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The orchids of Megamexico and their interactions with pollinators

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ABSTRACT

Objective: To describe the pollination syndromes of the orchids of Megamexico and the importance of the interactions between the orchids and their respective pollinators for the conservation of both groups.
Design/Methodology/Approach: An exhaustive search was carried out on the pollinators of each of the orchids that grow in Megamexico. With the information sources available, a data matrix was prepared that includes orchids and all their pollinators. Subsequently, it was quantified which group of pollinators the orchids interact with the most. Finally, it is described what physiological adaptations and morphologies orchids have developed to attract specific pollinators.
Results: Orchids from Megamexico maintain close relationships with specific pollinators. Said interaction is mediated by the shape, size, production of aromas, nectar, and the color of the flower. Thus, four large groups of pollinators are those that interact with the orchids of Megamexico, with the Hymenoptera being the group of pollinators that pollinates the most orchid species in Megamexico and birds to a lesser extent.
Study Limitations/Implications: This study describes the importance of pollinators and their interactions with orchids for orchid prevalence.
Findings/Conclusions: It is of vital importance to include orchid pollinators in conservation programs to ensure that interactions between orchids and pollinators continue to be effective and thus guarantee the permanence of the two groups.

Keywords: Conservation, ecological interactions, Megamexico, pollination syndrome.

INTRODUCTION

Megamexico is a biogeographic region that stands out in the world for having an important diversity and endemism of plants (Rzedowski, 1991). Among this diversity, the Orchidaceae family stands out, which turns out to be an important component of the vegetation of this biogeographic region (Ames and Correl, 1985; Hágsater *et al.*, 2005; Gutiérrez-Rodríguez *et al.*, 2022). Orchidaceae is the most diverse family of angiosperms

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(Christenhusz and Byng, 2016). It is made up of 30,000 species grouped into 736-880 genera (Chase *et al.*, 2015). Due to its way of life, it contains plants that are epiphytes (which grow on trees without causing them any damage), lithophytes (grow on rocks), geophytes (grow on the ground) and saprophytes (they are terrestrial, but they need fungi to survive).

THE DIVERSITY OF ORCHIDS IN MEGAMEXICO

In Megaméxico the presence of 1,732 species is reported, which in turn belong to 189 genera, 36 subtribes and 17 tribes (Gutiérrez-Rodríguez *et al.*, 2022). This great diversity has been possible thanks to climatic heterogeneity, topographic complexity, geological history, and the vast diversity of vegetation types in Megaméxico, which are some of the conditions that have favored the diversification and prevalence of many orchid species (Gutiérrez -Rodriguez *et al.*, 2022).

The diversity of existing species in Orchidaceae is a product of their ability to exploit a wide range of ecological niches (Ricklefs and Renner, 1994), their habitat specialization (Gravendeel *et al.*, 2004) and the ecological interactions that occur in this group. Several studies have linked orchid diversity to specialized interactions with mycorrhizal fungi and to a greater extent with specific pollinators (van der Pijl and Dodson, 1966; Dressler, 1981; Tremblay, 1992; Cozzolino and Widmer, 2005 Jersáková *et al.*, 2006; Borba *et al.*, 2011; Zhang *et al.*, 2017).

IMPORTANCE OF INTERACTION WITH POLLINATORS

Without a doubt, the flower is the most attractive part of orchids, which is why, together with its structures, they have been the subject of numerous studies (*e.g.* Dressler, 1961; van Der Pijl and Dodson, 1966; Castro and Singer, 2019). Notably, Charles Darwin (1885) was one of the first to examine orchid flowers and their pollination strategies. Orchids depend on their floral morphology to be pollinated (Schiestl and Schlüter, 2009). For this purpose, they have developed flowers with very particular shapes, structures, colors, and fragrances that are important in the life cycle of orchids to attract pollinators and thus achieve pollination (Hágsater *et al.*, 2005; Castro and Singer, 2019).

