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ORIGINAL ARTICLE

The Neglected Pollinators: Understanding the Importance of Lesser-Known Insect Taxa in Pollination

Shedding light on overlooked pollinators: Global insights into floral interactions of velvet ants (Hymenoptera: Mutillidae and Myrmosidae)

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Abstract

Plant–animal interactions constitute a recurrent and central focus in ecological research, with pollination representing one of its most extensively studied aspects. While certain insect orders have traditionally received considerable attention due to their abundance as flower visitors and their efficiency in pollination, it is undeniable that the significance of other less popular and neglected flower visitors cannot be overlooked. In this regard, velvet ants (Hymenoptera: Mutillidae and Myrmosidae) constitute an excellent study model, as the knowledge of their ecology (e.g., their feeding preferences) is still very limited despite being reported as common flower visitors. In this study, we conducted a comprehensive global review of velvet ant floral visitation patterns using citizen science data, literature records and unpublished data. We used network metrics to explore their flower-visit preferences on a global scale, as well as depending on the bioregion where the interaction was recorded and the sex of the velvet ants. In addition, we explored their potential role as pollen vectors examining the number of photographic records where velvet ants had pollen attached to their bodies. Our analyses revealed that velvet ants are generalist flower visitors of a wide range of plant families, with Apiaceae, Asteraceae, Euphorbiaceae, Rhamnaceae and Fabaceae as the most visited. Despite differences in flowering plant and velvet ant composition across bioregions causing differences in plant-velvet ant interactions, velvet ants visited flowering plants in a generalistic way across the globe. Males and females seemed to visit different plant communities, with males being more generalist than females. Furthermore, 42.7% (likely an underestimation) of the photographic records of velvet ants visiting flowers showed pollen attached to their bodies in the same way as in other pollinating insects, suggesting the same potential role as pollinators. There remains ample scope for ongoing investigation to comprehensively assess the importance of numerous arthropods, including velvet ants, not only as flower visitors but also as potential pollinators.

KEYWORDS
Apiaceae, bipartite graph, ecology, interaction network, neglected pollinators, specialization

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[Corrections added on 5 August 2024, after first online publication: new article subcategory has been included in this version.]

1 | INTRODUCTION

Dynamic relationships between plants and animals are currently among the most widely studied ecological interactions (Vázquez et al., 2009). They represent key ecological processes in many terrestrial ecosystems throughout the world, including pollination and seed dispersal, among others. Thus, the study of plant–animal interactions is essential for understanding the functioning of ecological systems and community structure, as well as for their own management and conservation (Bronstein et al., 2006; Rico-Gray & Oliveira, 2007; Waser & Ollerton, 2006).

Among plant–animal interactions, pollination is one of the most extensively studied interactions. To be considered a pollinator, an agent must facilitate the transfer of pollen from the male floral organs (stamens) to the receptive portion of the female organs (stigma) (Faegri & van der Pijl, 1979). Due to their wide distribution and diversity, four insect orders have received extensive research attention as pollinators: beetles (Coleoptera), flies (Diptera), butterflies and moths (Lepidoptera), and bees and wasps (Hymenoptera). Nevertheless, not all hymenopteran taxa have undergone comprehensive study. While bees have garnered significant attention as primary pollinators, a large portion of wasps remains relatively understudied (Brock et al., 2021). Wasp-mediated pollination, known as sphecophily, has been observed in certain plants. Notably, fig wasps of the Chalcidoidea superfamily engage in sphecophily with *Ficus* L. in a unique and specific way (Kjellberg et al., 2005). Additionally, wasps from the families Pompilidae, Scoliidae, Sphecidae, Thynnidae and Vespidae pollinate over 160 orchid species and other minor plant groups (Brock et al., 2021; Shuttleworth & Johnson, 2012). Thus, wasp pollination is indeed an especially important interaction, being comparable to bee pollination in terms of efficiency (Borchardt et al., 2024). Furthermore, many generalist wasp species forage for nectar and other floral resources, potentially contributing to pollination (Brock et al., 2021; Wardhaugh, 2015). In fact, nearly 800 plant species are visited by more than 600 different wasp species (Brock et al., 2021; Clemente et al., 2012; Fateryga, 2010; Gess & Gess, 2010; Mello et al., 2011; Santos et al., 2010), highlighting their significance as flower visitors and potential pollinators, despite these numbers being likely underestimated (Brock et al., 2021). Consequently, there are still many flower-wasp interaction records, especially those that contribute to pollination, that have yet to be studied. Knowledge of potential pollinating wasp species is essential for both the conservation of these hymenopterans and the plants they visit.

Mutillidae and Myrmosidae (Hymenoptera: Aculeata) are families that encompass solitary wasps commonly known as velvet ants. They are named for their appearance, which resembles true ants (Formicidae), and for the dense pilosity covering the body of most of the species (Brothers, 1995). Velvet ants are characterized by a strong sexual dimorphism, with winged males and wingless females (Deyrup & Manley, 1986), which leads to distinct behavioural patterns (Brothers, 1989; Polidori et al., 2010; Schmidt et al., 2021; Tormos et al., 2010). Until recently, the Myrmosidae family was included as a subfamily within Mutillidae; however, new molecular analyses revealed that they consist of two distinct families (Waldren et al., 2023). These two families are widely distributed, with over 4500 described species worldwide, their richness increasing towards tropical regions (Pagliano et al., 2020). Despite being such diverse and conspicuous families, the knowledge of their biology and ecology remains limited (e.g., Brothers, 1989; Ronchetti & Polidori, 2020; Williams et al., 2024).

