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Review Article

Pollination of Guatemalan orchids – state of knowledge

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Abstract

This literature review aims to synthesise existing knowledge on research on pollination of orchid species in Guatemala. Orchids, known for their diverse and specialised interactions with pollinators, play a key role in the ecosystems of this Central American country. As a base for our research, we have used the orchid checklist published in 2018 where more than 1200 taxa have been listed. Then we conducted a systematic search of academic databases, including, but not limited to PubMed, Web of Science, Scopus and relevant botanical databases. From 1231 orchid species reported to occur in Guatemala and classified in 221 genera, we have found data on pollination of only 98 taxa, classified in 71 genera. Through an exhaustive survey of the relevant scientific literature, this review intends to provide a comprehensive summary of the available data, highlighting gaps in current knowledge and suggesting directions for future research. Research on pollination in tropical orchids presents a formidable challenge due to the immense diversity of species, the intricacies of pollination mechanisms, the elusive nature of pollinators and the susceptibility of these ecosystems to environmental changes. Despite these challenges, the importance of unravelling these mysteries is underscored by the critical role orchids play in tropical ecosystems and their potential implications for conservation and biodiversity.

Key words: Biodiversity, flora of Guatemala, Orchidaceae, pollinators, pollination research, review

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Introduction

Guatemala, with its remarkably varied topography and ecosystems, has long captivated the attention of researchers seeking to unravel the complexities of its biodiversity. Over the years, a multitude of studies have contributed to our understanding of the myriad species that inhabit this region, as well as the ecological processes that govern their existence.

Research in Guatemala has been diverse, spanning disciplines such as ecology, botany, zoology, genetics and environmental science. Studies have ranged from taxonomic explorations of new species to in-depth analyses of ecosystem dynamics and the impacts of anthropogenic activities. The collaborative efforts of local and international researchers have significantly expanded our knowledge base, revealing the intricacies of Guatemala's unique flora and fauna. However, as in other countries in the region, pollination research seems to be still rather neglected (see data presented by Ackerman et al. (2023)). A substantial portion of research in Guatemala has focused on cataloguing and describing new species, contributing to the global understanding of biodiversity. Taxonomic studies have uncovered previously unknown flora and fauna, enriching our appreciation of the country's biological diversity. Research has delved into the intricate relationships between species and their environments, examining the ecological roles different organisms play in various habitats. Understanding the dynamics of ecosystems, from the coastal regions to the highland cloud forests, has been crucial for devising effective conservation strategies. Investigations into the conservation status of key species and ecosystems have highlighted the vulnerabilities and threats faced by Guatemala's biodiversity. Deforestation, habitat loss, climate change and other anthropogenic impacts demand urgent attention to safeguard the nation's natural heritage (Dix and Dix 2007). Recognising the importance of local communities in biodiversity conservation, some studies have explored the integration of indigenous knowledge into conservation practices. Collaborative initiatives that involve local residents have proven instrumental in preserving both cultural traditions and biological diversity.

Amidst the rich tapestry of Guatemala's diverse ecosystems lies a fascinating yet often overlooked phenomenon: the complex dance of orchid pollination. Orchids have long fascinated botanists, ecologists, nature lovers and others with their dazzling colours, shapes and scents. Located in the heart of Central America, Guatemala is home to an incredible variety of orchid species, each with its unique breeding strategy. From the misty highlands to the sun-bathed lowlands, the country hosts a breath-taking array of orchids, estimated at ca. 1,300 species (Archila et al. 2018). Guatemala's diverse ecosystems, from cloud forests to tropical jungles, provide ideal niches for orchids to thrive and each species is uniquely adapted to its specific habitat. Guatemala's orchid diversity not only contributes to the country's ecological richness, but also underscores its role as a global hotspot for orchid enthusiasts eager to explore the wonders of these intricate and enticing botanical gems. Orchids have evolved diverse and sophisticated mechanisms to ensure successful pollination, highlighting the intricate relationships between these plants and their pollinators (Ackerman et al. 2023). The co-evolution of orchids with specific pollinators has resulted in a fascinating array of shapes, sizes and types of behaviour that contribute to the incredible diversity of the orchid family. Orchids employ a remarkable variety of strategies to attract pollinators and the specific pollinators can vary widely amongst different orchid species. They have evolved to attract specific pollinators through their unique shapes, colours and fragrances. Some common orchid pollinators include bees, wasps, flies or hummingbirds.

While orchids are a diverse and ecologically important plant group, many orchid species in Guatemala still have not been studied. Orchid pollination can be highly specialised and understanding these relationships is crucial for conservation efforts, especially in the face of environmental changes. This article provides a thorough and critical overview of the current state of knowledge about pollination biology of Guatemalan orchids, summarising decades of scientific research on this fascinating phenomenon. We synthesise findings from a variety of studies to define how much we know about the reproductive strategies of these unique plants. With this comprehensive review, we aim to provide a holistic understanding of current scientific knowledge, identify research gaps and provide insights that can serve as the basis for future research. By addressing existing knowledge gaps and highlighting emerging challenges, we aim to inspire a renewed commitment to the ongoing exploration and conservation of Guatemala's extraordinary biodiversity.

Methodology

As a base for our research, we have used the orchid checklist published by Archila et al. in 2018 where more than 1200 taxa have been listed. Then we conducted a systematic search of academic databases, including, but not limited to PubMed, Web of Science, Scopus and relevant botanical databases. We utilised a combination of keywords such as "orchids", "pollination", "Guatemala" and related terms to ensure a comprehensive coverage of relevant literature. We have defined clear inclusion and exclusion criteria to filter the retrieved articles and included studies that specifically focus on the pollination of orchid species that are known to occur in Guatemala, encompassing various aspects such as floral morphology, pollinator behaviour and ecological interactions. We have excluded studies that did not provide solid data such as reports of pollinia transfer. Subsequently, we have performed an initial screening based on titles and abstracts to identify potentially relevant articles. After this initial screening, we thoroughly evaluated the full texts of selected articles to determine their suitability for inclusion in the review. As a result, we have included in our meta-analysis about 150 scientific publications. Then we extracted relevant information from the selected articles, including details about orchid species studied, pollinators identified, floral traits involved in pollination and ecological contexts. Finally, we have organised the extracted data into a structured framework for analysis.

Results

From 1231 orchid species reported to occur in Guatemala and classified in 221 genera, we have found data on pollination of only 98 taxa, classified in 71 genera (classification *sensu* Archila et al. (2018); detailed results presented in Table 1). Most of the information found was rather scarce and incomplete and only a few studies were conducted in Guatemala itself (see Fig. 1). Gathered data showed that, only for 22 genera (100% representatives), at least one pollinator is known and for as many as 150 genera, not a single effective pollinator has been documented. It should be noted that these 22 genera consist of 1–2 species only. We include also a summary of data on known pollinators taking into account the classification at the level of subtribes (Table 2).