Orchids are one of the most amazing and intriguing examples of pollinator interactions (Tremblay, 1992) and are among the most specialized plants with respect to their pollination (Schiestl and Schlüter, 2009; Phillips *et al.*, 2009, 2011; Castro and Singer, 2019; Lipińska *et al.*, 2022). It is estimated that about 60% of orchids interact with a single species of pollinator (Tremblay, 1992). This suggests that there is an important adaptation process in this family towards pollinators (Cozzolino and Widmer, 2005). The fascinating interaction between plants and pollinators is driven by different interests. Orchids need reliable pollen dispersal and pollination at minimal costs; while pollinators seek floral rewards that can be harvested as quickly and efficiently as possible (van der Kooi *et al.*, 2021).

Orchids display various adaptations that restrict access to floral rewards in many ways, from morphological to mechanical, including chemical barriers. Furthermore, pollinators were not left behind and developed strategies that allowed them to maintain the exploitation of floral resources to their benefit (van der Kooi *et al.*, 2021). Among these strategies there are morphological, behavioral and/or physiological modifications (Danfort *et al.*, 2019). Just to mention a few of the adaptations is body size that determines whether or not a pollinator can enter the flower and access the rewards. While physiological adaptations allow pollinators to exploit rewards efficiently and without having negative effects on reward toxicity (Danfort *et al.*, 2019). The success of pollination depends on how the pollinator interacts with the sexual organs of the flower, something that also depends on its morphological and temporal adjustment (Simon Porcar *et al.*, 2018).

ORCHID POLLINATION STRATEGIES

Pollinators have played an important role in the evolution of the Orchidaceae, and this is evidenced by the complex pollination mechanisms that are unique to orchids (van der Pijl and Dodson, 1966; Tremblay, 1992). This relationship between orchids and pollinators has given rise to a great diversity of floral morphologies that have been linked to specialization in pollination (van der Pijl and Dodson, 1966; Dressler, 1981; Tremblay, 1992; Jersáková *et al.*, 2006).

Orchids have developed strategies to ensure pollination and thus have effective propagation (van der Pijl and Dodson, 1966b). As in other plant families, orchids produce flower oils, nectar, and perfumes in order to attract pollinators (Ackerman, 1986; Dressler, 1982). In orchids, the production of oils and resins only occurs in five subtribes: Bifrenariinae, Catasetinae, Cyrtopodiinae, Maxillariinae and Oncidiinae. It should be noted that all are exclusive to the Neotropics. Similarly, the number of flowers, the size of the inflorescence and the density of the flowers play an important role in the pollination process (Willmer, 2011). Among the pollinators of orchids are: Coleoptera (beetles), Diptera (flies and mosquitoes), Hymenoptera (bees, bumblebees, and wasps), Lepidoptera (butterflies and moths) and some birds (hummingbirds). Likewise, some orchids present self-pollination (van der Pijl and Dodson, 1966; Williams, 1982).

Various studies indicate that more than 30% of orchids are pollinated by deception systems (van der Pijl and Dodson, 1966; Ackerman, 1986b; Tremblay *et al.*, 2005; Jersáková *et al.*, 2006). Orchids that use deception to attract pollinators employ different mechanisms ranging from feeding deception to floral and sexual mimicry (several times leading to pseudocopulation) (Jersáková *et al.*, 2006). This deception consists of imitating odors and visual stimuli to deceive pollinators that are looking for food or reproduction (Cozzolino and Widmer, 2005). Thus, non-reward orchid flowers have a complex morphology, in many cases having the appearance of the female pollinator. In this case it is known as sexual deception syndrome (van der Pijl and Dodson, 1966; Dressler, 1993; Ayasse, 2006). On the other hand, when there are structures in the flower that resemble food and that deceive the pollinator, it is known as food deception syndrome (Ackerman, 1986a, b).