Velvet ants are ectoparasitoids of the immature stages of other aculeate hymenopterans, dipterans, heteropterans, coleopterans, and cockroaches (Brothers, 1989; Brothers et al., 2000; Ronchetti & Polidori, 2020), exhibiting varying degrees of host taxonomic specialization (Ronchetti & Polidori, 2020). There is not much information in the literature regarding their feeding habits except for punctual observations and a few laboratory experiments. On the one hand, adult males primarily feed on sugary solutions such as nectar (Brothers, 1972, 1995) and are commonly observed foraging on flowers (Lelej, 1985), extrafloral nectaries (Quintero & Cambra, 2001; Robertson, 1929) and honeydew from aphids (Homoptera) (Invrea, 1964; Krombein, 1951). On the other hand, females have a broader dietary range. Along with foraging for nectar from flowers and extrafloral nectaries (Brothers, 1972; Calixto et al., 2018; Lenko, 1970; Luz et al., 2016; Wilson et al., 2010) and collecting honeydew (e.g., Invrea, 1964; Krombein, 1951), they exploit resources found within the nest cells of their hosts. Laboratory and natural observations indicate that females feed on moist pollen masses within bee host cells as well as the body fluids of adult and immature hosts (Brothers, 1972; Jordan, 1935; Mellor, 1927; Neal, 1884; Scholz, 1879). Despite differences in feeding habits, both males and females are considered common flower visitors (Hennessey & West, 2018; Invrea, 1964; Lelej, 1985), albeit this is to a lesser extent for the females. Lelej (1985) compiled Eurasian records of male velvet ants collected on different flowers. A total of 40 wasp species were reported on the flowers of 14 plant families, with Apiaceae inflorescences being the most frequently visited, as already suggested by other studies (e.g., Bischoff, 1920; Muskovits & György, 2011; Standfuss & Standfuss, 2012). However, despite host group preferences in host-velvet ant interactions being assessed in literature (Ronchetti & Polidori, 2020), no studies so far have attempted to quantitatively explore the flower visit patterns of these two wasp families. Furthermore, although they have been documented as frequent flower visitors, their role as potential pollinators remains largely unexplored.

In order to improve the knowledge of the ecology of velvet ants and their flower visit patterns, the main goals of this work are: (i) to quantitatively assess flower visit preferences using interaction network metrics of velvet ants at a global scale; (ii) to determine which plant families are most frequently visited by velvet ants and whether these patterns vary depending on the region and the sex of the velvet ants; and (iii) to provide further comments and considerations about the potential role of this insect group as pollinators.

2 | MATERIALS AND METHODS

2.1 | Data collection

The data used in this study were obtained through a comprehensive search across all photographic observations worldwide uploaded to the citizen science platforms iNaturalist (iNat; https://www.inaturalist.org/) and Biodiversidad Virtual (BV; https://www.biodiversidadvirtual.org/) until September 30th, 2023. The database included all records of velvet ants located on flowers. Additionally, a review of global literature on Mutillidae and Myrmosidae was conducted to search for bibliographic records of these two families that were collected or observed feeding on flowers and extrafloral nectaries. This review excluded instances where the individuals interacted with other parts of the plant (such as branches or leaves), fed on honeydew or where the part of the plant involved in the interaction was not specified. Finally, unpublished records from the authors and those from other collaborators were included in the database. For each flower-visit event, we recorded both the velvet ant and the plant species to the lowest possible identifiable taxonomic level, the sex of the velvet ant, the month of the observation, the location, and whether the velvet ant had pollen grains attached to its body. In this last case, we also recorded in which part of the body the pollen was found. Velvet ants were identified based on external diagnostic characters by various specialists (mainly by Kevin A. Williams, Rafael Matias, Marcello Romano, Denis J. Brothers and the first author). Plant species were identified by the observers themselves and were later verified by the authors of this study.

2.2 | Statistical analyses

For statistical analyses, records of velvet ants feeding on extrafloral nectaries were discarded in order to focus on flower interactions. We deem our analyses to be exploratory because of the nature of our data, which were gathered from disparate sources and present differing sampling sizes and efforts depending on the bioregion and taxa. However, given the size and coverage of our dataset, we consider them an acceptable representation of plant-velvet ant interactions and a good baseline for future research. In order to be able to generalize across our dataset and because a good taxonomic resolution was not always available, flowering plant data was always kept at the family level. In this work, two sets of analyses were carried out to explore the relationship between velvet ants and flowering plants. First, we studied whether velvet ant-flowering plant interactions differed by biological region and studied the general topology of a global interaction network pooling all available data. Then, we evaluated velvet ant sex bias on flower preference. For these analyses, Mutillidae and Myrmosidae data were pooled together except when explicitly stated otherwise, in most cases because there was not a lot of data available from the Myrmosidae. All analyses were conducted in R 4.3.1 (R Core Team, 2022). Interaction networks between plants and velvet ants were built using the 'bipartite' V2.18 package (Dormann et al., 2008). Details on the equations and calculations of species-level metrics can be found in Dormann (2011), and those involving the full network in Dormann et al. (2009). For better reproducibility of our results, we recommend using the R package 'checkpoint' (Ooi et al., 2022) set to January 2024. This allows the utilization of the same version of the R packages that were used at the time of analysing our data. The data and code supporting this study are available at 10.5281/zenodo.10569918.

2.3 | Global and bioregional interaction networks

Firstly, a global network was built pooling all available data regardless of geographical origin (therefore including the bioregions that were excluded in the individual bioregion analyses). To account for differences in interaction sampling across taxa and to reduce bias, we considered the interactions in this network as binary when calculating network metrics, thus not taking into consideration the frequency at which the same plant-velvet ant interaction took place. The only exception was in the calculation of the network specialization index (H_2'). The following metrics were calculated at the network level: mean number of species, mean number of links, mean number of shared partners, partner diversity (using Shannon's index), niche overlap (for both plants and wasps), connectance and H_2'. To assess whether plant-velvet ant interactions were different across bioregions, a one-way PERMANOVA with 9999 permutations was conducted using PAST 4.0.3 (Hammer et al., 2001) on a Bray-Curtis distance similarity matrix. Bioregion was used as the only predictor. Similarly, differences across velvet ant composition (assessed at the genus level for both Mutillidae and Myrmosidae) and plant family composition were sought across bioregions using the same approach. When statistically significant differences were detected in the PERMANOVA, a pairwise analysis was conducted to detect which bioregions were different from each other. Pairwise *p*-values were corrected using Bonferroni. Additionally, H_2' was calculated for each bioregion separately. Both for this and the PERMANOVAs, only bioregions with more than five unique interactions were considered. *Smicromyrme*/*Physetopoda* doubtful entries were removed, and abundance was used to calculate the distance matrix. Moreover, some adjustments needed to be made to some abnormally high abundance interaction records. Namely, the data extracted from Williams et al. (2019), and Hennessey and West (2018) were particularly problematic, as these sources recorded a high abundance of two mutillid species on *Euphorbia* spp. and *Helianthus annuus*, respectively. Such high abundance of these two specific mutillid-flowering plant interactions was disproportionate to the rest of the data, and notably affected the topology of the networks. Hence, the abundance of these records was reduced so that only a single interaction remained (i.e. abundance = 1).