Discussion

The previous attempt to summarise knowledge on pollination of the Guatemalan orchids was presented by Dix & Dix during the 1st International Congress of Neotropical Orchidology that was held in San José, Costa Rica, in May 2003. In their conference abstract published in Lankesteriana (Dix and Dix 2003), the authors stated that direct observation has enabled them to identify pollinators for 118 species of orchids, representing 16% of the 734 confirmed taxa in Guatemala (number of taxa follows Dix and Dix (2000)). For another 233 species (32%), the literature allowed them to suggest the categories represented by the pollinators.

Table 1. Summary of data known pollinators taking into account the classification at the genus level.

No	Orchid genus	Subtribe	Species number in Guatemala	Species with known pollinator	Species with known pollinator [%]	Pollinator species	Pollinator – functional group	Report type	Reference
1	*Arundina* Blume	Arundiinae Dressler	1	1	100%	*Megachile yaeyamaensis*, *Nomia pavonura*, *Thyreus takaonis*, *Apis mellifera*, *Megacampsomeris mojiensis*, *Rhynchium quinquecinctum*	bees, wasps	Pollinator observation	Sugiura (2014)
2	*Benzingia* Dodson	Huntleyinae Schltr.	1	1	100%	*Euglossa heterosticta*		Pollinator observation	Roubik and Hanson (2004)
3	*Brassavola* R. Br	Laeliinae Benth.	1	1	100%	*Manduca sexta*, *Protambulix strigilis*	moths	Pollinator observation	Chipka (2009)
4	*Catasetum* Rich. *ex* Kunth	Catasetinae Schltr.	2	2	100%	*Centris mexicana*, *Eulaema meriana*, *E. cingulata*, *Exaerete frontalis*, Euglossini, *Eulaema polychroma*	bees	Pollinator observation and floral attractants (chemistry)	Whitten et al. (1986), Damon and Salas-Roblero (2007), Cancino and Damon (2007), Damon et. al. (2012), Hernández-Ramírez (2021)
5	*Cischweinfia* Dressler & N. H. Williams	Trichopiliinae Pfitzer	1	1	100%	Euglossini	bees	Pollinator observation	Williams (1982)
6	*Clowesia* Lindl.	Catasetinae Schltr.	2	2	100%	*Euglossa viridissima*, *Euplusia mexicana*	bees	Pollinator observation	Aguirre León (1979), Dodson (1975)
7	*Comparettia* Poepp. & Endl.	Comparettiinae Schltr.	1	1	100%	*Colletes* sp., *Amazilia tzacatl*, *Chorostilbon maugaeus*	bees, hummingbirds	Pollinator observation and floral attractants (nectar availability)	van der Pijl and Dodson (1966), Rodríguez-Robles et al. (1992), Icones Orchidacearum 5 & 6
8	*Cycnoches* Lindl.	Catasetinae Schltr.	2	2	100%	Euglossini: *Euglossa tridentata*, *Eulaema cingulata*, *Euglossa mixta*	bees	Pollinator observation and floral attractants (chemistry)	Damon and Salas-Roblero (2007), Damon et al. (2012), Cancino and Damon (2007)
9	*Cypripedium* L.	Cypripediinae Meisn.	2	2	100%	*Trigona* spp., Halictidae *Lasioglossum nyctere*	bees	Pollinator observation	Szlachetko et al. (2017), Lozano-Rodríguez et al. (2018)
10	*Dichromanthus* Garay	Spiranthinae Lindl.	1	1	100%	*Amazilia berylina*, *Hylocharis leucotis*	hummingbirds	Pollinator observation	Sarmiento and Romero (2000), Hágsater et al. (2005)
11	*Eulophia* R. Br.	Cymbidiinae Benth	1	1	100%	*Centris* spp., *Centris bicornuta*, *C. inermis*, *C. minuta*, *C. rubella*, *C. spilopoda*, *C. varia*, *Xylocopa muscaria*, *Megachile* sp.	bees	Pollinator observation and floral attractants (chemistry)	Jürgens et al. (2009)
12	*Kefersteinia* Rchb. F	Huntleyinae Schltr.	1	1	100%	Euglossini	bees	Pollinator observation	Damon et al. (2012)
13	*Macradenia* R. Br.	Macradeniinae Mansf.	1	1	100%	*Euglossa hemiehlora*, *E. villosiventris*	bees	Pollinator observation	Dressler (1993), van der Cingel (2001)
14	*Mormolyca* Fenzl	Maxillariinae Benth.	1	1	100%	*Nannotrigona testaceicornis*, *Scaptotrigona* sp.	bees	Pollinator observation and floral attractants (chemistry)	Singer et. al. (2004), Flach et. al. (2006)
15	*Oeceoclades* Lindl.	Cymbidiinae Benth	1	1	100%	Nymphalidae, *Heliconius ethilla narcaea*, *Heliconius eratophyllis*	butterflies	Pollinator observation	Aguiar et al. (2012)
16	*Plectrophora* H. Focke	Oncidiinae Benth.	1	1	100%	*Eulaema meriana*	bees	Pollinator observation	Damon et. al. (2012)
17	*Polycycnis* Rchb. F	Stanhopeinae Benth.	1	1	100%	*Eulaema speciosa*	bees	Pollinator observation	Dressler (1977)