POLLINATION SYNDROMES IN ORCHIDS

In Orchidaceae, it has been documented that each subtribe or even each genus have specific pollinators according to the characteristics that the flowers present (van der Pijl and Dodson, 1966; Tremblay, 1992; Bogarin *et al.*, 2018). For example, it has been reported that flies are the pollinators of the Pleurothallidinae (Albores-Ortiz and Sosa, 2016; Bogarin *et al.*, 2018); Euglossine bees are pollinators of Catasetinae, Stanhopeinae and some representatives of Beltiinae, Lycastinae, Oncidiinae and Zygopetalinae; all from the Neotropics (Dressler, 1968; Parra *et al.*, 2016). On the other hand, some members of Habenariinae are pollinated by Lepidoptera and Orchidinae by Hymenoptera (Inda *et al.*, 2012), just to mention a few. Furthermore, orchids may share pollinators with other orchids or even with plants from other families (Ackerman, 1983).

Pollination efficiency is tied to how the pollinator interacts with the sexual organs of the flower, which is determined by its morphological and temporal adjustment (Simón-Porcar *et al.*, 2018). Pollination mechanisms in orchids have been extensively studied and have been grouped according to taxonomic groups of pollinators and flower morphology in the so-called "orchid pollination syndromes" (van der Pijl and Dodson, 1966; Tremblay, 1992). These syndromes clearly show the adaptations between the flower and the animals that pollinate them (van der Pijl and Dodson, 1966) (Table 1). The main characteristics of each of the groups of pollinators are described below.

Table 1. Comparison of pollination syndromes of orchids from Megaméxico.

Syndrome	Pollinator	Morphological adaptations of orchids	Flower coloring	Physiological adaptations	Notes	Examples
Melittophilous	Bees	Zygomophic flowers with complex nectar guides and platform-shaped lip for landing	Violet, blue, green, yellow, and white	Flowers that open during the day (may or may not close at night). Pleasant and fresh aromas	Some instead of nectar produce volatile essences	*Bletia, Laelia, Sobralia, Stanhopea, Vainilla*
Phalenophilous	Moths	Pollinia attach themselves to the feet of pollinators. No nectar guides. Flower does not erect, usually pendulous	White, cream, or greenish	Sweet scent and flowers open at night	They have short nectar tubes	*Epidendrum parkinsonianum, Coenoemersa, Habenaria, Platanthera*
Phsychophilous	Butterflies	Contain nectar in long narrow tubes, erect flower position, Zygomorphia not necessary	Bright colors, red, orange, yellow, pink, purple	The flowers open during the day. Pleasant and fresh aromas. Abundant nectar, usually in deep containers	Pollen sticks to the legs of pollinators	*Bletia, Epidendrum, Funkiella, Sacoila*
Ornithophilous	Birds	Nectar deep and occasionally protected. Pollen can be brown or dark colors	Predominant reddish colors. Red, orange, pink	No aroma or very faint aromas; hanging flowers	Pollen adheres to the beak	*Alamania, Arpophyllum, Comparettia falcata, Dichromanthus, Stenorrhynchos*
Miophilous/ sapromiophilous	Flies	Small flowers with transparent structures and may have hairs. Sometimes with mobile organs to the wind	dark purple, brown, and yellow colors with spots and lines	Strong aromas of decomposing matter	No nectar guides	*Bulbophyllum, Lepanthes, Pleurothallis, Stelis*
Cantharophilous	Beetles	Large flowers, sac-shaped lip	Mostly Yellow, green, purple	Nectar-producing	They usually eat part of the flower	*Cypripedium*

Hymenoptera

Bees, bumblebees, and wasps (Hymenoptera) are undoubtedly the taxonomic group that pollinates the most species of orchids, mainly members of the Apidae, Colletidae, Halictidae and Megachilidae tribes; and it is the only group that interacts with members of all five Orchidaceae subfamilies. Orchids took advantage of the great diversity of Hymenoptera and their cognitive abilities to diversify in the same way (Mondragón-Palomino and Theißen, 2009; Ramírez *et al.*, 2010). The orchid-hymenopteran interaction is one of the most fascinating in nature (Figure 1A). This great variety of mechanisms of attraction to pollinators can be through the generation of a) aromatic oils, b) nectar, c) nectar deception or d) sexual deception.

