



Eurasia Specialized Veterinary Publication

Entomological Research Letters

ISSN: 3108-639X

2025, Volume 5, Issue 2, Page No: 1-14

Copyright CC BY-NC-SA 4.0

Available online at: [www.esvpub.com/](http://www.esvpub.com/)

## Unveiling neglected pollinators: Worldwide perspectives on the floral associations of velvet ants (Hymenoptera: Mutillidae and Myrmosidae)

Daniel R. Cooper<sup>1</sup>, Melissa Hart<sup>2\*</sup>, Jonathan Miles<sup>1</sup>, Rebecca Stone<sup>2</sup>

<sup>1</sup>Department of Entomology, College of Agricultural Sciences, University of California Davis, Davis, United States.

<sup>2</sup>Department of Ecology and Evolutionary Biology, School of Biological Sciences, University of Queensland, Brisbane, Australia.

\*E-mail ✉ [melissa.hart@gmail.com](mailto:melissa.hart@gmail.com)

### ABSTRACT

Interactions between plants and animals are a fundamental theme in ecological studies, with pollination being among the most thoroughly investigated processes. Although certain insect groups have historically dominated pollination research due to their abundance and effectiveness, many lesser-known flower visitors also warrant attention. Velvet ants (Hymenoptera: Mutillidae and Myrmosidae) provide a compelling case study, as their ecological traits, including feeding behavior, remain poorly understood despite frequent reports of their visits to flowers. To address this gap, we assembled a worldwide synthesis of floral visitation by velvet ants, drawing on citizen science observations, published accounts, and unpublished datasets. Using network-based approaches, we examined patterns of floral use globally, across bioregions, and in relation to sex-specific visitation. Additionally, we evaluated their possible contribution to pollen transport by assessing photographic evidence of pollen adhered to their bodies. Our findings indicate that velvet ants act as broad generalists, interacting with diverse flowering plant families, particularly Apiaceae, Asteraceae, Euphorbiaceae, Rhamnaceae, and Fabaceae. While plant and velvet ant assemblages varied by region, the generalistic pattern of flower use persisted worldwide. Male and female velvet ants showed distinct floral associations, with males exhibiting broader preferences. Notably, pollen was present on 42.7% of images depicting velvet ants at flowers—likely an underestimate—paralleling observations in recognized pollinators and highlighting their potential role in pollination. These results underscore the need for further research into velvet ants and other overlooked arthropods to better understand their ecological significance as both flower visitors and possible pollinators.

**Keywords:** Apiaceae, Specialization, Bipartite graph, Ecology, Neglected pollinators, Interaction network

**Received:** 11 July 2025

**Revised:** 14 August 2025

**Accepted:** 17 August 2025

**How to Cite This Article:** Cooper DR, Hart M, Miles J, Stone R. Unveiling neglected pollinators: Worldwide perspectives on the floral associations of velvet ants (Hymenoptera: Mutillidae and Myrmosidae). *Entomol Res Lett.* 2025;5(2):1-14. <https://doi.org/10.51847/GDizD8REqR>

### Introduction

Ecological systems are shaped by numerous interactions between plants and animals, which serve as fundamental processes in terrestrial environments across the globe [1]. Among these, mechanisms such as seed dispersal and pollination are especially influential in maintaining ecosystem stability. Investigating such relationships is therefore critical not only for explaining how communities are organized but also for ensuring their long-term conservation and management [2–4].

Pollination, in particular, has long stood at the center of ecological research. An organism qualifies as a pollinator when it enables the transfer of pollen from stamens to stigmas, thereby facilitating plant reproduction [5]. Four

insect groups have dominated pollination studies: beetles, flies, lepidopterans (butterflies and moths), and hymenopterans (bees and wasps). While bees are widely celebrated for their pollinating efficiency, wasps—though diverse—remain comparatively underexplored [6]. Pollination mediated by wasps, known as sphecophily, is nonetheless well documented. The fig–fig wasp mutualism (Chalcidoidea and *Ficus* spp.) is a classic example of extreme specialization [7]. Beyond this, families such as Pompilidae, Scoliidae, Sphecidae, Thynnidae, and Vespidae have been identified as pollinators for numerous orchids and other plants [6, 8]. Generalist nectar-foraging wasps also interact with a wide range of flowers, extending their potential importance in pollination networks [9]. Estimates suggest that more than 600 wasp species interact with close to 800 flowering plants worldwide [6, 10–14], although the true numbers are likely far greater. Recognizing the diversity of wasp–plant associations is therefore essential, both for the protection of wasps and for the plants reliant on them.

Within Aculeata, the solitary wasps of the families Mutillidae and Myrmosidae—commonly known as velvet ants—offer an intriguing case study. Their dense hair and ant-like form inspired their common name [15]. They exhibit marked sexual dimorphism: males are winged, whereas females lack wings, resulting in distinct behavioral roles [16–20]. Once treated as a single lineage, recent phylogenomic work has separated Myrmosidae from Mutillidae, confirming them as independent families [21]. Collectively, they are remarkably diverse, with over 4,500 recognized species that peak in richness in tropical regions [22]. Yet, despite their conspicuousness, our ecological understanding of velvet ants remains fragmentary [17, 23, 24].

The life history of velvet ants is defined by their role as ectoparasitoids, developing within the brood of other insects including aculeate hymenopterans, coleopterans, dipterans, heteropterans, and even cockroaches [17, 23, 25]. Their degree of host specificity varies among taxa [23]. Adult feeding ecology, however, remains poorly described. Males are mainly nectar feeders, frequently observed on flowers, extrafloral nectaries, or consuming honeydew [15, 26–31]. Females exploit a broader set of resources, including nectar, extrafloral nectaries, honeydew, as well as provisions inside host cells such as pollen masses and host fluids [26, 32–39]. Despite their parasitic habits, both sexes are consistently recorded as flower visitors, though females appear less frequently in this role [27, 30, 40]. For instance, Lelej (1985) reported 40 Eurasian velvet ant species visiting flowers of 14 plant families, with Apiaceae being especially frequent, a pattern echoed by subsequent studies [27, 41–43]. Yet, despite documentation of host preferences, no systematic quantitative analysis has assessed their floral visitation. Likewise, their potential contribution to pollination remains largely speculative.

This study was designed to bridge these knowledge gaps by: (i) applying network-based approaches to analyze velvet ant floral visitation patterns globally; (ii) identifying the plant families most often visited and testing whether associations differ across regions or between sexes; and (iii) considering their potential ecological role as pollinators.

## Materials and Methods

### *Data collection*

To build the dataset, we compiled information from multiple sources. First, we retrieved all available photographic records of velvet ants on flowers from two global citizen science platforms—iNaturalist (<https://www.inaturalist.org/>) and Biodiversidad Virtual (<https://www.biodiversidadvirtual.org/>)—up to September 30, 2023. Next, we conducted a thorough literature search for references to Mutillidae and Myrmosidae observed or collected while feeding on flowers or extrafloral nectaries. Records where individuals were noted only on non-reproductive plant structures (e.g., branches or leaves), feeding on honeydew, or with the feeding structure unspecified, were excluded. Additional unpublished records contributed by the authors and external collaborators were also incorporated.

