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ORIGINAL ARTICLE

Integration of an Invasive Plant in Hummingbird and Flower Mite Networks Is Driven by Ecological Fitting and Generalization

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ABSTRACT

Most plant communities worldwide include exotic plants, which did not evolve with local organisms. The central goal of this study is to test if native organisms expanding their interactions to novel hosts are usually generalists or specialists. Here we studied new associations between hummingbirds, flower mites and *Musa velutina* (Musaceae), an exotic plant native to northeast India currently invading lowland forests in Costa Rica. Hummingbirds are pollinators, but flower mites feed on nectar without contributing to pollen transfer. Flower mites hitch rides on hummingbird beaks to colonize new flowers. To determine the original diet breadth of hummingbird and flower mite species, we assembled hummingbird and flower mite interactions at La Selva Biological Station. We identified four hummingbird species visiting *Musa velutina*. DNA barcode analyses identified only one species of flower mite colonizing flowers of *M. velutina*. All new associations with *M. velutina* involved generalist hummingbird and flower mite species. *Musa velutina* displays both male and female flowers. Although flowers of both sexes were equally visited by hummingbirds, mites were 15 times more abundant in male than in female flowers. We hypothesize that this is the result of constant immigration coupled with mite population growth. Only half of the mites hitching rides on hummingbird beaks emigrate to newly opened flowers. Our results show that *M. velutina* integration to a plant community occurs mainly by establishing interactions with generalists.

The Introduction of exotic species is affecting the structure and composition of native ecosystems worldwide. Exotic plants may also affect functional ecosystem attributes, for example, the structure of plant–pollinator networks (Frost et al. 2019). Traits evolved by exotic plants in their original habitats may facilitate the assembly of novel interactions in novel locations. This complementarity of not coevolved traits is known as ecological fitting (Agosta and Klemens 2008; Janzen 1985). Novel interactions between exotic plants and native organisms, besides affecting the life history of native organisms, also represent an opportunity to understand processes involved in the integration of novel species in plant communities.

One prediction of ecological fitting is that native generalists have an advantage over specialists to exploit novel host plants (Agosta and Klemens 2008). Most studies report generalist pollinators interacting with exotic plants (Lopezaraiza-Mikel et al. 2007; Memmott and Waser 2002). In contrast, empirical studies also support the opposite prediction. In insect pollinator networks, specialist insects are more likely to interact with exotic plants than generalists (Stouffer et al. 2014).

In the neotropics, hummingbirds (Family Trochilidae) pollinate more than 7000 plant species (Leimberger et al. 2022). Many exotic plants introduced to the neotropics display convergent traits associated with hummingbird pollination, such as tubular corollas and flowers of bright colors (Sánchez and Lara 2024). It is common for hummingbirds to visit exotic plants as soon as they learn that these plants are a reliable source of nectar (Sánchez and Lara 2024). Although exotic plants eventually become well integrated into plant-hummingbird networks, floral traits and plant relative abundance are poor predictors of the success of plants in attracting hummingbirds (Maruyama et al. 2016).

Hummingbirds are also associated with a group of neotropical floral parasites, the hummingbird flower mites (Acari: Mesostigmata: Ascidae) (Baker and Yunker 1964). This group of mites feeds on nectar and pollen without apparently contributing to pollination (Baker and Yunker 1964; Colwell 1973). This guild of tiny nectar thieves uses hummingbirds' electrostatic fields to cling to hummingbird beaks and hitch rides to newly opened flowers (García-Robledo et al. 2025).

This study focuses on guilds of hummingbirds and flower mites at La Selva Biological Station, a tropical lowland forest in Costa Rica. In our study site, we observed hummingbirds visiting flowers of the pink banana, *Musa velutina* H. Wendl. & Drude, Musaceae, Zingiberales (Figure 1A). This plant is originally from northeast India, and after its introduction to Costa Rica, it became one of the most aggressive invasive plants in lowland and montane forests (Valverde 2013).