2.4 | Flower preference of velvet ants based on sex

The Morisita-Horn dissimilarity index was used to compare the proportion of all female and male velvet ants found in each flowering plant family (i.e. the contribution of each plant family to female and male diets). This index uses proportions, which scale the flower visits from both males and females despite most records belonging to male Mutillidae and Myrmosidae. It ranges from zero (no differences) to one (completely different). Moreover, this index is resilient to undersampling and uneven sample sizes between groups, and it is more sensitive to large proportions than to small ones, therefore minimizing the relevance of plant families for which there is limited available data. Aiming for generalization and given the nature of our data, all available data across all bioregions was used and velvet ants were grouped by family (i.e. Mutillidae and Myrmosidae). However, since there was only a single female record for Myrmosidae, this family was excluded. Plants were considered at the family level. Besides calculating the Morisita-Horn dissimilarity between flower communities visited by all male and female Mutillidae, a permutation-based null model was also run following the methodology and code from Roswell et al. (2019). This model shuffled the sex of the wasps while maintaining the total number of males, females and overall combined visits to each flowering plant family, thus calculating the expected Morisita-Horn dissimilarity index under random chance. A total of 9999 permutations were used in this null model, and a 95% confidence interval was calculated. Additionally, two bipartite networks were built to illustrate the interactions between Mutillidae sexes and flowering plants. For this, all data were considered regardless of their geographical origin, but visitation frequencies were disregarded, as we intend to make generalizations across mutillid genera, and not how often the same taxon visits the same plant family. The relevance of each flowering plant species across all its partners was quantified as the sum of dependencies of each species (Bascompte et al., 2006) based on these networks. This was calculated for each plant family in relation to its interactions with males and females of mutillids treated at the genus level. Network specialization (H_2') was

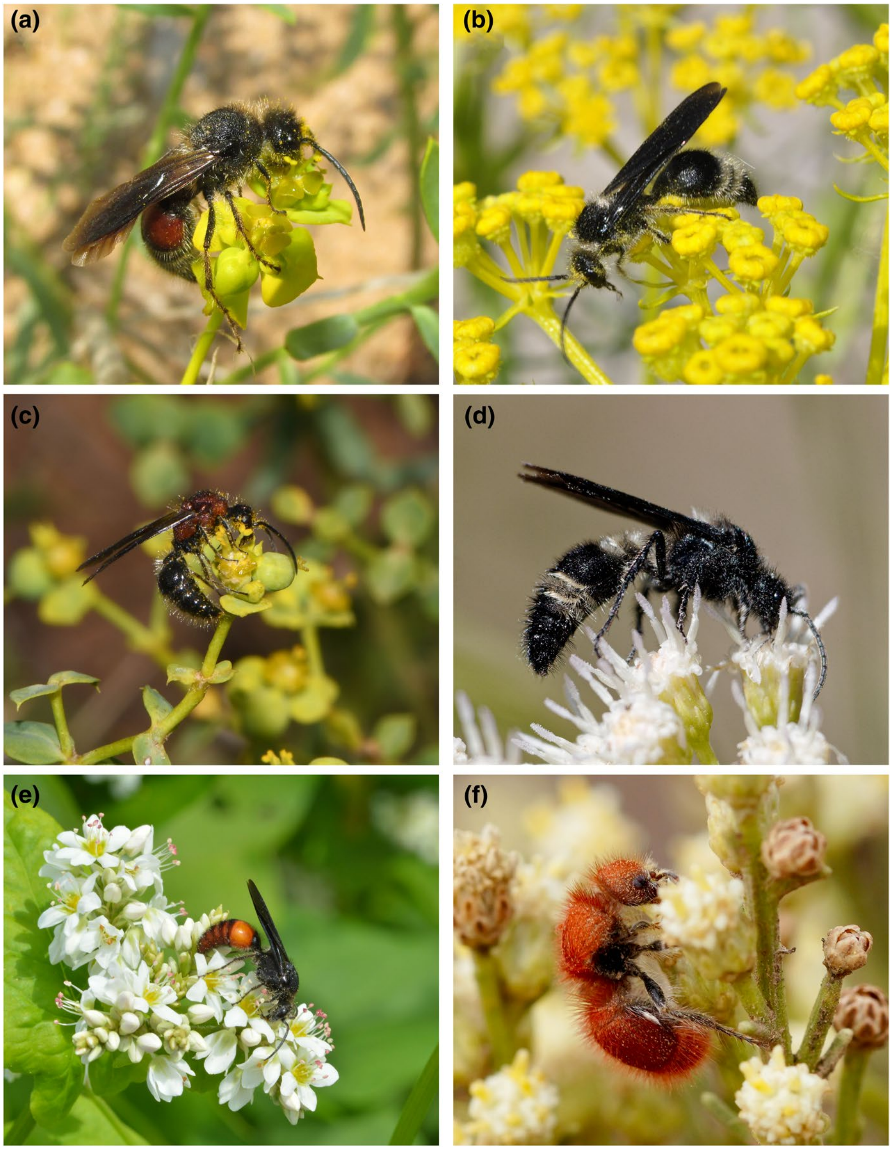

FIGURE 1 Examples of velvet ants visiting flowers and carrying pollen. (a) ♂ *Tropidotilla litoralis* (Russia, Asia; Author: Alexander Fateryga). (b) ♂ *Nemka viduata andalusiana* (Spain, Europe; Author: Francisco Rodríguez Luque “Faluke”). (c) ♂ velvet ant of tribe Smicromyrmini (France, Europe; Author: André Miquet). (d) ♂ *Tallium* sp. (Argentina, South America; Author: Quentin Vandemoortele). (e) ♂ *Timulla vagans* (United States, North America; Author: Sydney Penner). (f) ♀ *Sphaeropthalma unicolor* (United States, North America; Author: Glenn Perelson). [Colour figure can be viewed at wileyonlinelibrary.com]