For each flower-visit event, we recorded: the velvet ant and host plant taxa (to the finest identifiable level), sex of the velvet ant, month of observation, location, and whether pollen grains were visible on the insect’s body. When pollen was present, we further documented its position on the body. Velvet ant identifications were based on diagnostic morphological features and verified by specialists (notably Kevin A. Williams, Rafael Matias, Marcello Romano, Denis J. Brothers, and the first author). Plant identifications were initially provided by observers and subsequently cross-checked by the study authors.

### *Statistical analyses*

To ensure the focus remained strictly on flower-based interactions, records of velvet ants feeding at extrafloral nectaries were excluded. Because our dataset combined heterogeneous sources with uneven sampling effort across taxa and regions, we treated the analyses as exploratory. Nonetheless, the large number and wide coverage of records make them a reasonable baseline for examining plant–velvet ant associations. Given that plant identifications were not always resolved to species level, analyses were standardized at the family level.

We conducted two main sets of analyses: (i) evaluation of interaction differences among bioregions and description of the overall structure of a global network pooling all records, and (ii) assessment of sex-related variation in flower visitation patterns. Data from Mutillidae and Myrmosidae were analyzed jointly unless explicitly distinguished; in most cases, Myrmosidae records were too scarce for separate analysis. All analyses were performed in R 4.3.1 [44]. Plant–velvet ant interaction networks were generated using the ‘bipartite’ v2.18 package [45]. Species-level metric formulas are described in Dormann (2011), while full-network metrics follow Dormann *et al.* (2009) [46, 47]. For reproducibility, we recommend using the ‘checkpoint’ package fixed to January 2024, ensuring identical package versions to those used in this study [48]. All data and scripts are publicly available at 10.5281/zenodo.10569918.

#### *Global and bioregional interaction networks*

A global interaction network was first constructed using all records regardless of geographic origin (thus including some bioregions later excluded from regional analyses). To minimize sampling biases and account for uneven data representation, interactions were treated as binary when computing most network metrics, except for the network-level specialization index ( $H^2$ ), which incorporated frequencies. The following network metrics were calculated: average number of species, mean number of links, number of shared partners, partner diversity (Shannon index), niche overlap (for plants and wasps), connectance, and  $H^2$ .

To test for bioregional variation, we applied a one-way PERMANOVA with 9,999 permutations in PAST v4.0.3 using Bray–Curtis distance matrices [49]. Bioregion was the predictor variable. Similar analyses were conducted to examine whether velvet ant composition (at the genus level for both families) and plant family composition varied among regions. When PERMANOVA identified significant differences, pairwise comparisons were carried out with Bonferroni correction. Additionally,  $H^2$  was computed separately for each bioregion that contained more than five unique interactions. Records with doubtful *Smicromyrme*/*Physetopoda* identifications were excluded, and abundance data were used to construct distance matrices.

To correct for distortions introduced by disproportionately abundant records, adjustments were made. Specifically, data from Williams *et al.* (2019) and Hennessey & West (2018) contained unusually high counts of mutillid visits to *Euphorbia* spp. and *Helianthus annuus* [40, 50]. Because these inflated values skewed network structure, their abundances were standardized so that each interaction was represented only once (abundance = 1).

#### *Flower preference of velvet ants by sex*

To evaluate sex-based differences in floral resource use, we applied the Morisita–Horn dissimilarity index, which compares the proportional representation of female and male velvet ants across different flowering plant families (i.e., the contribution of each family to their respective diets). This metric, which ranges from 0 (identical composition) to 1 (entirely distinct), is robust to unequal sampling intensity and imbalanced group sizes. It also gives more weight to major contributors than to plant families with only a few records, thereby reducing the influence of underrepresented taxa. Because our dataset was inherently heterogeneous, all available records from every bioregion were pooled, and analyses were conducted at the family level for plants. Velvet ants were classified by family, although Myrmosidae was excluded from the comparison due to having just a single female observation.

Beyond the observed dissimilarity between male and female Mutillidae flower-visiting patterns, we constructed a null model to determine whether differences deviated from random expectation. This model, following the procedure outlined in Roswell *et al.* (2019), permuted wasp sex while preserving the total counts of male, female, and combined visits for each plant family [51]. We ran 9,999 permutations to generate a distribution of expected Morisita–Horn values and obtained a 95% confidence interval.

Additionally, two bipartite interaction networks were created to visualize associations between flowering plant families and male or female Mutillidae. For these networks, geographical origin was not considered, and interaction frequencies were disregarded to allow for broader generalizations across mutillid genera rather than repeated visits to the same host. Plant importance within each network was quantified as the cumulative sum of

dependency values across all velvet ant partners [52]. Finally, network-level specialization ( $H^2$ ) was calculated separately for males and females, this time incorporating interaction frequencies.

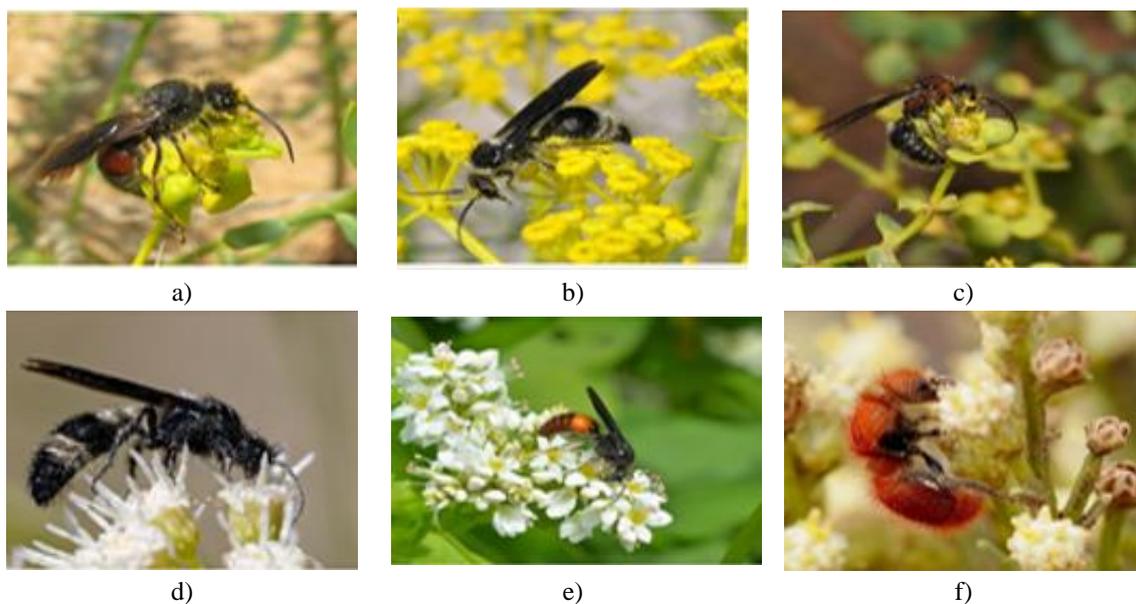
## Results and Discussion

### Data collection

Our survey encompassed 63,433 photographic records of velvet ants (Mutillidae and Myrmosidae) obtained worldwide—61,357 from iNaturalist, 2,076 from Biodiversidad Virtual, plus all available literature. Only a small fraction of these records (542; 0.9%) documented individuals visiting flowers (**Figure 1**), distributed as follows: 250 from iNaturalist, 184 from published literature, 65 from unpublished datasets contributed by the authors and collaborators, and 43 from BV. Full details of these records are provided in Data S1.