The central goal of this study is to determine if the integration of *Musa velutina* in the pollination network is driven by interactions with generalists or specialists. Using the analogy of hummingbird species as "flight connections" between plants, if *Musa velutina* is visited by generalist hummingbirds, these generalized flight connections will increase the connectivity with other plant species and the chance of more flower mite species to colonize *M. velutina*. If *M. velutina* is visited by specialist hummingbirds, fewer flight connections may limit mite transportation to the novel host. Although hummingbirds carry on their beaks a mix of generalist and specialist flower mites, we expect that only generalist mites will colonize *M. velutina*.

Musa velutina is monoecious, producing at first female flowers, which only offer nectar. After a few days, plants shift to produce male flowers, which offer both nectar and pollen. We are interested in determining if hummingbird flower mites prefer flowers only offering nectar or flowers offering a mix of nectar and pollen. By combining this information, we determined if colonization of *M. velutina* by flower mites is limited by available dispersal routes or by intrinsic preferences of generalist and specialist floral parasites encountering an exotic plant.

1 | Methods

1.1 | Study Site and Species

We performed this study at La Selva Biological Station (10°25′ 19.2″ N, 84°0′54″ W), a tropical rain forest on the Caribbean slope of Costa Rica (McClearn et al. 2016). Elevation at La Selva ranges from 35 to 137 m.a.s.l. Rainfall varies from 152.0 mm in March to 480.7 mm in July (McDade 1994). The average annual temperature is 23.6°C (McDade 1994).

At La Selva, the flowers of at least 32 plant species are visited by 14 species of hummingbirds (Table S1). Inside the flowers, hummingbird flower mites feed on pollen and nectar, and hitch rides on hummingbird beaks to colonize new flowers (Baker and Yunker 1964; Colwell 1973) (Figure 1B). Previous studies incorrectly reported that hummingbird flower mites are extremely specialized, and a single mite species is usually associated with each host plant (Colwell 1986). Using the DNA barcode CO1, we discovered that flower mites in many cases are generalists, and flowers usually host a mix of generalist and specialist flower mite species (Bizzarri et al. 2022, 2023; G. García-Franco et al. 2001; Kress 2022).

Musa velutina H. Wendl. & Drude (Musaceae) is native to Assam and the eastern Himalayas (Govaerts et al. 2021). *Musa velutina* was initially introduced to Trinidad in 1938 (Cheesman 1949). This species was documented for the first time in Costa Rica

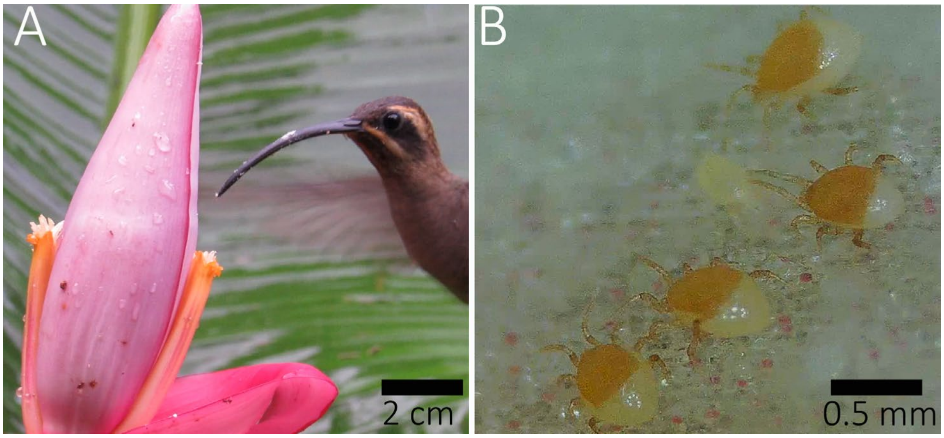

FIGURE 1 | Study organisms. (A) *Phaethornis longirostris* visiting a male inflorescence of *Musa velutina*. (B) Hummingbird flower mites feeding on nectar and pollen inside a flower.

in 1987, at a locality near La Selva Biological Station (Avalos et al. 2021). At La Selva, *M. velutina* is currently invading primary and secondary forests, usually in areas close to rivers (Balderama et al. 2011).