Smells play an important role in attracting some species of pollinators. One of the most studied cases is that of Euglossine bees (Apidae: Euglossini), which are known to actively collect floral perfumes that they probably use during courtship (Ramírez *et al.*, 2002; Eltz *et al.*, 2005). Within Orchidaceae, this pollination mechanism is restricted to the Epidendroideae subfamily, within the Catasetinae, Stanhopeinae subtribes and part of the Zygopetaliinae and Oncidiinae (Castro and Singer, 2019).

The Euglossini are exclusive to the Neotropics, they are distributed from Mexico to northern Argentina (Parra *et al.*, 2016). These bees learn and remember the chemicals they collect, their innate odor preferences and memory seem to prevent over-collection (Eltz *et al.*, 2006). It has been highlighted that the olfactory preferences of male euglossine bee species are a strong selection pressure towards orchid species (Roubik and Hanson, 2004). For this reason, orchids emit these substances to attract euglossine bees through a great diversity of aromas that vary intra- and interspecifically (Hetherington-Rauth and Ramírez, 2016).

Orchids pollinated by euglossine bees develop osmophores on the labellum (Franken *et al.*, 2016). High humidity and temperature levels can increase the metabolism of the scent glands (osmophores) of orchids, which translates into an accentuation of aromas (Téllez-Velasco, 2013). The orchids that emit these aromas grow mainly in tropical regions and their emission is generally higher in the morning, where the activity of euglossin bees is higher (Rodríguez-Flores *et al.*, 1995).

When male euglossin bees collect volatile compounds in the pollination process they are aided almost entirely by the intricate floral morphology of the orchid, which normally places the pollinator in the proper position. This position ensures precise placement of the orchid pollinarium in a specific area of the bee body, which in turn ensures successful deposition of the pollinia on the stigma later (Dressler, 1982).

On the other hand, some orchid species provide nectar as a reward to attract bees. Generally, in these orchids, the lip wraps around the column, forming a wide funnel-shaped tunnel into which the pollinator has to penetrate to carry out pollination. This type of flower is sometimes referred to as the throat type and is present in several groups of orchids not necessarily related, such as the genera *Bletia*, *Sobralia*, *Laelia* or *Cattleya*.

To attract bees, orchids also employ feeding deception, where they exploit the innate foraging behavior of pollinators. In this type of pollination, orchids signal that they are rewarding plants, such as the shape of the inflorescence, the color of the flower, the aroma, the nectar guides, and the spurs, this is usually especially effective for the bumblebees of the genus *Bombus* (Kunze and Gumbert, 2001). They also tend to flower gregariously in early spring, exhibit flower color polymorphism, and exploit newly emerged bees and bumblebees after hibernation (Heinrich, 1975). This strategy is particularly successful, since it is estimated that one third of orchids present this feeding deception mechanism (close to 10,000 species) (Ackerman, 1986a). Several experimental studies have shown that feeding cheating promotes cross-pollination, thus favoring genetic diversity, however, we still do not understand how it became such a successful strategy (Jersáková *et al.*, 2006).

Finally, orchids can attract pollinators in a spectacular form of floral mimicry: sexual deception. Hitherto known exclusively in orchids, the flowers mimic the mating signals (physical or chemical) of certain insect species and are pollinated by sexually excited males, who mistake the flower for a female and pollinate it during "pseudocopulation" (Jersáková *et al.*, 2006). Orchid species that perform sexual deception may have widely open flowers that expose the lip, which mimics or at least part of the female insects. Interestingly, many sexually deceptive orchids have flowers with green, red or white colorations (Gaskett, 2011).

Within Orchidaceae, this pollination strategy is exclusive to the Orchidoideae and Epidendroideae subfamilies (Castro and Singer, 2020). Examples of this fascinating interaction of orchids with hymenoptera are orchids of the genera *Lepanthes* (Blanco and Barbosa 2005), *Trigoninium*, *Mormolyca* (Singer *et al.*, 2004), *Telipogon*, *Tolumnia* and *Trichoceros* are pollinated by the melipona bee *Plebeia droryana* (Apidae: Meliponini) (Singer, 2002; Chase, 2009; Martel *et al.*, 2016).

