Review

By land and by tree: Pollinator taxa diversity of terrestrial and epiphytic orchids

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Abstract—There are approximately 30,000 species in the family Orchidaceae, with some species growing terrestrially and others growing as epiphytes. Though the pollination biology of many of these species is not well known, there has been a diversity of taxa recorded as orchid pollinators. Insects, birds, and even a record of a mammal species have been documented as successful pollinators, while some orchids are able to reproduce without the use of a pollen vector. The goal of this review is to provide an overview of orchid pollination tactics, with references to more specific studies of each, and to analyze a large subset of publications to determine differences in pollinator taxa and specificity between epiphytic and terrestrial orchid genera.

This review examines pollination data from over 400 orchid species, including 74 epiphytic and 83 terrestrial orchid genera. Two pollinator taxa, Coleoptera and Hymenoptera (Class: Insecta), were found to pollinate significantly more terrestrial than epiphytic orchid genera, while other taxa showed no significant differences. Hymenoptera were the dominant taxa of pollinator in regards to the overall number of species recorded; however, based on species interaction webs that were built, the Lepidoptera (Class: Insecta) have stronger interactions with the orchid species they pollinate, suggesting a more specific relationship between the two.

Keywords—Orchidaceae, epiphyte, terrestrial, bipartite, species interaction

Introduction

The Orchidaceae is one of the largest flowering plant families, with nearly 30,000 species globally (Brown 2005). Orchids grow terrestrially, as lithophytes, or as epiphytes. A single epiphytic orchid species may grow on numerous tree species or on a small number of host taxa, depending on location, availability of tree hosts, and branch or bark suitability (Mújica et al. 2018). Orchids are highly diverse, with highly variable pollination systems, some of which can be extremely specialized. These specialized pollination systems have been linked to the high diversification of orchid species and has been a topic of interest since Darwin published on the topic in the 1800s (Darwin 1877; Tsai et al. 2008). The earliest record of orchid pollination is from an extinct bee species (*Proplebei dominicana*) discovered in amber with pollinia from the now extinct *Meliorchis caribea* orchid. The amber, collected from the Dominican Republic, was dated as 15-20 million years old (Ramírez et al. 2007). One axis of variation in orchid pollinator relationships is the diversity of pollinator taxa, which ranges from a single species to a diverse set of taxa.

This study has two main aims. First, we provide a brief review of orchid pollination strategies and the diversity of pollinators. Second, we report on a quantitative survey of pollinator diversity in terrestrial vs. epiphytic species. We conducted a literature review for publications relating to successful, documented orchid pollination. This provided us with information on the orchid species involved, how it grows (epiphytic or terrestrial), and the taxa of pollinators that have been recorded. We used these data to compare pollinator relationships in terrestrial and epiphytic orchids. This provides insight into the specificity of recorded pollinating taxa to the more than 150 orchid genera included.

Orchid Pollination Overview

Reproductive Morphology

Orchid flowers are often phenotypically highly specialized (van der Pijl & Dodson 1966). A distinctive feature is the fusion of the stamens and pistil into a single structure referred to as the column (van der Cingel 2001; Roberts & Dixon 2008). Reduction in stamen number has led to orchid groups with three, two or, for the vast majority (99%) of species, one stamen (van der Pijl & Dodson 1966; Kocyan & Endress 2001). Below the column is a petal that has been modified into a labellum, or lip, which acts as a landing area for pollinators and directs them to the (presumed) nectar source within the flower (van der Cingel 2001; Brown 2005). As a pollinator moves towards the nectar source, it comes into contact with the pollen. Unlike the loose pollen grains of most flowering plant families, most orchids have pollen aggregated into compact structures called pollinia. The pollinia are borne in the male anther cap, and there is often a sticky structure, viscidium, that helps the pollinia adhere to a pollinator as it visits the flower (van der Cingel 2001; Roberts & Dixon 2008). The stigma is located on the underside of the column. If pollination is successful, the ovary of the flower will begin to swell and form a seed pod filled with thousands or even millions of small seeds (Soguillon & Rosario 2007; Roberts & Dixon 2008).

Deception

Many orchids attract pollinators by deception in the form of physical mimicry or chemical cues, often providing no nectar or other reward for the pollinator (Coleman 1927; Roy & Widmer 1999; Wong & Schiestl 2002; Cozzolino & Widmer 2005; Jersáková et al. 2016). One example of deception through mimicry is *Ophrys apifera* and other *Ophrys* species or 'bee orchids'. The lip of *Ophrys* flowers resemble a female bee sitting on the flower, and male bees are deceived into attempting to copulate with the flower, thus effecting pollination (Devey et al. 2008).