The final dataset contained information on 124 taxa spanning 40 genera of Mutillidae and Myrmosidae. Of the flower-visiting records, 466 individuals (86.0%) were males, 72 (13.3%) were females, and 4 (0.7%) were of undetermined sex. Biogeographic distribution of these events was uneven: 0.85% in the Afrotropical region, 1.57% in Australasia, 0.36% in Indomalaya, 44.75% in the Nearctic, 2.17% in the Neotropics, and 50.30% in the Palearctic.

Evidence of pollen transport was present in 132 cases (42.7% of flower-visiting observations, representing 0.2% of all photographic records reviewed). Pollen grains were most often found adhering to body pilosity on the head, antennae, thorax, abdomen, and legs. However, as most photographs captured dorsal views, potential pollen loads on the ventral side could not be assessed. Verification of entomological collection specimens revealed that pollen attachment to ventral body surfaces does indeed occur, supporting this likelihood.



**Figure 1.** Examples of velvet ants recorded while visiting flowers and transporting pollen. (a) Male *Tropidotilla litoralis* (Russia, Asia; photo by Alexander Fateryga). (b) Male *Nemka viduata andalusiana* (Spain, Europe; photo by Francisco Rodríguez Luque “Faluke”). (c) Male velvet ant from the tribe Smicromyrmini (France, Europe; photo by André Miquet). (d) Male *Tallium* sp. (Argentina, South America; photo by Quentin Vandemoortele). (e) Male *Timulla vagans* (United States, North America; photo by Sydney Penner). (f) Female *Sphaerophthalma unicolor* (United States, North America; photo by Glenn Perelson).

### Global interaction networks

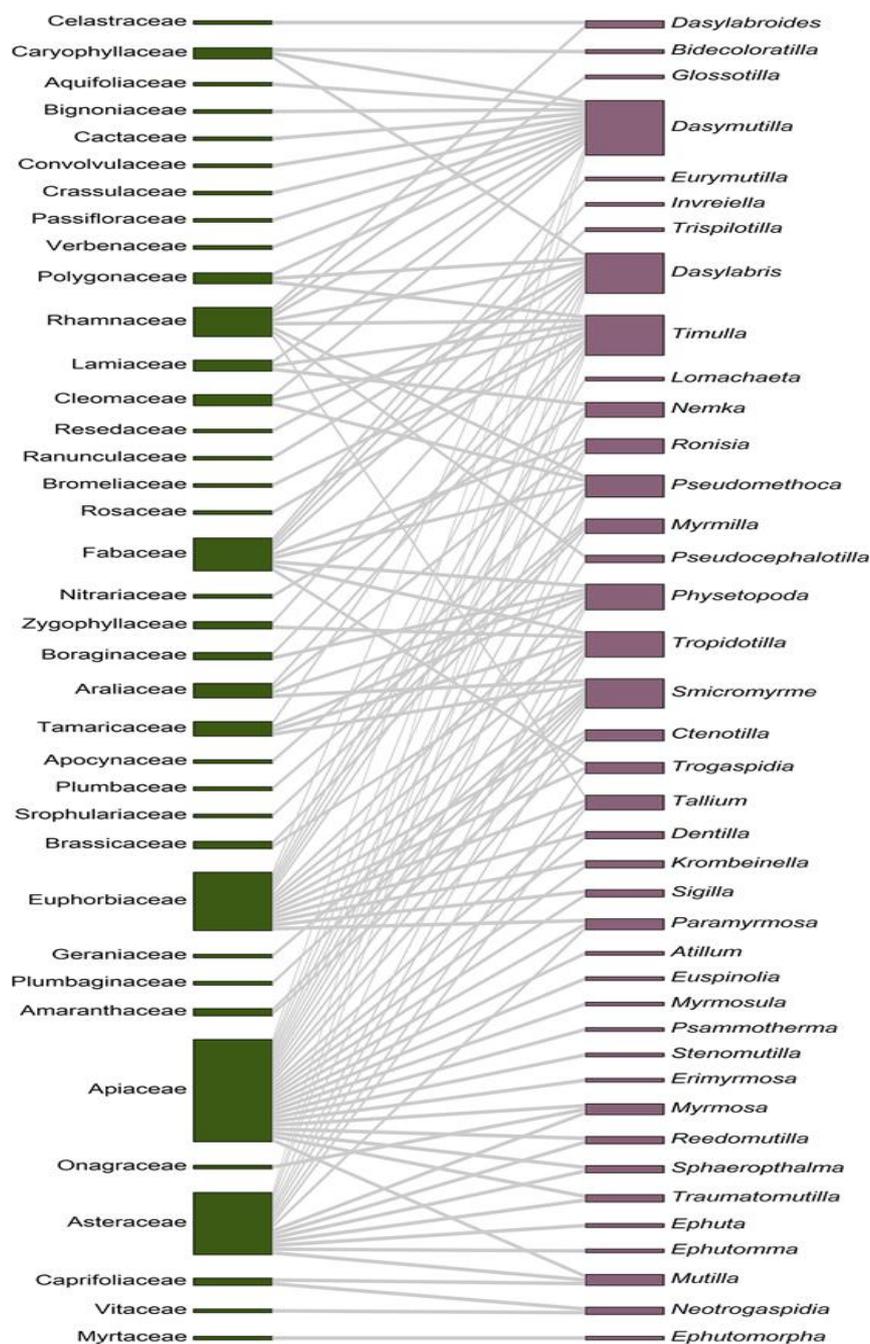
When combining all records into a single dataset, the network comprised 40 genera of velvet ants linked to 37 families of flowering plants. Among plant families, Apiaceae emerged as the most frequently visited, followed by Asteraceae, Euphorbiaceae, Rhamnaceae, Fabaceae, and several others with lower representation (**Figure 2**).

On average, each network node was connected to 1.67 nodes from the opposite trophic level. Velvet ants shared an average of 0.93 partners, compared with 0.52 for plant families. This indicates that velvet ants interacted with

a broader array of plant partners than plants did with velvet ant genera. Partner diversity, measured by Shannon's index, was higher for velvet ants (0.81) than for plants (0.64), though this difference may partially reflect unequal taxonomic resolution between the two groups.

The calculated niche overlap was 0.28 for velvet ants and 0.13 for plant families. Since the index spans from 0 (no overlap) to 1 (complete overlap), these values suggest that velvet ants exhibit greater redundancy in their interactions, whereas plant families engage in more specialized relationships. Consequently, the extinction of a single velvet ant genus would likely cause fewer cascading losses among plants than the disappearance of an entire plant family would have on velvet ants.

Overall, network connectance was estimated at 0.09, while the specialization index ( $H^2$ ) reached 0.49, reflecting an intermediate level of specialization across the global velvet ant–plant interaction network.



**Figure 2.** Bipartite diagram illustrating the complete set of recorded associations between velvet ant genera (right side) and families of flowering plants (left side) across all biogeographic regions. Interaction frequency (i.e., the number of times a given genus was observed on flowers from a particular plant family) was not considered in this representation.