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18	*Sacoila* Raf.	Stenorrhynchidinae Szlach.	1	1	100%	*Archilochus colubris*	hummingbirds	Pollinator observation	Catling (1987)
19	*Sievekingia* Lindl. *ex* Rchb. f.	Stanhopeinae Benth.	1	1	100%	*Euglossa crassipunctata*, *E. cybelia*, *E. mixta*, *E. sapphirina*, *Euplusia mussitans*, *E. duckei*	bees	Pollinator observation	Dressler (1976)
20	*Stanhopeastrum* Rchb. f.	Stanhopeinae Benth.	2	2	100%	*Eulaema luteola*, *Euplusia schmidtiana Euglossa* sp., *Euglossa flammea*	bees	Pollinator observation	Dressler (1968)
21	*Trichocentrum* Poepp. & Endl.	Trichocentrinae Schltr.	1	1	100%	Euglossini	bees	Pollinator observation	Damon et al. (2012)
22	*Unciferia* Luer	Pleurothallidinae Lindl.	2	2	100%	Phoridae, Chloropidae	flies	Pollinator observation	Karremans and Díaz Morales (2019)
23	*Cohniella* Pfitzer	Oncidiinae Benth.	3	2	67%	*Centris* sp.	bees	Pollinator observation	Cetzal-Ix et al. (2013)
24	*Aspasia* Lindl.	Oncidiinae Benth.	2	1	50%	Euglossini		Pollinator observation	Ackerman (1983)
25	*Cochleanthes* Raf.	Huntleyinae Schltr.	2	1	50%	Euglossini, *Eulaema* sp.	bees	Pollinator observation	Salguero and Pupulin (2019)
26	*Corymborkis* Thouars	Tropidiinae Pfitzer	2	1	50%	*Phaethornis squalidus*	hummingbirds	Pollinator observation and floral attractants (histochemistry)	Vieira et al. (2007)
27	*Ionopsis* Kunth	Ionopsidinae Pfitzer	2	1	50%	*Ceratina* sp., *Paratrigona lineata*, *Nannotrigona testaceicornis*, *Paratetrapedia flaveola*, *Augochlora* sp.	bees	Pollinator observation and floral attractants (chemistry)	Aguiar and Pansarin (2018), Aguiar et al. (2021)
28	*Laelia* Lindl.	Laeliinae Benth.	2	1	50%	*Bombus medius*	bees	Pollinator observation	Flores et al. (1996)
29	*Leochilus* Knowles & Westc.	Leochilinae Szlach.	4	2	50%	Halictidae: *Lasioglossum* sp., Polybiine: *Stelopolybia areata* and *S. hamiltoni*, Polistinae, *Pachoniderus nassidens*	bees, wasps	Pollinator observation	Chase (1986)
30	*Meiracyllium* Rchb. f.	Meiracylliinae Dressler	2	1	50%	Euglossini	bees	Pollinator observation	Damon et al. (2012)
31	*Senghasia* Szlach.	Huntleyinae Schltr.	2	1	50%	Euglossini	bees	Pollinator observation	Damon et. al. (2012)
32	*Arpophyllum* Lex.	Arpophyllinae Dressler	5	2	40%	*Amazilia tzacatl*	hummingbirds	Pollinator observation	Karremans 2023, Icones Orchidacearum 5 & 6
33	*Dryadella* Luer	Pleurothallidinae Lindl.	3	1	33%	*Drosophila* sp.	flies	Pollinator observation	Icones Orchidacearum 5 & 6
34	*Masdevallia* Ruiz & Pav	Pleurothallidinae Lindl.	6	2	33%	*Zygothrica* sp.	flies	Pollinator observation	Lipińska et al. (2019)
35	*Rossioglossum* (Schltr.) Garay & G.C. Kenn.	Oncidiinae Benth.	3	1	33%	*Centris* sp.	bees	Pollinator observation	van der Pijl and Dodson (1966)
36	*Sarcoglottis* C. Presl	Cyclopogoninae Szlach.	7	2	29%	*Eulaema atleticana*, *E. niveofasciata*, *Euglossa variabilis*, *E. viridissima*, *E. tridentata*	bees	Pollinator observation and floral attractants (chemistry)	Damon and Salas-Roblero (2007), Albuquerque et. al. (2021)

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37	*Stanhopea* J. Frost ex Hook	Stanhopeinae Benth.	30	8	27%	*Euplusia mexicana*, *Eufriesia coerulescens*, *Eulaema cingulata*, *Eufriesea ornata*, *Euglossa viridissima*, *Euglossa variabilis*, *E. tridentate*, *E. atrovenata*, *E. townsendi*, *Eufriesia* sp.	bees	Pollinator observation	Dodson (1975), Icones Orchidacearum 5 & 6, Dressler (1968), Williams and Whitten (1983), Damon et. al. (2012), Damon and Salas-Roblero (2007)
38	*Ornithidium* Salisb. ex R. Br.	Maxillariinae Benth.	4	1	25%	*Amazilia cyanocephala*	hummingbirds	Pollinator observation and floral attractants (SEM, TEM, chemistry, histochemistry)	Lipińska et al. (2022)
39	*Phragmipedium* Rolfe	Phragmipediinae Szlach.	4	1	25%	Self-pollinating	N/A	N/A	Dressler and Pupulin (2011)
40	*Prescottia* Lindl.	Prescottiinae Dressler	4	1	25%	Pyralidae	moths	Pollinator observation	Singer and Sazima (2001)
41	*Spiranthes* Rich.	Spiranthinae Lindl.	4	1	25%	*Bombus* spp., *Apis mellifera*, *Augochlorella striata*	bees	Pollinator observation	Catling (1983)
42	*Vanilla* Mill.	Vanillinae Lindl.	9	2	22%	*Eulaema polychroma*, *E. meriana*, *Euglossa viridissima*, *Euglossa* spp., *Eulaema* spp., *Eufriesea* spp.	bees	Pollinator observation and floral attractants (chemistry)	Vega et al. (2022 and references therein)
43	*Acropera* Lindl.	Stanhopeinae Benth.	5	1	20%	Euglossini	bees	Pollinator observation	Damon et al. (2012)
44	*Corallorhiza* Gagnebin	Corallorhizinae E.G. Camus, Bergon & A. Camus	5	1	20%	*Empis* sp., *Andrena* sp.	flies, bees	Pollinator observation	Kipping (1971), Luer (1975)
45	*Guarianthe* Dressler & W.E. Higgins	Laeliinae Benth.	5	1	20%	*Euglossa viridisima*	bees	Pollinator observation	Pemberton (2007)
46	*Myrmecophila* Rolfe	Laeliinae Benth.	5	1	20%	*Eulaema polychroma*, *Xylocopa* sp.	bees	Pollinator observation and floral attractants (chemistry)	Parra-Tabla et al. (2009)
47	*Notylia* Lindl.	Notyliinae Benth.	5	1	20%	*Euglossa viridissima*, *E. variabilis*, *E. tridentata*	bees	Pollinator observation and floral attractants (chemistry)	Damon and Salas-Roblero (2007), Damon et. al. (2012), Cancino and Damon (2007)
48	*Trichosalpinx* Luer	Pleurothallidinae Lindl.	10	2	20%	*Forcipomyia* sp.	flies	Pollinator observation and floral attractants (SEM, histochemistry)	Bogarín et al. (2018)
49	*Cyclopogon* C. Presl	Cyclopogoninae Szlach.	12	2	17%	*Augochlora nausicaa*, *Caenaugochlora cupriventis*	bees	Pollinator observation and floral attractants (SEM, chemistry, histochemistry)	Benitez-Vieyra et al. (2006), Wiemer (2009), Juárez et al. (2016)
50	*Trichopilia* Lindl.	Trichopiliinae Pfitzer	6	1	17%	Euglossini	bees	Pollinator observation	Damon and Salas-Roblero (2007)
51	*Triphora* Nutt.	Triphorinae (Dressler) Szlach.	6	1	17%	*Bombus* sp.	bees	Pollinator observation	Williams (1994)
52	*Barkeria* Knowles & Westc.	Laeliinae Benth.	7	1	14%	*Xylocopa tabaniformis*, *Amazilia tzacatl*, *Hylocharis leucocollis*	bees, hummingbirds	Pollinator observation and floral attractants (SEM, TEM, FM, LM, Histochem)	Van der Pijl (1966), Stpiczyńska et al. (2021), Warford (1993)
53	*Brassia* R. Br.	Oncidiinae Benth.	7	1	14%	*Pepsis* sp.	wasps	Pollinator observation	Pupulin and Bogarin (2005)