Lepidoptera

Pollination syndromes that are carried out by Lepidoptera are divided into two groups: sphingophilic when pollinated by moths and psychophilous when pollinated by butterflies (van Der Pijl & Dodson 1966). Lepidoptera pollinate about 10% of orchids, of which 85% are nectar-producing species (Figure 1D). Thus, the orchid flowers that are characteristic of this pollination syndrome are those that produce nectar; on which these pollinators feed. The flowers are adapted with a tubular-shaped nectary where pollinators enter their mouthparts called a proboscis for nectar absorption. Orchids that present this pollination syndrome are more common in tropical areas.

The sphingophilic flowers usually present white, beige or very light greenish colors. Likewise, the flowers usually open at night and have odors that are attractive to moths. Examples of this syndrome are the species of *Platanthera*, *Habenaria* and some *Epidendrum*, to mention a few. For their part, psychophilic flowers present bright colors such as orange, red, pink, purple, etc. They contrast with the sphingophiles by opening their flowers during the day and producing fresh aromas that attract butterflies. Some species of *Epidendrum*, *Sacoila*, *Funkiella* and some *Bletia* are examples of this pollination syndrome.

Thus, the orchids that are pollinated by Lepidoptera all have a structure that resembles a small tube, which is located at the base of the lip, whether it is spur-shaped as in *Habenaria* or a narrow tunnel product of the fusion of the column with the base of the lip as in many species of *Epidendrum* (Hágsater *et al.*, 2005). These small tubes are adapted to be penetrated

Figure 1. Representation of pollination groups in orchids. A) Pollination by Hymenoptera (*Stanhopea tigrina* and *Euglossa viridissima*), B) Birds (*Comparettia falcata* with *Chlorostilbon maugaeus*), C) Diptera (*Lepanthes glicensteinii* and *Bradysia floribunda*) and D) Lepidoptera (*Epidendrum veroscriptum* and butterfly of the family Pieridae).

only by the pollinator's proboscis or beak. The flowers that present these structures are called "key-lock" flowers (Dressler, 1981). In several species, this tunnel enters the ovary or the pedicel and at the bottom there is a larger cavity that contains the nectar. The length of the tunnel has adapted to the size of the pollinator's proboscis. *Brassavola* and *Rhyncholaelia* are obvious examples of this situation.

Diptera

After Hymenoptera, the Diptera are the second most important group of orchid pollinators. Pollination carried out by flies and mosquitoes is called myophily (van der Pijl and Dodson, 1966; Christensen, 1994). Myophily is considered one of the most promiscuous and widespread pollination syndromes in angiosperms (van der Pijl and Dodson, 1966). Diptera participate in the pollination of the richest tribes in species of the family such as Dendrobiinae, Malaxidinae and Pleurothallidinae (Ackerman *et al.*, 2022).

The flowers that present this pollination syndrome are very small and with different colors ranging from purple-pink and yellow with spots and lines. Furthermore, they do not produce nectar to attract pollinators (Borba *et al.*, 2011). In this case, the flowers produce fetid odors, which in many cases are not perceptible to humans, but are easy for flies to smell since they resemble rotten meat, decomposing fruits, etc. These orchids imitate being the food of the diptera that pollinate them. In many cases, the odor they emit attracts very specific pollinators (Christensen, 1994). An example of this syndrome is the species of *Stelis* where many of the species of the genus have dark colors in their flowers and frequently develop mobile structures and fetid odors (Figure 1C).

Lepanthes species are known to use sexual deception and are pollinated by fungus gnats of the family Sciaridae. The male mosquitoes, by confusing the flowers with the female mosquitoes, try to copulate with the flowers where, in addition, their genitals fit exactly in the appendages of the lip as they would with the female sexual organs of the female mosquito. Besides being amazing, this case demonstrates the incredible morphological adaptation of orchids to being pollinated by specific pollinators. All Pleurothallidinae and Cypripedioideae are examples of this type of pollination along with species belonging to the genera *Epipactis*, *Habenaria*, *Liparis*, *Malaxis*, *Corallorhiza*, to name a few.