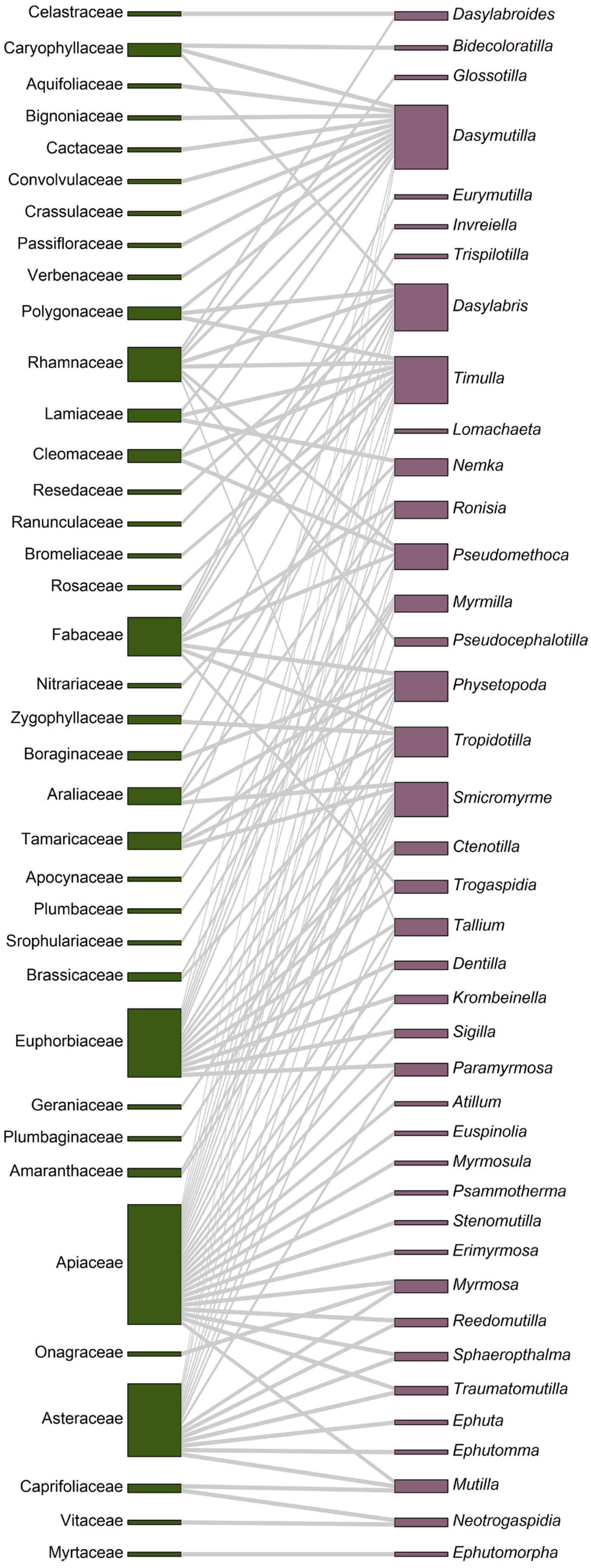

FIGURE 2 Bipartite network depicting all interactions between velvet ant genera (right) and flowering plant families (left) across all biological regions in our data. Interaction abundances (i.e. how many times a genus of velvet ant was found on a flower of the same plant family) were disregarded in this network. [Colour figure can be viewed at wileyonlinelibrary.com]

also calculated for each network (i.e., males and females separately), albeit taking into consideration their interaction frequency.

3 | RESULTS

3.1 | Data collection

We reviewed a total of 63,433 photographic records of velvet ants (Mutillidae and Myrmosidae) worldwide (2076 from BV and 61,357 from iNat) and all the available literature. Of these, only 542 records (0.9%) involved velvet ants visiting flowers (Figure 1): 250 from iNat, 184 from literature, 65 from our own and collaborators' data and 43 from BV. A detailed list of all these records is provided in Data S1. In total, we have gathered data on 124 different taxa of these two velvet ant families from 40 genera, of which 72 were females (13.3%), 466 males (86.0%) and 4 (0.7%) had uncertain sex. Overall, 0.85% were recorded in the Afrotropical bioregion, 1.57% in Australasia, 0.36% in the Indomalayan region, 44.75% in the Nearctic, 2.17% in the Neotropics and 50.30% in the Palearctic. Pollen was attached to the bodies of velvet ants in 132 cases (42.7% of the 542 photographic records involving velvet ant-flower interactions and 0.2% of all photographic records reviewed). A summary of this is also provided in Data S1. Pollen was mainly attached to the pilosity of head, antennae, thorax, abdomen and legs. It is important to note that most photos were taken in dorsal view, making it impossible to check whether pollen was attached to the individuals' ventral side. This is likely to occur, as we have been able to verify some specimens deposited in entomological collections that have pollen attached to the ventral side of their bodies.

3.2 | Global interaction networks

When pooling all available data together, we obtained 40 velvet ant genera and 37 plant families. Among them, Apiaceae was the most visited plant family, followed by Asteraceae, Euphorbiaceae, Rhamnaceae, Fabaceae and other families to a lesser extent (Figure 2). Overall, each node of the network had an average of 1.67 links to the nodes of the other level. Velvet ants had a mean number of shared partners of 0.93, while that of flowering plants was 0.52. Not only did velvet ants have almost twice as many partners as plants, but their partners also showed a higher Shannon's diversity index (0.81) than those of plants (0.64), although this may be caused by the different taxonomic resolutions used for each level. The niche overlap for the velvet ants was 0.28, while that of flowering plants was 0.13. This index takes a value of 0 when there is no overlap in the interaction patterns within the same trophic level, and a value of 1 when this overlap is perfect. Therefore, these results hint that plant species tend to hold more specialized interactions than velvet ants and suggest redundancy at the higher trophic level in our system and thus that the loss of one genus of velvet ants would trigger fewer secondary extinctions at the plant level than the loss of a whole plant family would trigger at the velvet ant level. The connectance of the network was 0.09, and network specialization was 0.49.