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54	*Gongora* Ruiz & Pav.	Stanhopeinae Benth.	7	1	14%	*Euglossa purpurea*	bees	Pollinator observation	Dressler (1968)
55	*Lophiaris* Raf.	Oncidiinae Benth.	7	1	14%	*Centris* sp.	bees	Pollinator observation	Cen (2016)
56	*Mormodes* Lindl.	Catasetinae Schltr.	7	1	14%	*Euglossa viridissima*, *E. townsendi*, *E. tridentata*, *E. atrovenata*	bees	Pollinator observation and floral attractants (chemistry)	Damon and Salas-Roblero (2007), Damon et. al. (2012), Cancino and Damon (2007)
57	*Ornithocephalus* Hook.	Ornithocephalinae Schltr.	8	1	13%	*Paratetrapedia calcarata*	bees	Pollinator observation	van der Cingel (2001)
58	*Polystachya* Hook.	Polystachyinae Schltr.	8	1	13%	*Dialictus* sp., *Plebeia droryana*, *Tetragonisca angustula*, *Trigona spinipes*, *Paratetrapedia* aff. *fervida*	bees	Pollinator observation	Pansarin and Amaral (2006)
59	*Isochilus* R. Br.	Laeliinae Benth.	9	1	11%	*Hylocharis leucotis*	hummingbirds	Pollinator observation	Icones Orchidacearum 10
60	*Rhynchostele* Rchb. f.	Oncidiinae Benth.	9	1	11%	*Bombus* sp.	bees	Pollinator observation	Icones Orchidacearum 10
61	*Specklinia* Lindl.	Pleurothallidinae Lindl.	21	2	10%	*Drosophila hydei*, Cecidomyiidae, Phoridae	flies	Pollinator observation and floral attractants (SEM, TEM, chemistry)	Damon and Salas-Roblero (2007), Karremans et al. (2015 a, b),
62	*Bletia* Ruiz & Pav	Bletiinae Benth.	11	1	9%	*Euglossa hemichlora*, *Melipona* sp. *Thygater* sp.	bees	Pollinator observation	Dressler (1968)
63	*Dichaea* Lindl.	Dichaeinae Schltr.	23	2	9%	Euglossini	bees	Pollinator observation	Ackerman (1983)
64	*Oncidium* Sw.	Oncidiinae Benth.	23	2	9%	*Paratetrapedia* sp., *Centris mexicana*, *C. nitida*	bees	Pollinator observation	Damon and Salas-Roblero (2007), Pemberton and Liu (2008), Silvera (2002)
65	*Maxillaria* Ruiz & Pav	Maxillariinae Benth.	13	1	8%	*Trigona testacea*, *T. amalthea*	bees	Pollinator observation	van der Pijl and Dodson (1966)
66	*Govenia* Lindl.	Goveniinae Dressler	15	1	7%	*Salpigogaster* spp.	flies	Pollinator observation	Pansarin (2008)
67	*Sobralia* Ruiz & Pav.	Sobraliinae Schltr.	47	3	6%	Euglossini	bees	Pollinator observation	Damon and Salas-Roblero (2007), Damon et. al. (2012), Dressler (2012)
68	*Encyclia* Hook.	Laeliinae Benth.	32	2	6%	*Xylocopa nautlana*, *X. fimbriata*, *Euglossa atrovenata*, *E. mixta*, *Eulaema meriana*	bees, wasps	Pollinator observation and floral attractants (chemistry)	Cancino and Damon (2006), Damon and Salas-Roblero (2007)
69	*Habenaria* Willd.	Habenariinae Benth.	26	1	4%	*Anthoptus* sp.	moths	Pollinator observation	Kolanowska (2005)
70	*Stelis* Sw.	Pleurothallidinae Lindl.	36	1	3%	Sciaroidea	flies	Pollinator observation	van der Pijl and Dodson (1966)
71	*Epidendrum* L.	Epidendrinae Szlach.	113	1	1%	*Pseudosphinx tetrio*	moths	Pollinator observation and floral attractants (SEM, TEM, chemistry)	Knudsen and Tollsten (1993), Moya and Ackerman (1993), Ackerman and Montalvo (1990)
72	*Acianthera* Scheidw.	Pleurothallidinae Lindl.	14	0	0%				
73	*Acineta* Lindl.	Stanhopeinae Benth.	3	0	0%				
74	*Adeneleutherophora* Barb. Rodr.	Elleanthinae Szlach.	3	0	0%				
75	*Amparoa* Schltr.	Oncidiinae Benth.	1	0	0%				
76	*Anathallis* Barb. Rodr.	Pleurothallidinae Lindl.	8	0	0%				

