recording and were produced using a handheld Nikon D90 camera equipped with a 300-mm zoom lens. We filtered 7,917 still images and 102 videos to ensure that we report unambiguous records of legitimate or illegitimate feeding and bird species identification. Hummingbirds spend less than a second visiting *Cuphea* flowers. Consequently, our results may underestimate the accurate visitation rates of that species. To identify animal species, we used digital images. We captured no hawkmoths or hummingbirds for specimen depositions in museum collections.

4.4 *Ex situ* collection and flower displays

I. cavalcantei and *I. marabaensis* are perennial morning glories with woody stems and enlarged storage roots. Therefore, it was possible to maintain unique genotypes by vegetative propagation. Representative wild types and color variants from continuously expanding canga-mine boundaries were rescued for *ex situ* collection by excavating plant storage roots and replanting them in BioParque Vale Amazônia (Parauapebas, Pará, Brazil). *I. cavalcantei* is listed on the National Red List as a critically endangered species. The *ex situ* collection establishment followed The International Union for Conservation of Nature (IUCN, <https://iucn.org/>) guidelines for endangered species. The soils at BioParque Vale Amazônia, located within a mountainous rain forest, were distinct from canga soils; nevertheless, morning glories grew well, which was consistent with our common garden experiments (Babiychuk et al., 2017) and showed that in a greenhouse, *I. cavalcantei* and *I. marabaensis* grew the best on agricultural grade soil mixes. However, maximal exposure to the sun was critical to ensure compact growth and abundant flowering. Thus, plants were planted next to and climbed over a wire fence that was exposed to the sun from approximately 9 am to 5 pm. The flower colors, shapes, and sizes recorded in canga kept true in the *ex situ* collection, ruling out the possibility that the local native environment, e.g., soils and water availability, was the key cause of color, size, and shape variation. The *ex situ* collection comprised individuals of i) *I. cavalcantei* with intense red “wild type” (n = 3), pink (n = 6), purple (n = 3), and white (n = 2) flowers; ii) *I. marabaensis* with “wild type” pale lavender (n = 2), white (n = 3), and intense pink (n = 2) flowers;

and iii) *I. cavalcantei* × *I. marabaensis* hybrids with magenta-colored flowers (n = 5). *I. cavalcantei* flower color/shape variants and *I. cavalcantei* × *I. marabaensis* hybrids occurred in fragments of sympatric cangas N4 and N5. It was important to characterize the flower visitor assemblages of the color variants and hybrids. Producing respective datasets in fragments of cangas N4 and N5 was impractical due to study site access difficulties, i.e., ongoing mining operations. We could follow the visitation of color variants and hybrids at the *ex situ* collection, in which we reconstructed, to some extent, the sympatry as found in the wild. However, the pollinator species composition differed from canga; e.g., we have not sighted black-throated mango, grey-breasted sabrewing, long-tailed hermit, and glittering-throated emerald, as well as ello sphinx hawkmoth at the *ex situ* site. To address those technical problems, we decided to offer pollinators in canga the entire range of flowers preserved at *ex situ* collection using artificial flower displays. To prepare displays with flowers from the *ex situ* collection, we used a 15-mL laboratory plastic tube filled with water to prevent flower wilting. We placed tubes in tube racks at random. Available tube racks were orange in color. On some displays, we covered racks with green paper. We did not notice a difference between “green” and “orange” racks regarding visitation by foraging animals. At dawn, we detached freshly opened flowers from a plant and placed them in water for transportation to canga. In the wild, we hung tube racks on branches of shrubs, which *I. cavalcantei* climbs at ca. 1.5 m above the ground, i.e., at the level with surrounding *I. cavalcantei* flowers, or placed on rocks at the height of ornithophilous *C. annulata* bushes favored by the short-billed hummingbird species. We presented displays to pollinators in cangas N1, N2, N3, N4, N6, and N8 and at *ex situ* collection (Supplementary Table S4). In canga N4 fragment 1, it was only possible to present displays at the canga-forest boundary. At other sites, we tested displays in more open canga areas. We directed a Nikon COOLPIX P7800 camera, fixed on a tripod, at a flower display, and we recorded 20-min-long videos in a continuous series. Displays comprised i) “wild types”, i.e., intense red *I. cavalcantei* and pale lavender *I. marabaensis* flowers; ii) flower color variants of both species; and iii) magenta-colored flowers of natural interspecies hybrids. One striking interspecies difference between *I. cavalcantei* and *I. marabaensis* flowers is the structural strength of the corolla limbs. Smaller flowers of *I. cavalcantei* are very rigid, presumably due to high cellular turgor pressure. In large *I. marabaensis* flowers, the corolla limb is weak and floppy, e.g., wind and rain easily distort flower shapes and damage corolla tissues. We hypothesized that such flower biomechanical properties could interfere with the hummingbird hovering flight that generates an air wake (Wolf et al., 2013), which could induce corolla limb flapping, affecting plant–hummingbird pairwise interactions. To check the working hypothesis, we also included *I. marabaensis* flowers with surgically trimmed corolla limbs (“cut limb” flowers).

4.5 Statistical analysis

To determine whether visitation rates differ among flower color types, we calculated the number of visits per flower and performed

non-parametric statistical tests for each of the four main floral visitors (*H. longirostris*, *P. superciliosus*, *H. auritus*, and *E. ello*). We conducted a Kruskal–Wallis rank-sum test for each visitor to evaluate whether visitation rates varied significantly across flower colors. When significant differences were identified ($p < 0.05$), we carried out pairwise comparisons using Dunn's test with Bonferroni correction for multiple testing, implemented through the `DunnTest()` function in the R package *FSA*. We separately analyzed each floral visitor by subsetting the dataset, and we performed the statistical tests iteratively within a loop. We assigned letters to flower colors based on the adjusted p-values: flower colors that did not differ significantly ($p \geq 0.05$) shared the same letter, while those with significant differences ($p < 0.05$) received different letters. We performed all analyses in R version 4.3.2 using the *FSA*, *dplyr*, and *readr* packages.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#). Further inquiries can be directed to the corresponding author.

Author contributions

EB: Investigation, Writing – review & editing, Project administration, Funding acquisition, Writing – original draft, Resources, Visualization, Conceptualization, Formal analysis, Methodology. JT: Methodology, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. LT: Methodology, Writing – review & editing, Investigation, Resources. VI-F: Writing – review & editing, Conceptualization, Project administration, Funding acquisition, Formal analysis, Data curation. SK: Methodology, Data curation, Conceptualization, Supervision, Formal analysis, Writing – original draft, Writing – review & editing.

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Conflict of interest

LT is an employee of the multinational mining company Vale S.A. Vale S.A. did not influence the study design, data analysis, or the interpretation of the results.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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