3.3 | Bioregional interaction networks

Only three out of six bioregions contained more than five unique interaction records in our dataset and were thus included in the analyses. Namely, these were the Nearctic ($n=39$), Neotropical ($n=11$) and Palaearctic ($n=71$) bioregions. The composition of plant-velvet ant interactions was statistically different across these bioregions (one-way PERMANOVA, $F=31.49$, $p<0.001$). In fact, all bioregions were different from each other (all $p<0.001$). Regarding velvet ant genus composition across bioregions, the same bioregions as in the interaction PERMANOVA remained. Velvet ant genus composition differed across bioregions (one-way PERMANOVA, $F=5.65$, $p<0.001$). Namely, there were differences between the Palaearctic and the Nearctic and Neotropical bioregions ($p<0.05$), but not between the Nearctic and the Neotropical ($p=0.62$). Plant-wise, though, statistical differences were found between the Nearctic and Neotropical regions ($p<0.001$) and Neotropical and Palearctic regions ($p<0.001$) but not between the Palaearctic and the Nearctic ($p=0.35$). The network specialization index was 0.20–0.21 for all the bioregions.

3.4 | Flower preference of mutillids based on sex

According to the Morisita-Horn dissimilarity index, the diet of male and female mutillids differed by 43.48%, which was significantly more than what was expected by random chance (Figure 3a). This suggests that male and female mutillids visit different plant communities. When assessing these communities through bipartite networks (Figure 3b) and calculating the relevance of all plant families to males and females (Table 1), Apiaceae is the most relevant plant family to both sexes of Mutillidae, and especially to males, for which it is almost threefold as relevant as Asteraceae, their second most relevant plant family. For females, Fabaceae is the second most relevant plant family, followed by Asteraceae and Euphorbiaceae. Males interacted with plants in a more generalistic way than females ($H_2'=0.40$ and $H_2'=0.82$, respectively).

4 | DISCUSSION

The results of this study contribute to deepening the knowledge of velvet ants ecology. We have quantitatively assessed flower visit patterns of these insects for the first time, confirming this group as flower visitors of many plant families worldwide, and suggesting a potential role of mutillids and myrmosids as pollinators of a great array of plant species. Moreover, we have found differences in plant interactions between male and female velvet ants, which is likely explained by the divergence in their biological needs.

For many hymenopterans, including parasitoids like velvet ants, floral resources such as nectar and pollen serve as nutritional sources (Jervis et al., 1993; Russell, 2015). Thus, it is common to find these wasps visiting flowers (Hennessey & West, 2018; Invrea, 1964; Lelej, 1985). Similar to many hymenopteran species, velvet ants may exhibit preferences for certain plant species with specific characteristics that make them more attractive to them (e.g., Fateryga, 2010; Hermes & Köhler, 2006; Wäckers, 2004). Understanding these feeding preferences is crucial for the conservation of these animals, which provide essential ecosystem services to humans by acting as pollinators and biological control agents (Brock et al., 2021). Our quantitative analysis reveals that a wide range of flowering plant species is visited by velvet ants worldwide. We gathered records of this insect group interacting with the flowers of 37 plant families. Of these, the umbels of the Apiaceae predominated as the most visited and therefore were potentially the most used for feeding, followed by Asteraceae, Euphorbiaceae, Rhamnaceae, Fabaceae and other families to a lesser extent. This is consistent with previous works on velvet ants (e.g., Bischoff, 1920; Lelej, 1985; Muskovits & György, 2011; Standfuss & Standfuss, 2012). In fact, similar flower visitation patterns have also been observed for other hymenopterans, such as other parasitoids (Jervis et al., 1993; Zemenick et al., 2019) and vespids (Fateryga, 2010; Hermes & Köhler, 2006; Somavilla & Köhler, 2012). We hypothesize that the flower preference patterns found in our study may be determined by floral architecture and attractiveness in combination with velvet ant mouth morphology (Lelej et al., 2016). Apiaceae, along with most of the other predominant plant families recorded in this study, display open floral systems (i.e., nectar and pollen are fully exposed, with no

FIGURE 3 (a) Morisita-Horn dissimilarity index observed between males and females of mutillids (red dot), as well as the dissimilarity index expected by random chance (grey). This index ranges from 0 (when there are no differences between the elements that are being compared) to 1 (when the two elements compared are completely different). (b) Bipartite networks depicting the relationship between flowering plants and female (left) and male (right) mutillids. Note that interactions are not weighted, and therefore differences in line width between plots are caused by the size of the network and not by any numerical difference. Plant families in common between males and females appear in the middle, with a background shaded in green that connects both networks. [Colour figure can be viewed at wileyonlinelibrary.com]