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77	*Ancipitia* (Luer) Luer	Pleurothallidinae Lindl.	1	0	0%				
78	*Aspidogyne* Garay	Goodyerinae Klotzsch	3	0	0%				
79	*Aulosepalum* Garay	Spiranthinae Lindl.	1	0	0%				
80	*Barbosella* Schltr.	Pleurothallidinae Lindl.	2	0	0%				
81	*Beloglottis* Schltr.	Spiranthinae Lindl.	4	0	0%				
82	*Brachionidium* Lindl.	Pleurothallidinae Lindl.	2	0	0%				
83	*Brachystele* Schltr.	Spiranthinae Lindl.	1	0	0%				
84	*Buccella* Luer	Pleurothallidinae Lindl.	1	0	0%				
85	*Bulbophyllum* Thouars	Bulbophyllinae Schltr.	5	0	0%				
86	*Calanthe* R. Br	Bletiinae Benth.	1	0	0%				
87	*Callistanthos* Szlach.	Stenorrhynchidinae Szlach.	1	0	0%				
88	*Camaridium* Lindl.	Maxillariinae Benth.	1	0	0%				
89	*Campylocentrum* Benth.	Angraecinae Summerh.	10	0	0%				
90	*Caularthron* Raf.	Laeliinae Benth.	1	0	0%				
91	*Chelyorchis* Dressler & N.H. Williams	Oncidiinae Benth.	3	0	0%				
92	*Chondroscaphe* (Dressler) Senghas & G. Gerlach	Huntleyinae Schltr.	1	0	0%				
93	*Christensonella* Szlach., Mytnik, Górniak & Śmiszek	Maxillariinae Benth.	1	0	0%				
94	*Chysis* Lindl.	Chysiinae Schltr.	7	0	0%				
95	*Coelia* Lindl.	Coeliinae Dressler	5	0	0%				
96	*Coryanthes* Hook.	Stanhopeinae Benth.	11	0	0%				
97	*Cranichis* Sw.	Cranichidinae Lindl.	11	0	0%				
98	*Crossoliparis* Marg.	Malaxidinae Benth. & Hook. f.	1	0	0%				
99	*Cryptarrhena* R. Br.	Cryptarrheninae Dressler	2	0	0%				
100	*Cryptocentrum* Benth.	Maxillariinae Benth.	1	0	0%				
101	*Cuitlauzina* La Llave & Lex.	Oncidiinae Benth.	3	0	0%				

No	Orchid genus	Subtribe	Species number in Guatemala	Species with known pollinator	Species with known pollinator [%]	Pollinator species	Pollinator – functional group	Report type	Reference
102	*Cyrtochiloides* N.H. Williams & M.W. Chase	Oncidiinae Benth.	1	0	0%				
103	*Cyrtopodium* R. Br.	Cyrtopodiinae Benth.	1	0	0%				
104	*Deiregyne* Schltr	Spiranthinae Lindl.	4	0	0%				
105	*Dimerandra* Schltr.	Epidendrinae Szlach.	1	0	0%				
106	*Dracontia* (Luer) Luer	Pleurothallidinae Lindl.	7	0	0%				
107	*Dracula* Luer	Pleurothallidinae Lindl.	2	0	0%				
108	*Dresslerella* Luer	Pleurothallidinae Lindl.	4	0	0%				
109	*Echinosepala* Pridgeon & M.W. Chase	Pleurothallidinae Lindl.	2	0	0%		flies	Floral attractants (SEM,TEM, chemistry)	Cardoso-Gustavson et al. (2017), Arévalo-Rodrigues et al. (2021)
110	*Elleanthus* C. Presl	Elleanthinae Szlach.	2	0	0%				
111	*Encabarcenia* Archila & Szlach.	Laeliinae Benth.	4	0	0%				
112	*Epistephium* Kunth	Vanillinae Lindl.	1	0	0%				
113	*Eriopsis* Lindl.	Eriopsidinae Szlach.	1	0	0%				
114	*Eurystyles* Wawra	Spiranthinae Lindl.	3	0	0%				
115	*Evelyna* Poepp. & Endl.	Elleanthinae Szlach.	1	0	0%				
116	*Funkiella* Schltr.	Stenorrhynchidinae Szlach.	3	0	0%				
117	*Galeandra* Lindl. & F.A. Bauer	Cyrtopodiinae Benth.	4	0	0%				
118	*Galeoglossum* A. Rich. & Galeotti	Prescottiinae Dressler	1	0	0%				
119	*Galeottia* A. Rich. & Galeotti	Zygopetalinae Schltr.	1	0	0%				
120	*Galeottiella* Schltr.	Galeottiellinae Salazar & M.W. Chase	1	0	0%				
121	*Goniochilus* M.W. Chase	Leochilinae Szlach.	1	0	0%				
122	*Goodyera* R. Br.	Goodyerinae Klotzsch	3	0	0%				
123	*Gracielanthus* Tamayo & Szlach.	Spiranthinae Lindl.	2	0	0%				
124	*Habenella* Small	Habenariinae Benth.	2	0	0%				
125	*Hapalorchis* Schltr.	Spiranthinae Lindl.	1	0	0%				

No	Orchid genus	Subtribe	Species number in Guatemala	Species with known pollinator	Species with known pollinator [%]	Pollinator species	Pollinator – functional group	Report type	Reference
126	*Helleriella* A.D. Hawkes	Ponerinae Pfitzer	1	0	0%				
127	*Heterotaxis* Lindl.	Maxillariinae Benth.	5	0	0%				
128	*Hexalectris* Raf.	Bletiinae Benth.	3	0	0%				
129	*Homalopetalum* Rolfe	Ponerinae Pfitzer	2	0	0%				
130	*Houlletia* Brongn.	Stanhopeinae Benth.	1	0	0%				
131	*Huntleya* Bateman ex Lindl.	Huntleyinae Schltr.	2	0	0%				
132	*Jacquiniella* Schltr.	Epidendrinae Szlach.	6	0	0%				
133	*Javieria* Archila, Chiron & Szlach.	Laeliinae Benth.	6	0	0%				
134	*Kegeliella* Mansf.	Stanhopeinae Benth.	1	0	0%				
135	*Kionophyton* Garay	Spiranthinae Lindl.	2	0	0%				
136	*Kraenzlinella* Kuntze	Pleurothallidinae Lindl.	1	0	0%				
137	*Kreodanthus* Garay	Goodyerinae Klotzsch	3	0	0%				
138	*Lacaena* Lindl.	Stanhopeinae Benth.	1	0	0%				
139	*Lalexia* Luer	Pleurothallidinae Lindl.	2	0	0%				
140	*Lankesteriana* Karremans	Pleurothallidinae Lindl.	7	0	0%				
141	*Lepanthes* Sw.	Pleurothallidinae Lindl.	75	0	0%				
142	*Lepanthopsis* (Cogn.) Ames	Pleurothallidinae Lindl.	1	0	0%			Floral attractants (SEM, LM, histochemistry)	Bogarin et al. (2019)
143	*Leucohyle* Klotzsch	Trichopiliinae Pfitzer	1	0	0%				
144	*Liparis* Rich.	Malaxidinae Benth. & Hook. f.	8	0	0%				
145	*Lockhartia* Hook.	Lockhartiinae Schltr.	4	0	0%			Floral attractants (SEM, TEM, LM, histochemistry, chemistry)	Blanco et al. (2013), Silvera (2002)
146	*Lockhartiopsis* Archila	Lockhartiinae Schltr.	1	0	0%				
147	*Lophiarella* Szlach., Mytnik & Romowicz	Oncidiinae Benth.	2	0	0%				
148	*Lycaste* Lindl.	Lycastinae Schltr.	18	0	0%				
149	*Macroclinium* Barb. Rodr.	Notyliinae Benth.	3	0	0%				
150	*Malaxis* Sol. *ex* Sw.	Malaxidinae Benth. & Hook. f.	24	0	0%				