*Bioregional interaction networks*

Out of the six bioregions surveyed, only the Nearctic ( $n = 39$ ), Neotropical ( $n = 11$ ), and Palearctic ( $n = 71$ ) contained more than five unique interaction events and were therefore suitable for analysis. Statistical testing confirmed significant variation in plant–velvet ant interactions among these three regions (one-way PERMANOVA,  $F = 31.49$ ,  $p < 0.001$ ), with all pairwise comparisons showing clear differences (all  $p < 0.001$ ). When examining velvet ant genera, composition also varied among regions (one-way PERMANOVA,  $F = 5.65$ ,  $p < 0.001$ ). Specifically, the Palearctic fauna differed significantly from both the Nearctic and Neotropical groups ( $p < 0.05$ ), while the Nearctic and Neotropical assemblages were not significantly distinct ( $p = 0.62$ ). Plant family composition revealed a different pattern: significant differences were observed between Nearctic and Neotropical ( $p < 0.001$ ) as well as Neotropical and Palearctic regions ( $p < 0.001$ ), but no significant divergence emerged between the Palearctic and Nearctic ( $p = 0.35$ ). Across all three regions, the calculated network specialization index ( $H^2$ ) remained consistently low, ranging between 0.20 and 0.21.

*Flower preference of mutillids by sex*

Analysis with the Morisita–Horn dissimilarity index indicated that male and female mutillids differed in their floral associations by 43.48%, a deviation significantly greater than expected under random allocation (**Figure 3a**). This outcome highlights that males and females exploit distinct sets of plant families.

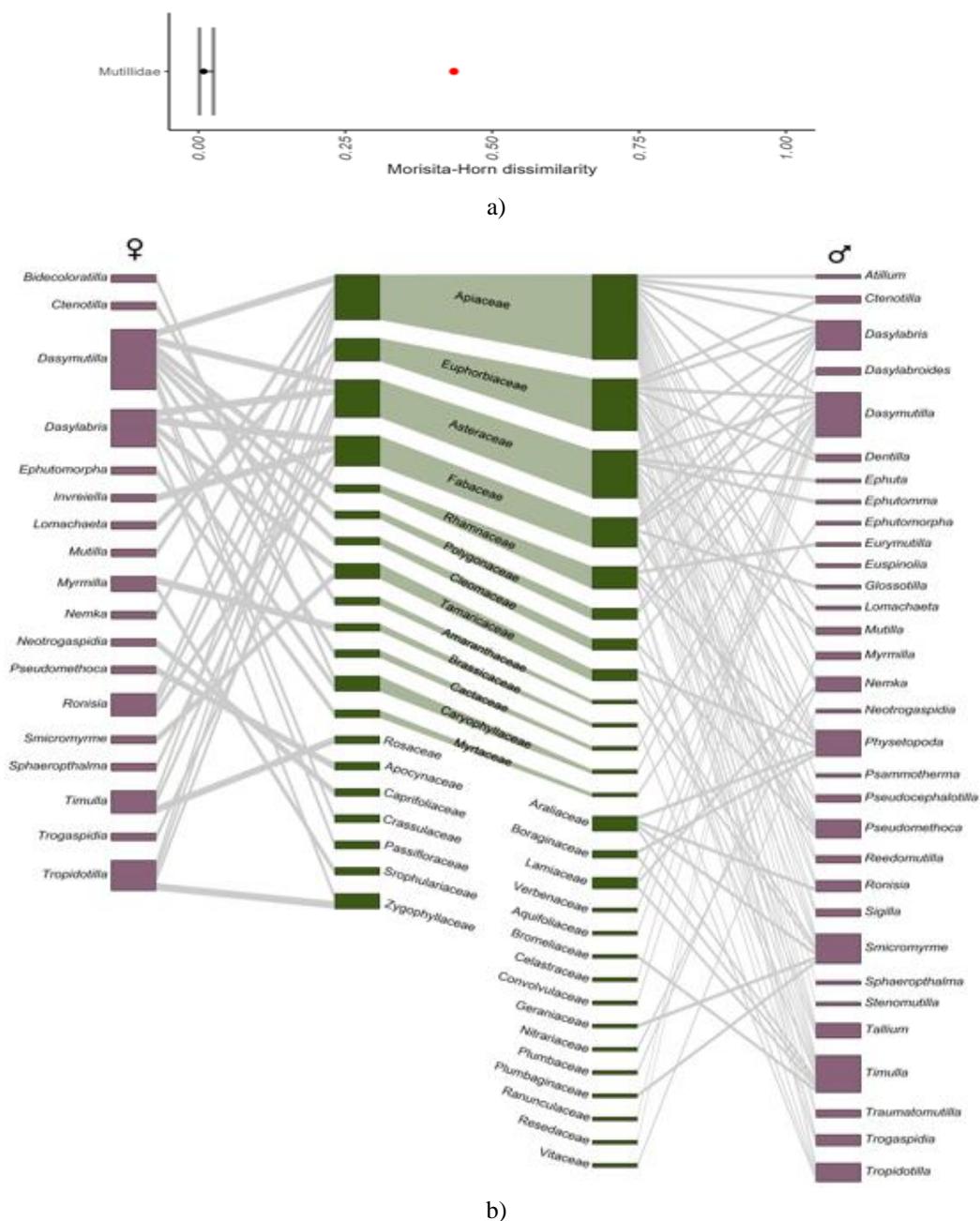
Bipartite networks depicting these sex-specific interactions (**Figure 3b**), together with measures of plant family importance (**Table 1**), showed that Apiaceae was the primary plant family visited by both sexes. However, its importance was particularly pronounced for males. Network specialization indices further supported this distinction, with  $H^2$  values of 0.40 for females and 0.82 for males, reflecting stronger generalism in male visitation patterns.

**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.** The term relevance corresponds to what Bascombe *et al.* (2006) define as species strength [52]. The final two columns display the ranked importance of each flowering plant family for male and female mutillids, arranged from lower to higher contribution.



**Figure 3.** (a) Morisita-Horn dissimilarity index comparing male and female mutillids is shown (red dot), alongside the dissimilarity expected under random conditions (grey). This index ranges from 0, indicating no differences between the compared elements, to 1, representing complete dissimilarity. (b) Bipartite networks

illustrating associations between flowering plants and female (left) versus male (right) mutillids. Interactions are unweighted, so variations in line thickness across plots reflect network size rather than any quantitative differences. Plant families shared by both sexes are positioned centrally, highlighted with a green background connecting the two networks.

This study provides novel insights into the ecological role of velvet ants by delivering the first quantitative evaluation of their flower visitation patterns. Our data confirm that these insects interact with numerous plant families across the globe, highlighting a likely contribution of mutillids and myrmosids to the pollination of a wide variety of plant species. Additionally, we observed that males and females differ in their floral associations, a pattern that likely reflects differences in their physiological and reproductive needs.

Floral resources such as nectar and pollen are essential nutritional components for many hymenopterans, including parasitoid species like velvet ants [53, 54]. Consequently, flower visitation is commonly reported for these insects [27, 30, 40]. Velvet ants, akin to other hymenopterans, appear to favor certain plant species whose traits—such as floral shape or reward accessibility—enhance their attractiveness [11, 55, 56]. Recognizing these preferences is crucial for conservation, as these insects provide vital ecosystem services both as pollinators and as biological control agents [6].