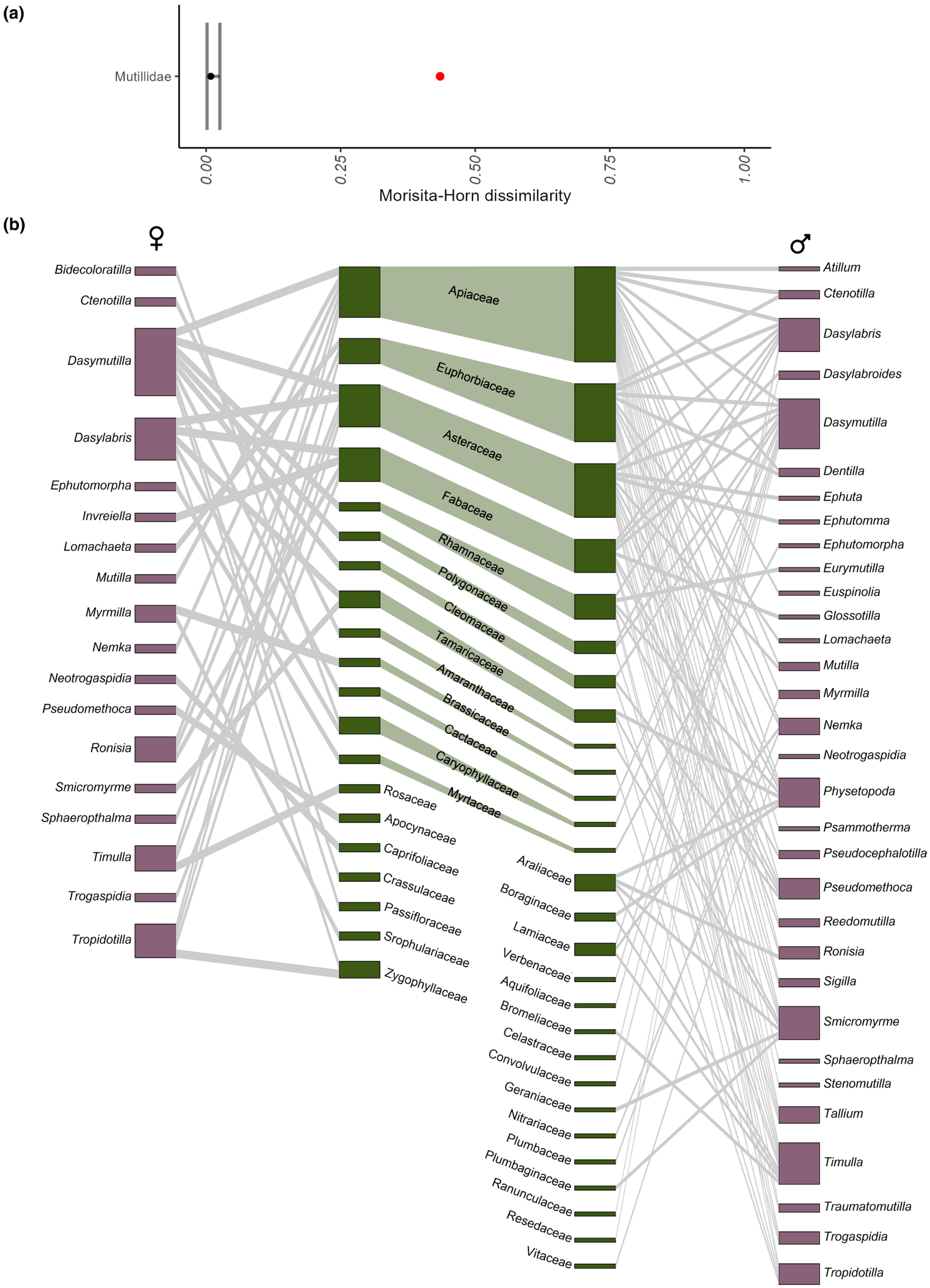
(a)
Mutillidae
0.00
0.25
0.50
0.75
1.00
Morisita-Horn dissimilarity
(b)
♀
♂
Bidecoloratilla
Ctenotilla
Dasymutilla
Dasylabris
Ephutomorpha
Invreiella
Lomachaeta
Mutilla
Myrmilla
Nemka
Neotrogaspidia
Pseudomethoca
Ronisia
Smicromyrme
Sphaeropthalma
Timulla
Trogaspidia
Tropidotilla
Apiaceae
Euphorbiaceae
Asteraceae
Fabaceae
Rhamnaceae
Polygonaceae
Cleomaceae
Tamaricaceae
Amaranthaceae
Brassicaceae
Cactaceae
Caryophyllaceae
Myrtaceae
Rosaceae
Apocynaceae
Caprifoliaceae
Crassulaceae
Passifloraceae
Srophulariaceae
Zygophyllaceae
Araliaceae
Boraginaceae
Lamiaceae
Verbenaceae
Aquifoliaceae
Bromeliaceae
Celastraceae
Convolvulaceae
Geraniaceae
Nitrariaceae
Plumbaceae
Plumbaginaceae
Ranunculaceae
Resedaceae
Vitaceae
Atillum
Ctenotilla
Dasylabris
Dasylabroides
Dasymutilla
Dentilla
Ephuta
Ephutomma
Ephutomorpha
Eurymutilla
Euspinolia
Glossotilla
Lomachaeta
Mutilla
Myrmilla
Nemka
Neotrogaspidia
Physetopoda
Psammotherma
Pseudocephalotilla
Pseudomethoca
Reedomutilla
Ronisia
Sigilla
Smicromyrme
Sphaeropthalma
Stenomutilla
Tallium
Timulla
Traumatomutilla
Trogaspidia
Tropidotilla

TABLE 1 Relevance of each plant family across all its partners towards the visits of male and female mutillids based on our data.

Plant	Relevance to females	Relevance to males	Relative relevance to females	Relative relevance to males
Apiaceae	3.04	10.80	1	1
Fabaceae	2.53	2.00	2	5
Asteraceae	1.91	4.85	3	2
Euphorbiaceae	1.58	4.44	4	3
Caryophyllaceae	1.20	0.08	5	28
Tamaricaceae	1.20	0.47	6	11
Amaranthaceae	1.00	0.13	7	22
Myrtaceae	1.00	1.00	8	7
Apocynaceae	1	NA	9	–
Caprifoliaceae	1	NA	10	–
Brassicaceae	0.50	0.20	11	17
Srophulariaceae	0.50	NA	12	–
Zygophyllaceae	0.45	NA	13	–
Rosaceae	0.33	NA	14	–
Cactaceae	0.13	0.08	15	29
Polygonaceae	0.13	0.30	16	14
Cleomaceae	0.13	0.38	17	13
Rhamnaceae	0.13	2.75	18	4
Crassulaceae	0.13	NA	19	–
Passifloraceae	0.13	NA	20	–
Vitaceae	NA	1.00	–	6
Araliaceae	NA	0.70	–	8
Celastraceae	NA	0.50	–	9
Plumbaceae	NA	0.50	–	10
Lamiaceae	NA	0.43	–	12
Nitrariaceae	NA	0.25	–	15
Boraginaceae	NA	0.24	–	16
Geraniaceae	NA	0.13	–	18
Plumbaginaceae	NA	0.13	–	19
Ranunculaceae	NA	0.13	–	20
Resedaceae	NA	0.13	–	21
Bromeliaceae	NA	0.10	–	23
Aquifoliaceae	NA	0.08	–	24
Bignoniaceae	NA	0.08	–	25
Convolvulaceae	NA	0.08	–	26
Verbenaceae	NA	0.08	–	27

Note: Relevance is also known as 'species strength' and was calculated as in Bascompte et al. (2006). The last two columns depict the relative importance of each plant family for male and female mutillids in an increasing fashion.

floral restrictions) (Müller, 1883), making them easily accessible to a large diversity of insect visitors, especially those with short mouthparts which are unable to access narrow tubular corollas (Gilbert & Jervis, 1998). Additionally, Apiaceae flowers are clustered in inflorescences, creating a more conspicuous display than scattered single flowers while at the same time providing a landing platform for insects (Proctor et al., 1996). Besides visual cues, flowering plants also exhibit attractive olfactory cues, as well as sugary rewards to their visitors in an effort to secure their pollination. In particular, Apiaceae and Asteraceae comprise high-aromatic species that produce volatile compounds which are attractive to insects (Hatt et al., 2019). Moreover, most flowers from these families also present bright yellow colours on their corollas, which are very attractive to wasps (Hatt et al., 2018; Reverté et al., 2016).