Musa velutina produces a single erect inflorescence. Bracts subtend groups of flowers, known as banana "hands". Each morning, a pink bract opens to expose a set of flowers. This species of wild banana is monoecious, with female and male flowers produced in the same inflorescence (Kirchoff 2017). At La Selva, we observed that plants first produce 1 to 6 female flower hands and transition to produce 7 to 40 male hands. Female and male hands have a similar number of flowers (Mean = 6 flowers, Min = 3, Max = 13, *N* = 28). Inflorescences produce flowers for about a month (Min = 11 days, Max = 49 days Mean = 29.1 days, *N* = 21).

In its native range, *Musa velutina* is pollinated by bats (Percival 1979). Female and male flowers produce nectar with a similar concentration, *ca*. 15%. However, female flowers produce less nectar than male flowers (Percival 1979). In Costa Rica, inflorescences are visited by hummingbirds and stingless bees in the genus *Trigona* (Valverde 2013).

1.2 | Hummingbird Interactions With Native Plants and *Musa velutina*

Hummingbird-plant interactions had been studied at La Selva for the last 50 years (Table S1). To determine which hummingbird species visit each native plant species in our study site, we assembled a qualitative hummingbird-plant interactions network by combining our observations with published interaction records (Table S1).

To determine which hummingbird species visit *Musa velutina*, we used high-resolution cameras (Canon PowerShot SX530 HS, Canon Inc. Tokyo, Japan). We modified the cameras for motion detection by installing in the SD cards the firmware Canon Hack Development Kit, available at http://chdk.wikia.com/wiki/CHDK (Juárez et al. 2023; Maguiña-Conde et al. 2023; Steen 2017). The cameras were placed at 3 to 4 m from inflorescences and recorded each visit for 5 s. We recorded visits from 6:00 a.m. to 1:00 p.m.

1.3 | Interactions of Hummingbird Flower Mites With Native Plants and *Musa velutina*

To determine the association between flower mite species and hummingbird-pollinated plants at La Selva, we collected flower mites from each native plant species. Mites were fixed in ETOH 95%. Individual mites were placed in 96 well plates. To identify mite species, we amplified the DNA barcode CO1 (Hebert et al. 2003). Mites were identified to genus by an expert taxonomist (Dr. Ricardo Bassini-Silva). We assembled a qualitative plant–hummingbird flower mite network by combining new interaction records in this study with interactions reported in one of our previous studies (see methods in Bizzarri et al. 2022, 2023). All sequences were deposited in GenBank (Accession Numbers. MW14554-MW147005 and PQ438945-PQ439121).

To determine which mite species are expanding their diets to *Musa velutina*, we collected flower mites from recently open flowers (see sample size in the results section). Mites were fixed in ETOH 95%, then sequenced to obtain the DNA barcode CO1. We identified the mite species colonizing *Musa velutina* by comparing mite CO1 sequences of individuals collected in *M. velutina* with our DNA barcode library. Sequence comparison was performed using the BLAST algorithm (Camacho et al. 2009). All analyses were performed using the program Geneious (Geneious-Prime-2023.2.1 2023).

1.4 | Hummingbird Visits to Male and Female *M. velutina* Flowers

To determine differences in the number of hummingbird visits to female and male flowers, we recorded the number of visits per flower hand. To ensure independence among samples, we only surveyed each inflorescence during either its female or male phases. To determine differences in the number of visits per flower, we performed a generalized linear model, including plant individuals and sex as factors, and the number of hummingbird visits as the response variable.