Birds

Orchid pollination by birds has only been reported in tropical regions (Ackerman *et al.*, 2022). In Megaméxico, hummingbirds (Trochilidae) are the only birds that pollinate orchids where members of the two largest subfamilies, Epidendroideae and Orchidoideae, pollinate (Figure 1B). Few orchid species (around 3% of species) have interactions with these fast-moving birds. However, most of the orchids that are pollinated by hummingbirds have some interesting and unique characteristics that we will mention below: These orchids are usually from high and/or cold areas, since a large part of the pollinating insects do not reach these areas because that do not have the ability to thermoregulate, this is an opportunity that hummingbirds that, having said ability, can take advantage of. Hummingbird-pollinated orchids tend to have bright colors with predominantly reddish tones, such as bright red, pink, purple, orange, yellow, or magenta. Most insects cannot perceive the red of the color spectrum and hummingbirds, having the ability to see those colors, can take advantage of this (Siegel, 2011).

Ornithophilous orchids usually have a callus that partially closes the floral tube at the level of the anther and the stigma (van Der Pijl and Dodson, 1966). The pollen sacs of most orchids are yellow, but this yellow would produce a high visual contrast with the color of the bill and hummingbirds would be stimulated to clean their bills, implying crossbreeding failure in orchids (Lipińska *et al.*, 2022). That is why, to avoid detection, a large part of the orchids pollinated by hummingbirds evolved to have a dark pollinarium (Dressler, 1971). Some examples of hummingbird-pollinated genera that have some of the characteristics mentioned above are *Elleanthus* and *Comparettia*. It is important to note that the curvature of some flowers coincides with the curvature of the beaks, which makes pollination more efficient (Castro and Singer, 2019).

Other Animal Interactions

Orchids not only interact with pollinating animals, but also with species with very particular functions. For example, some orchids of the genus *Myrmecophila* have hollow pseudobulbs that serve as homes for ants (Thien and Rico-Gray, 2004). These orchids in their mutualistic relationship provide shelter and food for the ants and these defend the plants from being defoliated by herbivores and fertilize the soil (Hágsater *et al.*, 2005).

These pseudobulbs have been reported to harbor at least nine species of ants, each species living in a different pseudobulb (Thien and Rico-Gray, 2004). This relationship can become so relevant that some orchids only grow directly on anthills, forming so-called ant gardens (Kleinfeldt, 1978). For example, *Epidendrum flexuosum* and *Coryanthes picturata*, the interaction with ants is essential and they are obligate myrmecophilous orchids, since for both species the anthills are a favorable environment for the germination and growth of these species while the roots of the plants give structure to the anthills and protect it (Morales-Linares *et al*., 2018).

THE POLLINATORS OF THE ORCHIDS OF MEGAMEXICO

In Megaméxico, bees are the main pollinators of orchids; pollinate 827 species of orchids, it should be noted that it interacts with species from the four Orchidaceae subfamilies present (Figure 2). The second most important group are flies pollinating 473 orchid species, followed by butterflies and to a lesser extent by hummingbirds and beetles (Figure 3). As for orchids, the Epidendroideae subfamily is the richest in species in the family and they present a wide range of shapes and colors in their flowers. Within this subfamily, each subtribe has particular traits and morphological adaptations of the flowers that allow them to be pollinated by certain groups of pollinators. For this reason, it is the group that interacts with all the groups of pollinators present in our study region (Figure 2). In Orchidoideae it interacts with all pollinators except wasps and beetles. In the case of Cypripedioideae it is pollinated by Diptera and beetles. Finally, the Vanilloideae only interact with bees

CONSERVATION IMPLICATIONS

Megamexico orchids and their respective pollinators coexist due to the interactions that occur between them. However, these interactions are threatened since the habitats of