No	Orchid genus	Subtribe	Species number in Guatemala	Species with known pollinator	Species with known pollinator [%]	Pollinator species	Pollinator – functional group	Report type	Reference
151	*Marsupiaria* Hoehne	Maxillariinae Benth.	1	0	0%				
152	*Matalbatzia* Archila	Oncidiinae Benth.	1	0	0%				
153	*Maxillariella* M.A. Blanco & Carnevali	Maxillariinae Benth.	10	0	0%			Floral attractants (SEM, TEM, chemistry, histochemistry)	Lipińska et al. (2021)
154	*Mesadenella* Pabst & Garay	Stenorrhynchidinae Szlach.	2	0	0%				
155	*Mesadenus* Schltr.	Spiranthinae Lindl.	3	0	0%				
156	*Mesospinidium* Rchb. f	Ionopsidinae Pfitzer	1	0	0%				
157	*Microchilus* C. Presl	Goodyerinae Klotzsch	3	0	0%				
158	*Microthelys* Garay	Spiranthinae Lindl.	4	0	0%				
159	*Myoxanthus* Poepp. & Endl.	Pleurothallidinae Lindl.	3	0	0%				
160	*Nageliella* L.O. Williams	Ponerinae Pfitzer	2	0	0%				
161	*Nemaconia* Knowles & Westc.	Ponerinae Pfitzer	3	0	0%				
162	*Nidema* Britton & Millsp.	Ponerinae Pfitzer	2	0	0%				
163	*Nitidobulbon* Ojeda, Carnevali & G.A. Romero	Maxillariinae Benth.	1	0	0%				
164	*Ocampoa* A. Rich. & Galeotti	Cranichidinae Lindl.	1	0	0%				
165	*Octomeria* R.Br.	Pleurothallidinae Lindl.	3	0	0%				
166	*Oestlundia* W.E. Higgins	Laeliinae Benth.	2	0	0%				
167	*Oestlundorchis* Szlach.	Stenorrhynchidinae Szlach.	7	0	0%				
168	*Orchidotypus* Kraenzl.	Pachyphyllinae Pfitzer	1	0	0%				
169	*Palumbina* Rchb. f.	Oncidiinae Benth.	1	0	0%				
170	*Paphinia* Lindl.	Stanhopeinae Benth.	1	0	0%				
171	*Pelexia* Poit. *ex* Lindl.	Cyrtopodiinae Benth.	9	0	0%				
172	*Peristeria* Hook.	Coeliopsidinae Szlach.	1	0	0%				
173	*Phloeophila* Hoehne & Schltr.	Pleurothallidinae Lindl.	1	0	0%				

No	Orchid genus	Subtribe	Species number in Guatemala	Species with known pollinator	Species with known pollinator [%]	Pollinator species	Pollinator – functional group	Report type	Reference
174	*Physosiphon* Lindl.	Pleurothallidinae Lindl.	2	0	0%				
175	*Platystele* Schltr.	Pleurothallidinae Lindl.	17	0	0%				
176	*Platythelys* Garay	Goodyerinae Klotzsch	4	0	0%				
177	*Pleurothallis* R. Br.	Pleurothallidinae Lindl.	3	0	0%				
178	*Ponera* Lindl.	Ponerinae Pfitzer	1	0	0%				
179	*Ponthieva* R. Br.	Cranichidinae Lindl.	13	0	0%				
180	*Potosia* (Schltr.) R. González & Szlach. *ex* Mytnik	Cyclopogoninae Szlach.	4	0	0%				
181	*Prosthechea* Knowles & Westc.	Laeliinae Benth.	18	0	0%				
182	*Pseudencyclia* Chiron & V.P. Castro	Laeliinae Benth.	9	0	0%				
183	*Pseudogoodyera* Schltr.	Spiranthinae Lindl.	2	0	0%				
184	*Psilochilus* Barb. Rodr.	Triphorinae (Dressler) Szlach.	2	0	0%				
185	*Psygmorchis* Dodson & Dressler	Oncidiinae Benth.	3	0	0%				
186	*Restrepia* Kunth	Pleurothallidinae Lindl.	7	0	0%				
187	*Restrepiella* Garay & Dunst.	Pleurothallidinae Lindl.	2	0	0%				
188	*Rhetinantha* M.A. Blanco	Maxillariinae Benth.	4	0	0%				
189	*Rhinorchis* Szlach.	Habenariinae Benth.	1	0	0%				
190	*Rhyncholaelia* Schltr.	Laeliinae Benth.	2	0	0%				
191	*Scaphosepalum* Pfitzer	Pleurothallidinae Lindl.	3	0	0%				
192	*Scaphyglottis* Poepp. & Endl.	Ponerinae Pfitzer	18	0	0%				
193	*Scelochilus* Klotzsch	Comparettiinae Schltr.	1	0	0%				
194	*Schiedeella* Schltr.	Stenorrhynchidinae Szlach.	10	0	0%				
195	*Schomburgkia* Lindl.	Laeliinae Benth.	1	0	0%				
196	*Selbyana* Archila	Lycastinae Schltr.	16	0	0%				
197	*Sepalosaccus* Schltr.	Maxillariinae Benth.	1	0	0%				