Our global analysis shows that velvet ants visit flowers from 37 different plant families. Apiaceae umbels emerged as the most frequently visited and likely the main source of nourishment, followed by Asteraceae, Euphorbiaceae, Rhamnaceae, Fabaceae, and several other families in smaller proportions. These results are consistent with prior studies on velvet ants [27, 41–43] and mirror patterns reported for other hymenopterans, including parasitoids [53, 57] and vespids [11, 55, 58].

We suggest that the observed flower preferences are shaped by both the structural traits of flowers and the morphology of velvet ant mouthparts [59]. Many of the commonly visited families, including Apiaceae, have open floral designs that expose nectar and pollen, allowing access even for insects with short mouthparts that cannot reach narrow tubular corollas [60, 61]. The inflorescence arrangement in Apiaceae further enhances visibility and provides a landing platform for visitors [62]. In addition to visual appeal, flowers offer olfactory signals and sugary rewards that attract pollinators. Apiaceae and Asteraceae, in particular, are highly aromatic, producing volatile compounds that insects find attractive, and their bright yellow corollas are known to be especially appealing to wasps [63–65].

To date, no research has specifically explored the potential role of velvet ants as pollinators. Even the most recent review on Sphecophily does not include Mutillidae or Myrmosidae within its scope. Some studies have considered these wasps merely as pollen thieves rather than legitimate flower visitors [6, 66]. Historically, pollination research has largely focused on a narrow set of insects, primarily bees, hoverflies, beetles, and butterflies. However, attention is gradually expanding to include less-studied flower visitors such as certain wasps, cockroaches, non-syrphid flies, and other neglected taxa [6, 8, 9, 67, 68].

Although flower visits by velvet ants appear rare when considering all photographic records reviewed (less than 1% of total observations), nearly 43% of cases in which they were recorded on flowers revealed pollen grains attached to their bodies. This suggests that their potential contribution to pollination should not be overlooked. Pollen can adhere to multiple parts of their bodies, including ventral regions typically hidden in field photographs, indicating that published observations likely underestimate their role. Supporting this, examination of entomological collections revealed specimens with pollen adhering to ventral surfaces, demonstrating that pollen can remain attached and well-preserved over long periods after collection. This raises the possibility of systematically investigating museum specimens to further assess their pollination potential.

Many velvet ants possess dense body hairs, and in some taxa, such as certain Sphaerophthalminae, the mesosomal hairs are plumose, resembling those of bees [15, 69]. Such adaptations may facilitate pollen transport. Given the critical ecosystem services provided by pollinator communities and the negative effects of anthropogenic pressures on them, it is important to expand our understanding of overlooked flower visitors [70, 71]. While velvet ants may not rival traditional pollinators in overall contribution, they represent a previously neglected component of pollination networks. This study represents an initial step toward addressing this knowledge gap, but further research is needed to clarify their effectiveness and relative importance as pollinators.

Analysis of network metrics can provide insights into community organization and heterogeneity in trophic interactions. At the global scale, interactions between plant families and velvet ant genera suggest that plant species tend to exhibit more specialized relationships than velvet ants. In other words, plants share fewer flower

visitors, while velvet ants visit flowers more broadly. Indeed, velvet ants showed a higher diversity of shared partners compared to plants. Network connectance was relatively low (0.09), reflecting the small proportion of realized interactions relative to all potential links, a pattern common in pollination networks [72]. This contrasts with flower-visitation networks of some social wasps, where connectance ranges from 15.90% to 21.24% [10, 14]. One possible explanation is that social wasps have more generalized feeding behaviors, consuming not only floral resources but also alternative foods such as animal carcasses, whereas adult velvet ants, particularly males, rely almost exclusively on floral resources [13, 14, 73].

The global network specialization index for velvet ants was 0.49, consistent with values reported for pollination networks [74]. At the bioregion level, this metric ranged consistently between 0.20 and 0.21, aligning more closely with ant-nectar interaction networks [74]. The stability of these specialization values across diverse regions, despite differences in local plant and velvet ant communities, indicates that velvet ants function as generalist flower visitors on a global scale. Variations in plant-velvet ant interaction patterns among bioregions are likely driven by regional differences in species richness, abundance, and diversity of both plants and velvet ants [1].

When network specialization was analyzed separately for males and females, we found values of 0.40 and 0.82, respectively. This indicates that females tend to interact with a narrower set of plant species than males. However, these differences may partly reflect disparities in sample sizes, since females are more challenging to observe on flowers. Previous research on parasitoid wasps has reported mixed outcomes regarding interaction specialization, with some studies highlighting generalized behavior and others noting apparent specialization [57]. To more accurately assess the specificity of velvet ant-plant interactions, future investigations should employ standardized and rigorous sampling protocols, ideally at finer, local scales, because visitation patterns are likely influenced by local variation in the abundance and diversity of both plants and velvet ants. For instance, plant communities with low species richness dominated by a few plants may favor highly specialized visitors [10, 75], whereas species-rich, resource-abundant habitats could reduce specialization due to competitive constraints on resource use [76]. Therefore, detailed local-scale studies are essential to complement our global, generalized network analyses that integrate geographically distant communities.

Sex was another key factor shaping floral visitation patterns and structuring plant-velvet ant networks. Extreme sexual dimorphism in mutillids, both in morphology and behavior, likely drives the exploitation of different ecological niches. Our data reveal distinct flower visitation patterns and degrees of specialization between males and females, suggesting potential differences in their feeding strategies. Similar sex-related foraging differences have been documented across a range of pollinating taxa, including insects (Coleoptera, Diptera, Hymenoptera, Lepidoptera), bats, and hummingbirds [51, 77].

We propose several hypotheses for these sex-specific patterns. One is the difference in foraging ranges: female mutillids are wingless (apterous), whereas males are winged and can travel longer distances. Consequently, males may encounter a wider variety of flowers, while females, restricted to shorter distances, might consistently visit fewer plant species. This limited mobility may also influence the efficiency of females as potential pollinators. Analogous to ant pollination systems, flowers visited by females might possess traits that facilitate effective pollination by small, ground-level, or apterous insects. Successful ant-pollination systems typically involve plants with small, bright, clustered flowers, exposed nectar and pollen, synchronized flowering, and few open flowers per individual [78]. Many plant families frequented by female mutillids—such as Apiaceae, Asteraceae, Euphorbiaceae, and Caryophyllaceae—exhibit these traits, featuring small, clustered, generalist flowers with accessible resources [60, 62].

Further research targeting individual plant species is needed to determine whether pollination by female mutillids parallels ant-mediated pollination systems and to clarify the role of female velvet ants as effective pollinators.

Another factor that may explain the divergent floral preferences between male and female mutillids is the variation in both the quantity and quality of floral resources across plant species, which likely reflects differences in their nutritional demands. Male velvet ants primarily require energy to sustain continuous flight in search of mates, so they may prioritize visiting a larger number of flowers that provide abundant rewards. In contrast, females need resources not only for their own energy requirements but also for reproduction, making them more selective with regard to the nutritional quality of the resources they exploit [77]. This distinction is particularly important for pollen foraging, since pollen quality can significantly affect offspring development, whereas nectar mainly varies in terms of volume and sugar concentration [77, 79, 80].