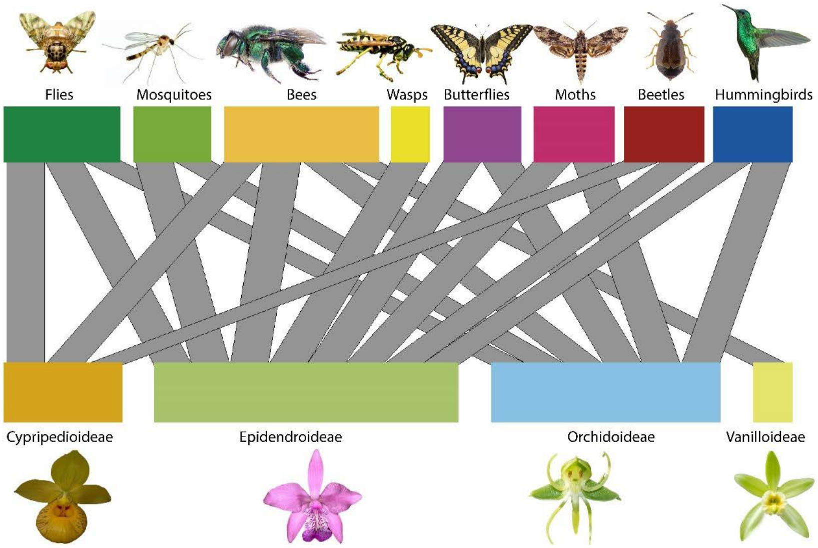

Figure 2. Network of interactions of orchids and pollinators of Megamexico. Lines represent interactions between pollinator groups and Orchidaceae subfamilies.

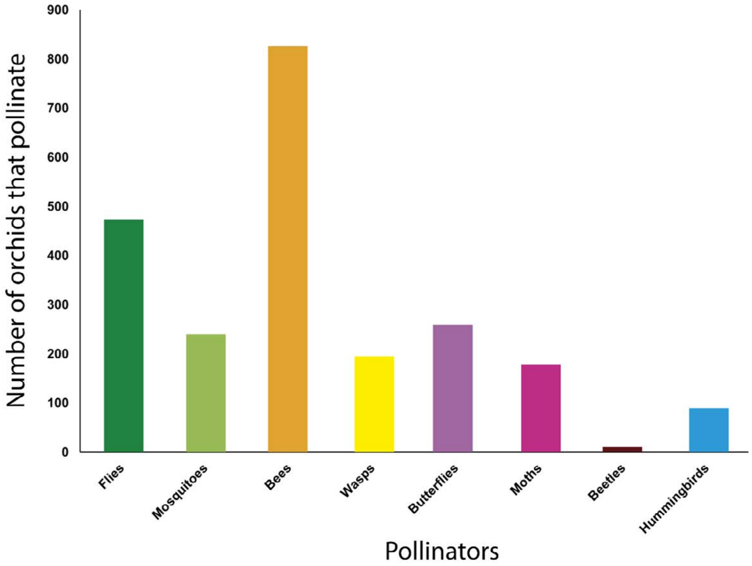

Figure 3. Representation of the number of orchids pollinated by each of the groups of pollinators.

the orchids and therefore of the pollinators are in danger; the causes and consequences of the loss of orchid habitats are listed in Gutiérrez-Rodríguez (2022). The disappearance of orchids or their pollinators will inevitably lead to the extinction of one, the other, or both. Both orchids and pollinators are affected to varying degrees by environmental fluctuations and disturbances in ecosystems. Therefore, habitat conservation is a critical factor that affects their permanence and, in that sense, their survival. We believe that an ecological study of orchid-pollinator interaction networks is imperative to understand how these interactions are structured, which are vital for the life cycles of both groups of organisms. The study of interactions between orchids and pollinators provides a fundamental basis for conservation proposals considering the habitat requirements not only of orchids but also of the organisms with which they interact.

We also believe that it is extremely important to call for more research on orchid pollination, since many groups have not been studied and little or nothing is known about their pollinators. In this sense, we encourage researchers and people in general to contribute to this gap that is little explored for many groups and we invite them to make more field observations on orchid pollinators and report them through the use of digital platforms such as the website of Naturalista (https://www.naturalista.mx/). Finally, we believe that it is very important to include orchid pollinators in conservation programs to ensure that interactions between orchids and pollinators continue to be effective and thus guarantee the permanence of the two groups.

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