No	Orchid genus	Subtribe	Species number in Guatemala	Species with known pollinator	Species with known pollinator [%]	Pollinator species	Pollinator – functional group	Report type	Reference
198	*Sigmatostalix* Rchb. f.	Oncidiinae Benth.	2	0	0%				
199	*Stacyella* Szlach.	Oncidiinae Benth.	1	0	0%				
200	*Stellilabium* Schltr.	Telipogoninae Schltr.	3	0	0%				
201	*Stenorrhynchos* Rich. *ex* Spreng.	Stenorrhynchidinae Szlach.	4	0	0%				
202	*Stenotyla* Dressler	Huntleyinae Schltr.	4	0	0%				
203	*Svenkoeltzia* Burns-Bal.	Stenorrhynchidinae Szlach.	1	0	0%				
204	*Tamayorkis* Szlach.	Malaxidinae Benth. & Hook. f.	1	0	0%				
205	*Telipogon* Kunth	Telipogoninae Schltr.	1	0	0%				
206	*Teuscheria* Garay	Bifrenariinae Dressler	2	0	0%				
207	*Triceratostris* Szlach. & R. Gonzalez	Spiranthinae Lindl.	1	0	0%				
208	*Trigonidium* Lindl.	Maxillariinae Benth.	2	0	0%				
209	*Trisetella* Luer	Pleurothallidinae Lindl.	1	0	0%				
210	*Tropidia* Lindl.	Tropidiinae Pfitzer	1	0	0%				
211	*Tubella* Archila	Pleurothallidinae Lindl.	7	0	0%				
212	*Tupacamaria* Archila	Cyrtopodiinae Benth.	1	0	0%				
213	*Verapazia* Archila	Pleurothallidinae Lindl.	8	0	0%				
214	*Warrea* Lindl.	Warreinae Szlach.	1	0	0%				
215	*Warscewiczella* Rchb. F	Huntleyinae Schltr.	1	0	0%				
216	*Wullschlaegelia* Rchb. f.	Wullschlaegelliinae (Dressler) Dressler	2	0	0%				
217	*Xanthoxerampellia* Szlach. & Sitko	Maxillariinae Benth.	4	0	0%				
218	*Xylobium* Lindl.	Xylobiinae Archila	4	0	0%				
219	*Zhukowskia* Szlach., R. González & Rutk.	Cyclopogoninae Szlach.	4	0	0%				
220	*Zootrophion* Luer	Pleurothallidinae Lindl.	1	0	0%				
221	*Zosterophyllanthos* Szlach. & Marg.	Pleurothallidinae Lindl.	9	0	0%				

Table 2. Summary of data known pollinators taking into account the classification at the subtribe level.

Subtribe	Species number in Guatemala	Species with known pollinator	Species with known pollinator (%)
Angraecinae Summerh.	10	0	0%
Arpophyllinae Dressler	5	2	40%
Arundiinae Dressler	1	1	100%
Bifrenariinae Dressler	2	0	0%
Bletiinae Benth.	15	1	7%
Bulbophyllinae Schltr.	5	0	0%
Catasetinae Schltr.	13	7	54%
Chysiinae Schltr.	7	0	0%
Coeliinae Dressler	5	0	0%
Coeliopsidinae Szlach.	1	0	0%
Comparettiinae Schltr.	2	1	50%
Corallorhizinae E.G. Camus, Bergon & A. Camus	5	1	20%
Coeliopsidinae Szlach.	1	0	0%
Cranichidinae Lindl.	25	0	0%
Cryptarrheninae Dressler	2	0	0%
Cyclopogoninae Szlach.	27	4	15%
Cymbidiinae Benth	2	2	100%
Cypripediinae Meisn.	2	2	100%
Cyrtopodiinae Benth.	15	0	0%
Dichaeinae Schltr.	23	2	9%
Elleanthinae Szlach.	6	0	0%
Epidendrinae Szlach.	120	1	1%
Eriopsidinae Szlach.	1	0	0%
Galeottiellinae Salazar & M.W. Chase	1	0	0%
Goodyerinae Klotzsch	16	0	0%
Goveniinae Dressler	15	1	7%
Habenariinae Benth.	29	1	3%
Huntleyinae Schltr.	14	4	29%
Ionopsidinae Pfitzer	3	1	33%
Laeliinae Benth.	104	8	8%
Leochilinae Szlach.	5	2	40%
Lockhartiinae Schltr.	5	0	0%
Lycastinae Schltr.	34	0	0%
Macradeniinae Mansf.	1	1	100%
Malaxidinae Benth. & Hook. f.	34	0	0%
Maxillariinae Benth.	49	3	6%
Meiracylliinae Dressler	2	1	50%
Notyliinae Benth.	8	1	13%
Oncidiinae Benth.	73	10	14%
Ornithocephalinae Schltr.	8	1	13%
Pachyphyllinae Pfitzer	1	0	0%
Phragmipediinae Szlach.	4	1	25%
Pleurothallidinae Lindl.	274	10	4%
Polystachyinae Schltr.	8	1	13%
Ponerinae Pfitzer	29	0	0%
Prescottiinae Dressler	5	1	20%
Sobraliinae Schltr.	47	3	6%
Spiranthinae Lindl.	33	2	6%
Stanhopeinae Benth.	64	14	22%
Stenorrhynchidinae Szlach.	29	1	3%
Telipogoninae Schltr.	4	0	0%
Trichocentrinae Schltr.	1	1	100%
Trichopiliinae Pfitzer	8	2	25%
Triphorinae (Dressler) Szlach.	8	1	13%
Tropidiinae Pfitzer	3	1	33%
Vanillinae Lindl.	10	2	20%
Warreinae Szlach.	1	0	0%
Wullschlaegelliinae (Dressler) Dressler	2	0	0%
Xylobiinae Archila	4	0	0%
Zygopetalinae Schltr.	1	0	0%

Figure 1. Pollinators in Guatemalan orchids **A** Fruit fly visiting *Specklinia* sp. flower **B** Hummingbird (*Amazilia cyanocephala*) pollinating *Ornithidium fulgens* (photo: Fredy L. Archila Morales) **C** Fly (*Zygothrica* sp.) pollinating *Masdevallia floribunda*.

According to their knowledge at the time, the most important orders in pollination were Hymenoptera, responsible for pollinating 46% of the species (Euglossini 16%) and Diptera, which pollinated 28%. This proportion is evident also in our results (see Fig. 2). Only 8% of orchid species were capable of self-pollination according to the authors. Unfortunately, to our best knowledge, these data have not been published and, thus, we are not able to comment on their findings. Since the methodology of their survey also remains unknown, we are not sure if, for instance, if the authors separated visitors from effective pollinators.

Studying pollination in tropical orchids presents a myriad of challenges that researchers must navigate to unravel the intricate relationships between these plants and their pollinators. The unique characteristics of tropical ecosystems, coupled with the specialised adaptations of orchids, contribute to the com-