Currently, no work has attempted to evaluate the role of velvet ants as pollinators. Even in the last review on Sphecophily (Brock et al., 2021), Mutillidae and Myrmosidae wasps were not considered. In contrast, some studies consider velvet ants only as pollen robbers (Jia et al., 2015). The study of pollination has historically been biased towards the same insect groups, namely bees, hoverflies, beetles and butterflies. However, some other forgotten flower visitors are slowly gaining attention from the scientific community, such as some understudied wasps (Brock et al., 2021; Shuttleworth & Johnson, 2012), cockroaches (Pérez-Gómez et al., 2023), non-syrphid flies (Orford et al., 2015) and many others (Wardhaugh, 2015). While flower visiting by velvet ants might be deemed a rare occurrence considering all the photographic records reviewed (less than 1%), in nearly 43% of the cases in which velvet ants were recorded on flowers, pollen grains were observed attached to their bodies. Based on this, it would be inattentive to overlook their potential role as pollinators. Furthermore, we have noted that pollen grains can be attached anywhere on their bodies, including the ventral side of physical specimens, which is usually not visible in pictures made in the field. This renders our observations as a likely underestimation. Consistent with this, we found some specimens located in entomological collections with pollen attached to the ventral side. We also want to point out that pollen is well preserved and attached to the body of collected specimens regardless of time since the collection of the individual. Thus, this opens up the possibility of examining entomological material from collections in search of evidence suggesting a role for them as potential pollinators. Most velvet ants have great hairiness (Brothers, 1995), and in some cases, such as in some Sphaeropthalminae, mesosomal hairs can be plumose as in bee species (Mason, 1993). This may facilitate the transport of pollen grains. Considering the ecosystem benefits offered by pollinator communities and the detrimental impact of human activities on them (Nath et al., 2023; Potts et al., 2010), it is imperative to broaden our understanding of overlooked flower visitors, even though their contribution to pollination may not be as important as that of other pollinator groups. In the specific case of velvet ants, we have taken the first step into this knowledge gap, but more studies are necessary to confirm their role as pollinators as well as their relative importance and contribution to pollination.

Network metrics may help to unravel important patterns of community organization and heterogeneity in trophic associations. Interactions between plant families and velvet ant genera, albeit diverse, suggest that plant species tend to hold more specialized interactions than velvet ants, at least when considering plant and velvet ant niche overlap in a global network across bioregions. This means that plants share fewer flower visitors, whereas velvet ants visit flowering plants more generally. In fact, velvet ants had a higher and more diverse number of shared partners than plants. Additionally, the connectance of the network was relatively low (0.09), since only a small number out of the total potential links actually occurred, as typically happens in pollination networks (e.g., Vizentin-Bugoni et al., 2018). This, however, contrasts with what has been found in flower-feeding networks of some social wasps (15.90%–21.24%, Clemente et al., 2012; Santos et al., 2010). A potential explanation for this could be the diverging feeding pattern of both groups. The diet of social wasps does not only involve floral resources, but also other food sources like animal carcasses, which makes their interactions with flowers more generalized (Mello et al., 2011; Menezes et al., 2022; Santos et al., 2010). In contrast, adult velvet ants are almost exclusively dependent on floral resources for feeding, especially males. The network specialization index of our global data was 0.49, which falls within the expected value range of pollination networks (Thompson et al., 2013). Nevertheless, when considering plant-velvet ant interactions at the bioregion level, this metric fluctuated consistently around 0.20–0.21. These network specialization index values match better those of ant-nectar interactions (Thompson et al., 2013). Consistency across all bioregions for this index despite regional differences in plant and velvet ant community composition suggests that velvet ants act as generalist flower visitors globally. We attribute the differences in plant-velvet ant interactions found among the different bioregions to differences in the abundance, richness and diversity of plant and velvet ant species across regions (e.g., Vázquez et al., 2009). Contrastingly, when calculating network specialization indexes for males and females separately, we obtained values of 0.40 and 0.82, respectively. This suggests that females are more specific in their interactions than males, although these differences may root from the diverging sample sizes of our networks caused by the difficulty of finding females on flowers. Previous studies with parasitoid wasps found mixed results regarding the specialization of the interactions, with some indicating generalization and others observing apparent specialization (see Zemenick et al., 2019 for references). To better understand the specialization relationship between velvet ants and plant species, further studies with standardized and rigorous data collection are needed, as well as those at a more local scale, since visitation patterns may be sensitive to local variations in plant and velvet ant abundance and diversity. For example, communities with lower plant species richness, where a few plant species dominate, may foster visitors with specialized habits (e.g., Blüthgen et al., 2008; Clemente et al., 2012). Conversely, higher wasp diversity in resource-rich habitats could limit the variation in the diversity of resources utilized by each wasp species due to competition (e.g., Heithaus, 1979). For this reason, further studies focusing on the understanding of these patterns at a more local scale are encouraged, as ours deals with the issue in a very generalized way by integrating geographically distant communities into the same network.