Similar patterns are observed in certain bee species, where females collect both nectar and pollen to provision their offspring, while males forage primarily for nectar to sustain flight, leading to sex-specific flower preferences

[51, 81]. In our study, Asteraceae ranked as the second most important plant family for males, likely because it contains high concentrations and proportions of essential amino acids compared to Apiaceae, Fabaceae, or Lamiaceae, supporting the notion that males prioritize energy acquisition for flight [82]. For females, Fabaceae was the second most important family, as many species in this family produce pollen that is protein-rich and highly nutritious, providing essential resources for offspring development [83, 84]. Observations and laboratory studies indicate that female mutillids feed not only on nectar but also on pollen and occasionally on their hosts [26, 36–39], suggesting that they seek nutrients unavailable in nectar alone.

A third explanation for sex-specific floral preferences may involve differences in sensory perception, such as the type of sensilla or the relative reliance on visual versus olfactory cues for locating flowers [85, 86]. Finally, the disparity in sample sizes between males and females in our dataset could also contribute to observed differences. Females were recorded much less frequently than males, possibly due to behavioral differences, which may have artificially inflated the H<sup>2</sup> index for females and may not fully capture the breadth of their interactions. It is also important to note that these sex-based analyses were conducted at the family level, pooling all Mutillidae records; individual genera or species may exhibit different patterns when examined separately.

## Conclusion

Although velvet ants have largely been overlooked in pollination research, our study emphasizes their role as flower visitors and highlights their potential importance for the pollination of a diverse array of plant species worldwide. Our findings indicate that velvet ants show clear preferences for certain plant families, including Apiaceae, Asteraceae, Euphorbiaceae, Rhamnaceae, and Fabaceae, though further research is required to clarify the mechanisms underlying these preferences. Despite regional differences in plant and velvet ant community composition, these insects display a generally generalist pattern of flower visitation on a global scale. Moreover, males and females appear to exploit different plant communities, though the causes of these sex-specific patterns remain largely unexplored.

While the effectiveness of velvet ants as pollinators is still uncertain, a substantial proportion of individuals were observed carrying pollen, suggesting they may contribute to pollination. This study underscores the need for additional research to better understand the ecological role of velvet ants. Key areas for future investigation include: (1) quantifying their contribution to pollination, (2) assessing their efficiency as pollen vectors, (3) elucidating the causes of sex-based differences in flower visitation, (4) examining how female foraging influences offspring development, (5) exploring specific plant-velvet ant interactions, including the potential use of historical insect collection data, and (6) collecting standardized data at local scales to refine knowledge of plant-velvet ant networks.

Addressing these questions is not only critical for understanding the ecological significance of these neglected pollinators, but also for the conservation of velvet ants themselves. This is particularly important given ongoing concerns about the global decline of pollinators and their essential role in sustaining ecosystem function.

**Acknowledgments:** None

**Conflict of Interest:** None

**Financial Support:** None

**Ethics Statement:** None

## References

1. Vázquez DP, Blüthgen N, Cagnolo L, Chacoff P. Uniting pattern and process in plant-animal mutualistic networks: a review. *Ann Bot.* 2009;103(9):1445-57. doi:10.1093/aob/mcp057
2. Bronstein JL, Alarcón R, Geber M. The evolution of plant-insect mutualisms. *New Phytol.* 2006;172(3):412-28. doi:10.1111/j.1469-8137.2006.01864.x
3. Rico-Gray V, Oliveira PS. *The ecology and evolution of ant-plant interactions.* Chicago (IL): University of Chicago Press; 2007.

4. Waser NM, Ollerton J, editors. *Plant-pollinator interactions: From specialization to generalization*. Chicago (IL): University of Chicago Press; 2006.
5. Faegri K, van der Pijl L, editors. *Principles of pollination ecology*. Pergamon Press Ltd; 1979. Chapter 16: Applied pollination ecology. p. 159-63.
6. Brock RE, Cini A, Sumner S. Ecosystem services provided by aculeate wasps. *Biol Rev*. 2021;96(4):1645-75. doi:10.1111/brv.12719
7. Kjellberg F, Jousselein E, Hossaert-McKey M, Rasplus JY. Biology, ecology, and evolution of fig-pollinating wasps (Chalcidoidea, Agaonidae). In: Raman A, Schaefer W, Withers TM, editors. *Biology, ecology and evolution of gall-inducing arthropods*. CRC Press; 2005. p. 539-72.
8. Shuttleworth A, Johnson SD. The *Hemipepsis* wasp-pollination system in South Africa: A comparative analysis of trait convergence in a highly specialized plant guild. *Bot J Linn Soc*. 2012;168(3):278-99. doi:10.1111/j.1095-8339.2012.01216.x
9. Wardhaugh CW. How many species of arthropods visit flowers? *Arthropod-Plant Interact*. 2015;9(6):547-65. doi:10.1007/s11829-015-9398-4
10. Clemente MA, Lange D, Del-Claro K, Prezoto F, Campos NR, Barbosa BC. Flower-visiting social wasps and plants interaction: network pattern and environmental complexity. *Psyche: J Entomol*. 2012;2012:478431. doi:10.1155/2012/478431
11. Fateryga AV. Trophic relations between vespidae wasps (Hymenoptera, Vespidae) and flowering plants in the Crimea. *Entomol Rev*. 2010;90:698-705. doi:10.1134/S0013873810060047
12. Gess SK, Gess FW. *Pollen wasps and flowers in southern Africa: SANBI Biodiversity Series 18*. Pretoria: South African National Biodiversity Institute; 2010.
13. Mello MA, de Mendonça Santos GM, Mechi MR, Hermes MG. High generalization in flower-visiting networks of social wasps. *Acta Oecol*. 2011;37(1):37-42. doi:10.1016/j.actao.2010.11.004
14. Santos GMM, Aguiar CML, Mello MA. Flower-visiting guild associated with the Caatinga flora: trophic interaction networks formed by social bees and social wasps with plants. *Apidologie*. 2010;41(4):466-75. doi:10.1051/apido/2009081
15. Brothers DJ. Mutillidae. In: Hanson PE, Gauld ID, editors. *The Hymenoptera of Costa Rica*. Oxford: Oxford University Press; 1995. p. 541-48.
16. Deyrup M, Manley D. Sex-biased size variation in velvet ants (Hymenoptera: Mutillidae). *Fl Entomol*. 1986;69(2):327-35. doi:10.2307/3494937
17. Brothers DJ. Alternative life-history styles of mutillid wasps (Insecta, Hymenoptera). In: Bruton MN, editor. *Alternative life-history styles of animals. Perspectives in vertebrate science, Vol 6*. Springer; 1989. p. 279-91. doi:10.1007/978-94-009-2605-9\_14
18. Polidori C, Mendiola P, Asís JD, Tormos J, Selfa J. Temporal asynchrony and spatial co-occurrence with the host: The foraging patterns of *Nemka viduata*, a parasitoid of digger wasps (Hymenoptera: Mutillidae and Crabronidae). *J Ethol*. 2010;28:353-61. doi:10.1007/s10164-009-0196-2
19. Schmidt JO, Schmidt LS, Schmidt DK. The paradox of the velvet-ant (Hymenoptera, Mutillidae). *J Hymenopt Res*. 2021;84:327-37. doi:10.3897/jhr.84.68795
20. Tormos J, Asís JD, Polidori C, Benítez A, Storino G. The mating behaviour of the velvet ant, *Nemka viduata* (Hymenoptera: Mutillidae). *J Insect Behav*. 2010;23:117-27. doi:10.1007/s10905-009-9200-5
21. Waldren GC, Sadler EA, Murray EA, Bossert S, Danforth BN, Pitts JP. Phylogenomic inference of the higher classification of velvet ants (Hymenoptera: Mutillidae). *Syst Entomol*. 2023;48(3):463-87. doi:10.1111/syen.12588
22. Pagliano G, Brothers DJ, Cambra R, Lelej AS, Lo Cascio P, Matteini Palmerini M, et al. Checklist of names in Mutillidae (Hymenoptera), with illustrations of selected species. *Boll Mus Reg Sci Natur Torino*. 2020;36(1-2):5-427.
23. Ronchetti F, Polidori C. A sting affair: A global quantitative exploration of bee, wasp and ant hosts of velvet ants. *PLoS One*. 2020;15(9):e0238888. doi:10.1371/journal.pone.0238888
24. Williams K, Pan AD, Wilson JS. *Velvet ants of North America*. Princeton (NJ): Princeton University Press; 2024.
25. Brothers DJ, Tschuch G, Burger F. Associations of mutillid wasps (Hymenoptera: Mutillidae) with eusocial insects. *Insectes Sociaux*. 2000;47:201-11. doi:10.1007/PL00001704