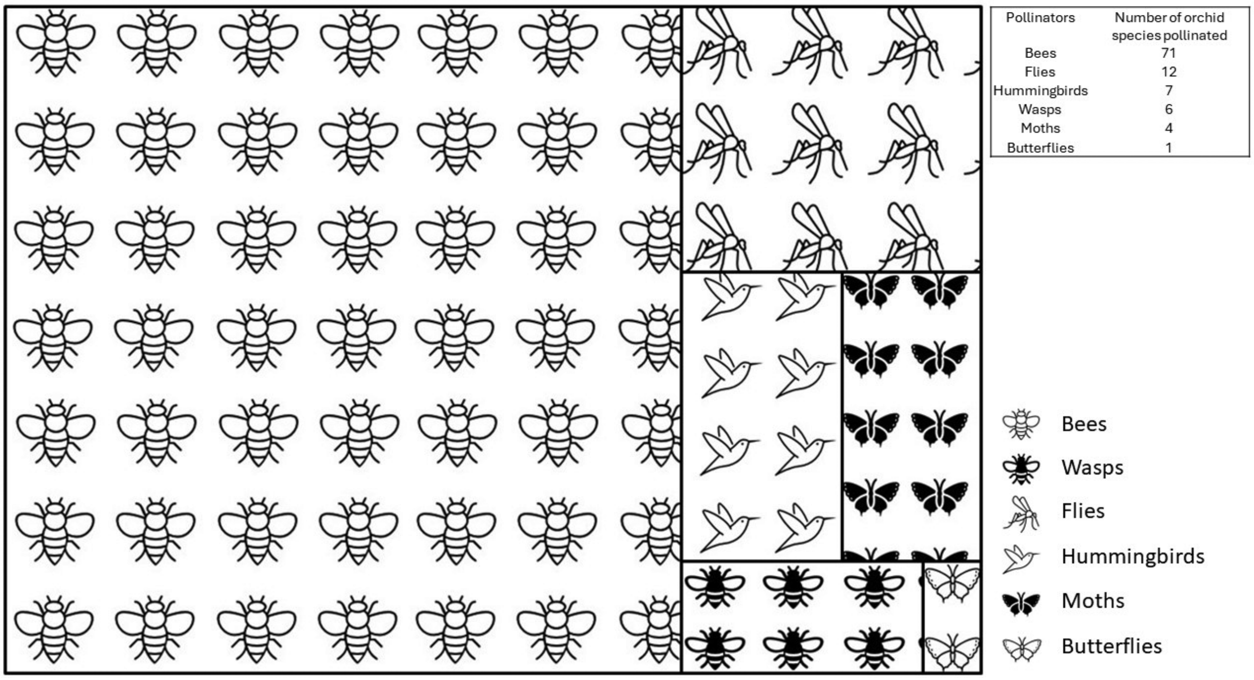

Figure 2. Visualisation of the contribution of different animal groups to the pollination of Guatemalan orchids.

plexity of this research endeavour. One of the primary difficulties lies in the sheer diversity of tropical orchid species (Ackerman et al. 2023). The tropics harbour an extensive array of orchid taxa, each with its distinct morphological and ecological traits. This high diversity often demands specialised knowledge and resources for accurate identification and classification, making it challenging for researchers to establish comprehensive datasets. Furthermore, the cryptic nature of many orchid species exacerbates the difficulty in locating and studying them in their natural habitats. Understanding the intricate pollination mechanisms of tropical orchids proves to be a formidable task. Many orchid species exhibit complex floral structures and employ diverse pollination strategies, including mimicry, deceit and rewards. Deciphering the specific cues that attract pollinators and elucidating the mechanisms that ensure successful pollination necessitate a detailed understanding of both the plant and the associated pollinator community. This complexity poses a significant barrier to researchers seeking to generalise findings across various orchid taxa. The elusive nature of tropical orchid pollinators adds another layer of complication to research efforts. Many orchids depend on specific pollinator species, which may be highly specialised or nocturnal (Ackerman et al. 2023). Identifying and studying these pollinators requires meticulous observation and often involves the use of advanced techniques, such as night-vision equipment and molecular analysis. As a result, access to specialised equipment and the expertise to operate it becomes crucial, making such studies resource-intensive and logistically challenging. Tropical orchids are also vulnerable to environmental changes, including habitat loss and climate fluctuations, which can impact both the plants and their pollinators (Dix and Dix 2007). Understanding the resilience of these intricate relationships in the face of environmental changes requires long-term monitoring and collaboration across disciplines, further complicating the research landscape.

In the study published by Ackerman et al. (2023), it was found that only half of the species records with known reproductive data are epiphytic. This finding is noteworthy considering that approximately 72% of orchid species exhibit epiphytic behaviour (Gravendeel et al. 2004), indicating a significant under-representation of these species in orchid pollination studies. The significant challenge for numerous studies concerning Orchidaceae, especially in tropical regions, is the fact that orchids are characterised by high diversity, yet fewer active pollination biologists work in the region compared to temperate areas (Ackerman et al. 2023). As reported in the mentioned paper, the majority of orchid pollination researchers operate in regions where orchid epiphytes are scarce or non-existent. This geographical bias is evident in the data, with temperate and subtropical latitudes being disproportionately represented due to intensive research activities in regions such as South Africa, southern Australia, Europe and northern America north of Mexico (Ackerman et al. 2023 and references cited therein). Conversely, tropical regions of Africa, Latin America, Temperate Asia and Tropical Asia are severely under-represented. Indeed, the disparity in the representation of scientists from the so-called Global South in the fields of ecology and evolution studies remains a critical issue. Despite the immense biodiversity and ecological significance of regions such as Africa, Latin America and parts of Asia, the voices and perspectives of researchers from these areas are often marginalised. According to Hughes et al. (2023), 83% of all top researchers in ecology and evolution are based in the top 12 countries, which are all European, North American or Australian. Limited access to resources, including funding and advanced research facilities, coupled with systemic barriers, such as language barriers and unequal academic networks, contribute to this imbalance. The consequences are profound, as indigenous knowledge and local expertise crucial for understanding and addressing ecological challenges are often overlooked. Rectifying this imbalance requires concerted efforts to amplify the voices of scientists from the Global South, foster equitable collaborations and dismantle systemic barriers that hinder their participation in global scientific discourse.

Conclusions

The complex and diverse orchid flora in Guatemala remains largely unexplored, particularly in terms of pollination biology. Despite their ecological and cultural significance, a comprehensive understanding of the pollination mechanisms employed by the majority of orchid species in this region eludes us. Research on pollination in tropical orchids presents a formidable challenge due to the immense diversity of species, the intricacies of pollination mechanisms, the elusive nature of pollinators and the susceptibility of these ecosystems to environmental changes. Despite these challenges, the importance of unravelling these mysteries is underscored by the critical role orchids play in tropical ecosystems and their potential implications for conservation and biodiversity. Future research endeavours should address these challenges collaboratively, combining expertise from ecology, botany and entomology to advance our understanding of tropical orchid pollination. Such investigations will not only contribute to our scientific knowledge, but also play a crucial role in developing effective conservation strategies for these enigmatic and often endangered plants.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: MML. Formal analysis: MML. Investigation: MML, CB. Supervision: MML. Writing – original draft: MML. Writing – review and editing: MML.

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Data availability

All of the data that support the findings of this study are available in the main text.

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