Mutillidae sex was another important factor shaping visit preference patterns and influencing the plant-wasp interaction network. Mutillids present extreme sexual dimorphism both in morphology and behaviour, which may lead to the exploitation of different ecological niches. We found diverging flower visitation patterns and specialization degrees between male and female mutillids, which may also point towards different feeding habits. Sex differences in foraging patterns have also been observed in many other pollinating animals, from insects (Coleoptera, Diptera, Hymenoptera and Lepidotera) to bats and hummingbirds (Roswell et al., 2019; Smith et al., 2019). We suggest a few hypotheses to address why velvet ant males and females show different flower preferences and specialization. Firstly, we suggest that this may be caused by differences in their foraging ranges, given that mutillid females are apterous while most males are winged and can cover longer distances. This could lead to an increased encounter rate between males and a broader range of flowers, whereas females, moving shorter distances, may have fewer opportunities to visit a diverse array of plants, being perhaps more consistent in their visit patterns due to this limitation (Smith et al., 2019). Moreover, sexual differences in dispersive ability, higher in males than in females, may also affect their efficiency as potential pollinators. Similar to ant pollination systems, flowers visited by female mutillids might exhibit specific traits that render them more suitable for effective pollination by apterous insects. Effective ant pollination systems require plants that are small, bright and clustered, with exposed floral resources, and high flowering synchrony with few open flowers per individual, among other characteristics (Domingos-Melo et al., 2017). Some of the plant families preferred by mutillid females, such as Apiaceae, Asteraceae, Euphorbiaceae or Caryophyllaceae, may fulfill these conditions, as they feature generalist, small, clustered and exposed flowers (Müller, 1883; Proctor et al., 1996). Further studies focusing on individual plant species are required to uncover whether pollination by female mutillids is comparable to ant pollination systems, as well as the potential role of female mutillids as pollinators.

Secondly, differences in floral resource quantity and quality among plant species may be the cause of such divergent floral preferences between mutillid sexes, mainly reflecting their different nutritional needs. Males primarily seek resources to obtain energy to invest in continuous flight in search of mates, and thus may prioritize a great number of flowers with abundant rewards over other flowering plants. Females, on the other hand, allocate resources both for energy and offspring production, and may therefore be more sensitive to reward quality (Smith et al., 2019). This sensitivity is expected to be more pronounced when foraging on pollen, which is known to vary in nutritional quality for developing offspring (e.g., Di Pasquale et al., 2013; Roulston & Cane, 2000), compared to when foraging on nectar, where rewards mostly vary via nectar volume and concentration (Smith et al., 2019). This is consistent with observations of certain bee species, where females collect both nectar and pollen for their offspring, while males primarily forage for nectar to fuel flight (Willmer & Stone, 2004), leading to diverging flower preferences between sexes (Roswell et al., 2019). Asteraceae, the second plant family with the most relative importance to males, contains the highest concentrations and proportions of essential amino acids compared to Apiaceae, Fabaceae or Lamiaceae families (Venjakov et al., 2022), thus supporting the hypothesis of male fuel acquisition for flight. In contrast, Fabaceae was the second most important plant family for females. The pollen of many Fabaceae species has been indicated as high quality and very rich in proteins compared to other species (Hanley et al., 2008; Roulston et al., 2000), and it can be beneficial for female Mutillidae, which need high-quality resources for offspring production. Laboratory experiments and natural observations indicate that besides sugar solutions such as nectar, females also feed on their hosts and pollen (Brothers, 1972; Jordan, 1935; Mellor, 1927; Neal, 1884; Scholz, 1879), suggesting that they forage for additional nutrients not present in nectar. A third hypothesis is that males and females differ in their sensory abilities related to the location of forage (e.g., the type of sensilla or the use of visual or olfactory systems to locate flowers), leading to such differences in flower preference (Dötterl et al., 2011; van Praagh et al., 1980). Finally, the observed differences between males and females may have been caused by the diverging sample size between sexes in our data, where females were observed at a much lower frequency than males, probably owing to the behavioural differences with males discussed above. This may have led to an unrealistic high H_2' for females, for which the limited scarcity of records may not give a complete overview of their interactions. Also, note that we calculated sex differences across the family Mutillidae by pooling all records. However, specific genera or species may show patterns different to those observed at the family level when assessed individually.

5 | CONCLUSION

Despite the fact that the role of velvet ants as potential pollinators has been largely neglected by research so far, this study highlights their role as flower visitors with potential implications for the pollination of a wide range of plant species worldwide. Our analyses reveal the preferences of this insect group for specific plant families such as Apiaceae, Asteraceae, Euphorbiaceae, Rhamnaceae or Fabaceae, although more research needs to be carried out to unravel the underlying reasons behind these preferences. Despite differences in flowering plant and velvet ant composition across bioregions, velvet ants visited flowering plants in a generalistic way across the globe. Males and females seem to visit different plant communities, although the reasons for this are still unexplored. Finally, although their role as effective pollinators is still uncertain, we can confirm that a great percentage of velvet ants had pollen attached to their bodies and thus could potentially contribute to pollination. Overall, this research underscores the need for further investigation into the ecological contributions of velvet ants. Namely, the following aspects deserve research efforts: (1) the contribution of velvet ants to pollination, including (2) the effectiveness of velvet ants as pollen vectors, (3) the reasons behind the differences between flower visitation patterns in male and female Mutillidae, including (4) the contribution of flower foraging on female offspring, (5) the further investigation of the specific interactions between velvet ants and flowering plants, potentially using historical data from insect collections as done with other pollinating insects, and (6) the collection of data at local scales and with standardized sampling protocols to deepen the knowledge on plant-velvet ant interaction networks. Obtaining answers to these issues is not only essential to understand more about the significance of these neglected pollinators, but is also crucial to the conservation of this specific insect group. This becomes particularly relevant in light of the growing concerns about the global decline of pollinators and the pivotal role they play in maintaining ecosystems.

AUTHOR CONTRIBUTIONS

Daniel Parejo-Pulido: Conceptualization; methodology; data curation; investigation; validation; formal analysis; supervision; visualization; resources; writing – original draft; writing – review and editing. **Joan Díaz-Calafat:** Conceptualization; methodology; software; data curation; investigation; validation; formal analysis; supervision; visualization; resources; writing – original draft; writing – review and editing. **Jairo Robla:** Conceptualization; methodology; data curation; investigation; validation; formal analysis; supervision; visualization; resources; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All the data used in this paper is included in Zenodo: 10.5281/zenodo.10569918 and in the Data S1 of this paper.

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