26. Brothers DJ. Biology and immature stages of *Pseudomethoca f. frigida*, with notes on other species (Hymenoptera, Mutillidae). *Univ Kansas Sci Bull.* 1972;50:1-38.
27. Lelej AS. The velvet ants (Hymenoptera, Mutillidae) of the USSR and neighboring countries. Nauka; 1985. (In Russian)
28. Quintero D, Cambra RA. On the identity of *Scaptopoda F. Lynch Arribálzaga*, new taxonomic changes and new distribution records for Neotropical Mutillidae (Hymenoptera), with notes on their biology. *Trans Am Entomol Soc.* 2001;127:291-304.
29. Robertson C. Flowers and insects: Lists of visitors to four hundred and fifty-three flowers. Science Press Print Comp; 1929.
30. Invrea F. Mutillidae – Myrmosidae. *Fauna d'Italia.* Vol. 5. Bologna: Edizioni Calderini; 1964.
31. Krombein KV. Wasp visitors of tulip-tree honeydew at Dunn Loring, Virginia (Hymenoptera: Aculeata). *Ann Entomol Soc Am.* 1951;44(1):141-3. doi:10.1093/aesa/44.1.141
32. Calixto ES, Sousa-Lopes B, Del-Claro K. Are rare velvet ants (Hymenoptera: Mutillidae) to feed on extrafloral nectar? *J Environ Anal Progress.* 2018;3:406-9. doi:10.24221/jeap.3.4.2018.2037.406-409
33. Lenko K. A singular method of feeding of mutillid wasps. *Entomol News.* 1970;81:152.
34. Luz DR, Rosa BB, Williams KA, Melo GAR. An uncommon feeding habit: Mutillid wasps (Hymenoptera, Mutillidae) visiting extrafloral nectaries in Malpighiaceae. *Braz J Biol.* 2016;76(2):551-3. doi:10.1590/1519-6984.01615
35. Wilson JS, Williams KA, Tanner DA, Pitts JP. Nectaring by nocturnal velvet ants (Hymenoptera: Mutillidae). *Southw Nat.* 2010;55(3):441-3. doi:10.1894/JC-33.1
36. Jordan R. Die Spinnennameise, *Mutilla europaea*, ein Bienenschadling! *Deutscher Imker.* 1935;47:421-7.
37. Mellor JEM. A note on the mutillid *Ephutomma continua* Fabr. and of *Bembex mediterranea* Hdl. in Egypt with a summary of the distribution and of some previously recorded habits of the Mutillidae. *Bull Soc Roy Entomol Egypte.* 1927;20:69-79.
38. Neal JC. Note on the habits of *Mutilla* sp. *US Dept Agr Div Entomol Bull.* 1884;4:87.
39. Scholz H. Bienenfeinde. *Deutscher Bienenfreund.* 1879;15:173-5.
40. Hennessey RD, West SA. Reproductive strategies of diurnal mutillid wasps (Hymenoptera: Mutillidae). *Contrib Sci.* 2018;526:181-8. doi:10.5962/p.320147
41. Bischoff H. Monographie der Mutilliden Afrikas. *Archiv für Naturgeschichte A.* 1920-21;86:1-830.
42. Muskovits J, György Z. Velvet ants of Hungary (Hymenoptera: Mutillidae). Kaposvár. 2011.
43. Standfuss L, Standfuss K. Zur Kenntnis der Spinnennameisen (Hymenoptera, Mutillidae) im Süden der Thessalischen Pilion-Halbinsel/Griechenland. *Entomofauna.* 2012;33:457-68.
44. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing; 2022. Available from: <https://www.R-project.org/>
45. Dormann CF, Gruber B, Fruend J. Introducing the bipartite package: Analysing ecological networks. *R News.* 2008;8(2):8-11.
46. Dormann CF. How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology.* 2011;1(1):1-20.
47. Dormann CF, Fruend J, Bluethgen N, Gruber B. Indices, graphs and null models: Analyzing bipartite ecological networks. *Open Ecol J.* 2009;2:7-24.
48. Ooi H, de Vries A, Microsoft. Checkpoint: Install packages from snapshots on the checkpoint server for reproducibility. R package version 102; 2022.
49. Hammer Ø, Harper DAT, Ryan PD. PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica.* 2001;4(1):9.
50. Williams KA, Cambra RA, Bartholomay PR, Luz DR, Quintero D, Pitts JP. Review of the genus *Lomachaeta* Mickel, 1936 (Hymenoptera: Mutillidae) with new species and sex associations. *Zootaxa.* 2019;4564(1):101-36. doi:10.11646/zootaxa.4564.1.4
51. Roswell M, Dushoff J, Winfree R. Male and female bees show large differences in floral preference. *PLoS One.* 2019;14(4):e0214909. doi:10.1371/journal.pone.0214909
52. Bascompte J, Jordano P, Olesen JM. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science.* 2006;312(5772):431-3. doi:10.1126/science.1123412
53. Jervis MA, Kidd NAC, Fitton MG, Huddleston T, Dawah HA. Flower-visiting by hymenopteran parasitoids. *J Nat Hist.* 1993;27(1):67-105. doi:10.1080/00222939300770051