1.5 | Hummingbird Mite Transit and Colonization of Male and Female *M. velutina* Flowers

To determine differences in mite colonization and migration from female and male *M. velutina* flowers, we counted the number of mites embarking or disembarking in each hummingbird visit. Videos were analyzed using the application Adobe Premiere Pro V24.1, Adobe Inc. San Jose, CA, USA (see methods in García-Robledo et al. 2025). Differences in the number of mites embarking or disembarking between male and female flowers were determined using a generalized linear model, including hummingbird species, flower sex and transit (i.e., embarking vs. disembarking) as factors.

To determine differences in the number of mites present in female and male flowers, we collected individual flowers in ETOH 95%, then counted the number of flower mites per flower. We tested for differences in the average number of flower mites using a Welch Two Sample t-test (Welch 1947). All analyses were performed using R studio and Program R (R Core Team 2025; RStudio Team 2024).

2 | Results

2.1 | Hummingbird Interactions With Native Plants and *Musa velutina*

At La Selva, 14 hummingbird species visit 34 native plant species. The most generalist hummingbird species is *Phaethornis longirostris*. This hummingbird species visits 72% of the native species at La Selva. The second most generalist hummingbird species is *Phaethornis striigularis*. This species visits 31% of all native plant species included in this study. We observed *P. striigularis* feeding at the base of the corollas of *Costus malortieanus* and *Aechmea mariae-reginae*. It remains unknown if flower mites can use this hummingbird species for transportation to these host plants. *Phaethornis striigularis* is also a nectar robber of the bat-pollinated plant *Merinthopodium neuranthum*. We never observed *P. striigularis* piercing the petals when feeding on these species. All other hummingbird species were recorded visiting between one and four host plants (Figure 2A).

After surveying 6 male and 4 female plants, we recorded 200 h of video. We observed the four most generalist hummingbird species visiting *M. velutina* (Figure 2A). We recorded 165 visits by *P. longirostris*, 137 visits by *A. tzacatl*, 24 visits by *P. striigularis* and two visits by *T. colombica*. All visits by *P. striigularis* were legitimate, suggesting that this hummingbird species contributes to flower mite transportation to the novel host (Figure 2A).

2.2 | Interactions of Hummingbird Flower Mites With Native Plants and *Musa velutina*

Based on 1884 DNA barcode sequences, we identified 19 flower mite species interacting with 17 host plants (Figure 2B). The most generalist flower mite species is *Proctolaelaps* sp1 (Figure 2B). The diet breadth of all other flower mites ranges from generalist species using seven host plants to specialist mites recorded in a single plant species (Figure 2B). Most plant species host a mix of generalist and specialist mite species (Figure 2B).

We sequenced 156 DNA barcodes from flower mites collected in 14 individuals of *M. velutina*. All individuals were identified as *Proctolaelaps* sp1, the most generalist flower mite species at La Selva (Figure 2B).

2.3 | Hummingbird Visits and Flower Mite Colonization of *Musa velutina*

There is no difference in the number of hummingbird visits between female and male flowers ($F_{sex} = 0.007$, $DF_{sex} = 25$, $P_{sex} = 0.09$, $F_{plant} = 1.22$, $DF_{plant} = 24$, $P_{plant} = 0.28$, Figure 3A). However, we detected a difference in the number of mites disembarking and embarking during hummingbird visits. In both female and male flowers, less than a half of the flower mites arriving to *M. velutina* eventually migrate to other inflorescences

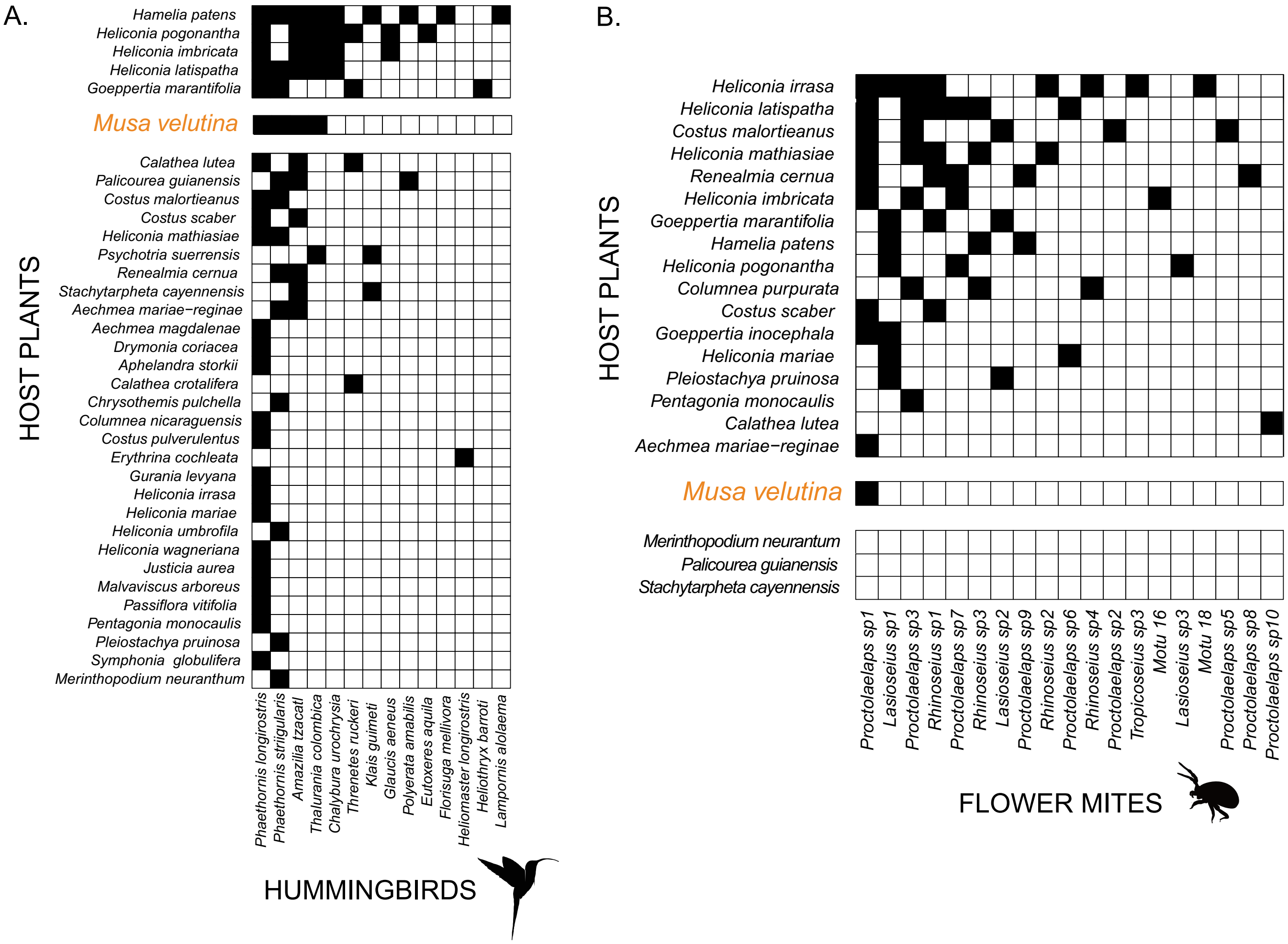

FIGURE 2 | Interactions between plants, hummingbirds and flower mites at La Selva Biological Station, Costa Rica. (A) Plant-hummingbird network. Black cells represent hummingbird species visiting each host plant. Hummingbird species visiting *Musa velutina* are highlighted in orange. References for each plant-hummingbird interaction are included in Table S1. (B) Plant-hummingbird flower mite network. Note three plant species at the bottom, with no record of flower mites. The only mite species expanding its diet to *Musa velutina* is highlighted in orange. Black cells represent mite species recorded in each host plant.