54. Russell M. A meta-analysis of physiological and behavioral responses of parasitoid wasps to flowers of individual plant species. *Biol Control*. 2015;82:96-103. doi:10.1016/j.biocontrol.2014.11.014
55. Hermes MG, Köhler A. The flower-visiting social wasps (Hymenoptera, Vespidae, Polistinae) in two areas of Rio Grande do Sul State, southern Brazil. *Rev Bras Entomol*. 2006;50(2):268-74. doi:10.1590/S0085-56262006000200008
56. Wäckers FL. Assessing the suitability of flowering herbs as parasitoid food sources: flower attractiveness and nectar accessibility. *Biol Control*. 2004;29(3):307-14. doi:10.1016/j.biocontrol.2003.08.005
57. Zemenick AT, Kula RR, Russo L, Tooker J. A network approach reveals parasitoid wasps to be generalized nectar foragers. *Arthropod-Plant Interact*. 2019;13:239-51. doi:10.1007/s11829-018-9642-9
58. Somavilla A, Köhler A. Preferência floral de vespas (Hymenoptera, Vespidae) no Rio Grande do Sul, Brasil. *EntomoBrasilis*. 2012;5(1):21-8. doi:10.12741/ebrasilis.v5i1.152
59. Lelej AS, Fateryga AV, Ivanov SP. The velvet ants (Hymenoptera: Mutillidae) of the Crimean Peninsula. *Far Eastern Entomologist*. 2016;314:1-24.
60. Müller H. Fertilisation of flowers (Translated by W. D'Arcy Thompson). London: Macmillan; 1883.
61. Gilbert F, Jervis MA. Functional, evolutionary and ecological aspects of feeding-related mouthpart specializations in parasitoid flies. *Biol J Linn Soc*. 1998;63:495-535. doi:10.1111/j.1095-8312.1998.tb00327.x
62. Proctor M, Yeo P, Lack A. The natural history of pollination. London: Harper Collins Publishers; 1996.
63. Hatt S, Xu Q, Francis F, Osawa N. Aromatic plants of East Asia to enhance natural enemies towards biological control of insect pests: A review. *Entomologia Generalis*. 2019;38(4):275-315. doi:10.1127/entomologia/2019/0625
64. Hatt S, Uyttenbroeck R, Lopes T, Chen J L, Piqueray J, Monty A, et al. Effect of flower traits and hosts on the abundance of parasitoids in perennial multiple species wildflower strips sown within oilseed rape (*Brassica napus*) crops. *Arthropod-Plant Interact*. 2018;12:787-97. doi:10.1007/s11829-017-9567-8
65. Reverté S, Retana J, Gómez JM, Bosch J. Pollinators show flower colour preferences but flowers with similar colours do not attract similar pollinators. *Ann Bot*. 2016;118(2):249-57. doi:10.1093/aob/mcw103
66. Jia X-C, Li J, Lu G-H, Wang Y-Q. The concrete evidence of flexistyly in *Plagiostachys*: Pollination biology of a wild ginger on Hainan Island, China. *Ecol Evol*. 2015;5(22):5364-77. doi:10.1002/ece3.1807
67. Pérez-Gómez Á, León-Osper M, Pareja D, Robla J. Flower visits of cockroaches (Insecta: Blattodea) in the Iberian Peninsula: Are they neglected pollinators? *J Appl Entomol*. 2023;147(8):565-76.
68. Orford KA, Vaughan IP, Memmott J. The forgotten flies: The importance of non-syrphid Diptera as pollinators. *Proc R Soc B*. 2015;282(1805):20142934.
69. Mason WRM. Key to superfamilies of the Hymenoptera. In: Goulet H, Huber JT, editors. *Hymenoptera of the World: An identification guide to families*. Ottawa: Research Branch Agriculture Canada Publication 1894/E: I-VII + 668 p.; 1993. p. 65-100.
70. Nath R, Singh H, Mukherjee S. Insect pollinators decline: An emerging concern of Anthropocene epoch. *J Apicul Res*. 2023;62(1):23-38.
71. Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE. Global pollinator declines: Trends, impacts and drivers. *Trends Ecol Evol*. 2010;25(6):345-53.
72. Vizentin-Bugoni J, Maruyama PK, de Souza CS, Ollerton J, Rech AR, Sazima M. Plant–pollinator networks in the tropics: A review. In: Dáttilo W, Rico-Gray C, editors. *Ecological networks in the tropics*. Cham: Springer; 2018. p. 73-91.
73. Menezes MR, Laviski BFS, dos Santos APL, de França ECB, Moreira MS, da Conceição R, et al. Flower visitation by bees, wasps and ants: Revealing how a community of flower-visitors establish interaction networks in a botanical garden. *Sociobiology*. 2022;69(4):e7894. doi:10.13102/sociobiology.v69i4.7894
74. Thompson AR, Adam TC, Hulgren KM, Thacker CE. Ecology and evolution affect network structure in an intimate marine mutualism. *Am Nat*. 2013;182(2):E58-E72. doi:10.1086/670803
75. Blüthgen N, Fründ J, Vázquez DP, Menzel F. What do interaction network metrics tell us about specialization and biological traits? *Ecology*. 2008;89(12):3387-99. doi:10.1890/07-2121.1
76. Heithaus ER. Flower-feeding specialization in wild bee and wasp communities in seasonal neotropical habitats. *Oecologia*. 1979;42:179-94. doi:10.1007/BF00344856
77. Smith GP, Bronstein JL, Papaj DR. Sex differences in pollinator behavior: Patterns across species and consequences for the mutualism. *J Anim Ecol*. 2019;88:971-85. doi:10.1111/1365-2656.12988

78. Domingos-Melo A, Nadia TL, Machado IC. Complex flowers and rare pollinators: Does ant pollination in *Ditassa* show a stable system in Asclepiadoideae (Apocynaceae)? *Arthropod-Plant Interact.* 2017;11:339-49. doi:10.1007/s11829-017-9499-3
79. Di Pasquale G, Salignon M, Le Conte Y, Belzunces LP, Decourtye A, Kretzschmar A, et al. Influence of pollen nutrition on honey bee health: Do pollen quality and diversity matter? *PLoS One.* 2013;8:e72016. doi:10.1371/journal.pone.0072016
80. Roulston T, Cane J. Pollen nutritional content and digestibility for animals. *Plant Syst Evol.* 2000;222:187-209. doi:10.1007/BF00984102
81. Willmer PG, Stone GN. Behavioral, ecological, and physiological determinants of the activity patterns of bees. *Adv Stud Behav.* 2004;34:347-466.
82. Venjakov C, Ruedenauer FA, Klein A-M, Leonhardt SD. Variation in nectar quality across 34 grassland plant species. *Plant Biol.* 2022;24:134-44. doi:10.1111/plb.13343
83. Hanley ME, Franco M, Pichon S, Darvill B, Goulson D. Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants. *Funct Ecol.* 2008;22:592-8. doi:10.1111/j.1365-2435.2008.01415.x
84. Roulston TH, Cane JH, Buchmann SL. What governs protein content of pollen: Pollinator preferences, pollen-pistil interactions, or phylogeny? *Ecol Monogr.* 2000;70:617-43. doi:10.1890/0012-9615(2000)070[0617:WGPCOP]2.0.CO;2
85. Dötterl S, Milchreit K, Schäffler I. Behavioural plasticity and sex differences in host finding of a specialized bee species. *J Comp Physiol A.* 2011;197:1119-26. doi:10.1007/s00359-011-0673-2
86. van Praagh JP, Ribí W, Wehrhahn C, Wittmann D. Drone bees fixate the queen with the dorsal frontal part of their compound eyes. *J Comp Physiol A.* 1980;136:263-6. doi:10.1007/BF00657542