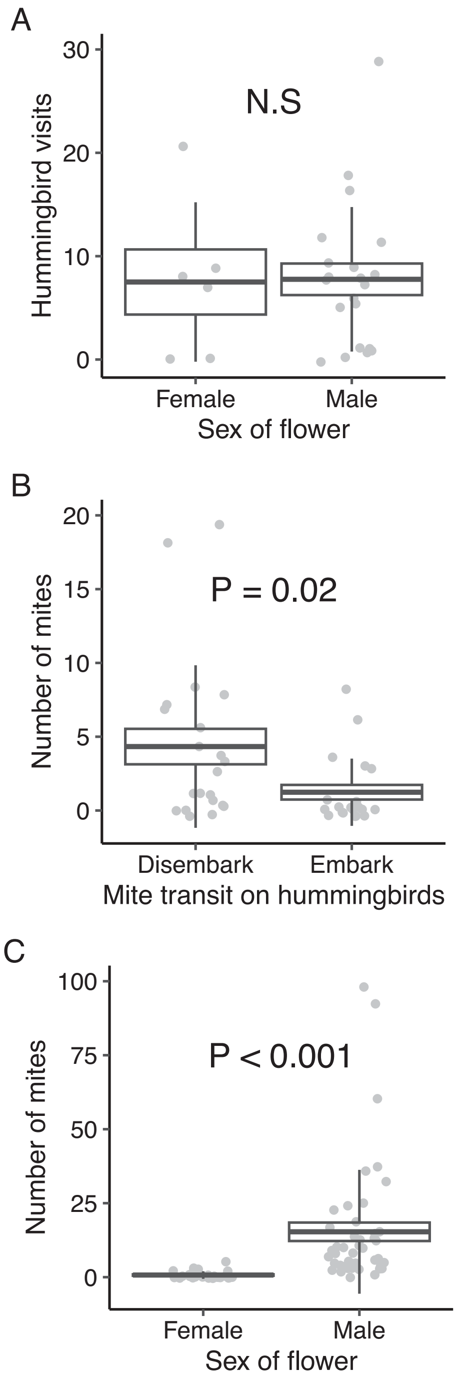

FIGURE 3 | Hummingbird visits and mite colonization of female and male flowers of *Musa velutina* (Mean, SE and SD). (A) Number of hummingbird visits to female or male flower hands. ($N_{\text{flowers} ♀}=36$, $N_{\text{flowers} ♂}=140$). (B) Number of mites disembarking or embarking from hummingbird beaks during each flower visit ($N_{\text{hummingbird visits} ♀}=66$, $N_{\text{hummingbird visits} ♂}=266$). (C) Number of flower mites inside female and male flowers ($N_{\text{flowers} ♀}=29$, $N_{\text{flowers} ♂}=45$).

($F_{\text{sex}}=0.0248$, $\text{DF}_{\text{sex}}=40$, $P_{\text{sex}}=0.87$, $F_{\text{transport}}=5.49$, $\text{DF}_{\text{transportt}}=24$, $P_{\text{transport}}=0.02$, Figure 3B). Male flowers harbor more mites than female flowers ($F=13.8$, $\text{DF}=1$, $p=0.0003$). Male flowers have on average 15 times more mites than a female flower (Figure 3C).

3 | Discussion

Our observations of generalist hummingbird species visiting *Musa velutina* represent another example of how hummingbirds usually incorporate novel hosts in their diets. In natural and urban settings, generalist hummingbirds tend to visit exotic plants (Sánchez and Lara 2024). One common feature in plant-pollinator networks is the presence of keystone pollinator species, i.e., species that serve as the only pollinators of many specialized plant species (Traveset et al. 2017). At La Selva, 40% of all hummingbird-pollinated plant species are only visited by *P. longirostris*. It is predicted that if the most important pollinator becomes extinct, the survival of plant species specialized to a single pollinator will depend on other pollinators eventually switching hosts or the plant's ability to self-pollinate or propagate vegetatively (Abrahamczyk et al. 2014; Johnson and Steiner 2000).

For the flower mite community, we found that 42% of mite species specialize on a single host plant. However, these specialized species were recorded on six different host plants. This specialization in different plant species may reduce the risk of secondary extinction in flower mite communities (Maia et al. 2021; Traveset et al. 2017).

We recorded three plant species that are not hosts of flower mites. *Merinthopodium neurantum* is bat pollinated and opens its greenish pendulous flowers at dusk (Bechler et al. 2024). The hummingbird *P. striigularis* robs nectar from *M. neurantum* flowers just before sunset. *Palicourea guianensis* (Rubiaceae) and *Stachytarpheta cayennensis* (Verbenaceae) open their flowers in the morning. Both plants are visited by hummingbirds during the day. More research is needed to determine which traits deter flower mites from colonizing these three plant species.

In this study, we were interested in determining if hummingbird species visiting both native plants and *Musa velutina* facilitate or constrain the potential colonization of flower mites. Because the three most generalist hummingbird species visit *M. velutina*, all flower mite species have the potential to colonize *M. velutina*. However, only one of the nineteen flower mite species was recorded in the novel host plant. Hummingbirds at La Selva may carry multiple mite species in their beaks (Bizzarri 2020). The two hummingbird species most frequently visiting *M. velutina*, i.e., *P. longirostris* and *A. tzacatl*, may carry on their beaks as many as eight mite species; one of them is *Proctolaelaps* sp1 (Bizzarri 2020). This shows that flower mites can select the plant species in which they disembark.

Previous studies in the laboratory reported that flower mites select their host plants using flower scents (Heyneman et al. 1991). These experiments might not be biologically relevant, as they report a very slow response of mites to floral scents. Mites selected their host after minutes or even hours of exposure to the scent cue (Heyneman et al. 1991). Hummingbird flower mites seem to use tactile cues to choose their host plants (Banker 2015). In a recent study, we discovered that flower mites are almost instantaneously attracted to electric fields generated by hummingbirds (García-Robledo et al. 2025). Because flowers are negatively charged, it is possible that flower mites can identify host plants by maybe combining electrical and chemical cues (García-Robledo et al. 2025).

Musa velutina produces nectar with sugar concentrations within the range of those reported for native species (McDade and Weeks 2004). Floral resources are scarce during the dry season (Stiles 1975, García-Robledo, obs. pers.). Because *M. velutina* flowers all year, this exotic species might become a key resource for hummingbirds and for at least one species of flower mite.

Although female flowers of *M. velutina* produce less nectar than male flowers, we did not observe any difference in the number of visits by hummingbirds. The number of mites disembarking in female and male flowers is also similar. This suggests that flower mites have similar probabilities of arrival to both female and male flowers. Colonization rates of *M. velutina* inflorescences are similar at both female and male phases. However, more mites were observed disembarking than embarking on hummingbird beaks. This suggests that only a fraction of the population of flower mites will eventually migrate to colonize novel hosts.

We recorded more flower mites in male than in female flowers. As shown in our previous results, the high abundance of flower mites in male flowers is not the result of intrinsic preferences of hummingbirds or flower mites (e.g., more hummingbird visits or more mites disembarking in male flowers). The observed higher abundance of flower mites in male flowers is more likely the result of an accumulation of mites disembarking during hummingbird visits and population growth during the time that inflorescences are producing flowers.

In conclusion, an exotic plant provides key resources to pollinators and nectar parasites. *Musa velutina* seems to be fully integrated in the plant-pollinator network at La Selva, with the most generalist pollinators connecting this exotic host with most native plant species. Associations between plants and flower mites are to some degree more specialized than interactions with hummingbirds. However, this study provides additional evidence showing that hummingbird flower mites are not extremely specialized, as suggested by previous studies (Colwell 1986). At least one flower mite species has the potential to colonize novel host plants through ecological fitting.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.9kd51c5t1.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.