In other cases, deception may be mediated by colour. Non-rewarding flowers of the orchid *Eulophia zeyheriana* in close proximity to the similarly coloured, and rewarding, flowers of *Wahlenbergia cuspidata* have similar visitation by pollinators. Based on similar spectral reflectance of the flowers, the bee pollinators of a *Lipotriches* sp. (Halictidae), the pollinator of *E. zeyheriana*, would likely not be able to differentiate between the two flowers (Peter & Johnson 2008). When *E. zeyheriana* was growing in closer proximity to *W. cuspidata*, they had higher pollination success, suggesting that they are using colour as a floral mimic to entice their bee pollinators (Peter & Johnson 2008).

Colour has also been studied in the rewardless orchid *Ionopsis utricularioides*, which exhibits floral colour polymorphism ranging from white to purple. This variation in the floral cue is thought to prevent pollinators from learning deceptive flowers based on colour. Studies suggest that a visitor of *I. utricularioides*, the stingless bee *Scaptotrigona depilis*, learned to avoid flowers displaying a colour morph that it had previously experienced as non-rewarding, while more commonly visiting a novel colour that did present a reward (Aguiar et al. 2020).

Orchid Floral Fragrance

Like many plants, orchids often secrete fragrances involved in pollinator attraction (Knudsen et al. 1993; Brown 2005; Dudareva & Pichersky 2006). Fragrance emission rate can differ over a 24 h period, as well as across locations, which can lead to difficulty in determining the floral volatiles for each species (Ray et al. 2018; Ray et al. 2019). Floral volatiles are very complex and while they may be used to advertise a nectar reward, they often mimic natural odours that are very specific attractants for different species. These adaptive mechanisms can be beneficial for the orchids to increase the likelihood of pollination success. One example is *Epipactis helleborine,* that has the typical shape of a wasp pollinated orchid and offers a large quantity of nectar as a floral reward. However, the floral fragrance mimics the volatiles of injured leaves and is attractive to wasps looking to consume the herbivore that has damaged the leaves (Brodmann et al. 2008).

In addition to prey attraction, the flower may release a chemical that the pollinator can use for defence or in mate attraction (Wong & Schiestl 2002). The orchid *Epidendrum paniculatum* releases pyrrolizidine alkaloids that some male Lepidoptera in the families Arctiidae and Nymphalidae use for seeking mates and defence (DeVries & Stiles 1990). DeVries & Stiles (1990) surveyed *E. paniculatum* in Costa Rica and found that 98% of the insects attracted to the flowers were male Lepidoptera that use pyrrolizidine alkaloids for attracting mates, and for predator defence.

Many orchids produce a fragrance that mimic the sex pheromones of female wasps, attracting the males. This is observed in numerous species that are pollinated by male thynnine wasps (Hymenoptera: Tiphiidae) (Alcock 1981; Peakall 1990).

POLLINATOR TAXA- ARTHROPODS

Orchids are pollinated by a diverse set of pollinators. Bees and wasps are the most common, but Lepidoptera, Diptera, Coleoptera, and other insect orders are known orchid pollinators (Statman-Weil 2001; Lehnebach & Robertson 2004; Micheneau et al. 2010; Stökl et al. 2011) van der Cingel (2001).

Among Hymenopteran pollinators, the euglossine bees (Hymenoptera: Apidae: Euglossini) have one of the closest relationships with orchids, with an estimated 650 or more tropical orchids pollinated exclusively by these bees (Ackerman 1983). The orchids release chemical compounds that both attracts and acts as a reward for male euglossine bees. The compounds do not mimic mating pheromones, but the bee collects the compounds and use them in compiling 'perfumes' used in courtship (Williams & Whitten 1983, Ackerman 1983). In the genus *Coryanthes,* the bee often becomes temporarily trapped inside the flower, where the orchid's pollinia attach to the departing bee (Williams & Dodson 1972, Ackerman 1983, Ramirez et al. 2010).

Two uncommon orders that have been documented as pollinators are Orthoptera and Thysanoptera. On Réunion Island off the coast of Madagascar, an unnamed species of raspy cricket (*Glomeremus* sp.; Orthoptera: Gryllacrididae) was documented as the sole pollinator of *Angraecum cadetii*, an epiphytic, endemic species (Micheneau et al. 2010). Three species of thrips (Thysanoptera) were found to be supplementary pollinators of terrestrial *Epipactis thunbergii* flowers in Japan (Suetsugu et al. 2019). Pollen of *E. thunbergii* is easily crumbled, allowing thrips to transfer the pollen in smaller masses (Suetsugu et al. 2019). Suetsugu et al. (2013) found one species of *Clubiona* spider (Araneae: Clubionidae) affecting pollinia transfer in the terrestrial *Neottianthe cucullata*, though the spider could have been feeding on part of the pollen and would thus be an unlikely effective pollinator. Authors noted visitation of small bees (*Lasioglossum* spp.), and presented the idea that the presence of the spider could even lower the chance of successful reproduction by preventing the true pollinators from reaching the flower (Suetsugu et al. 2013).

POLLINATOR TAXA- BIRDS

Hummingbirds (Family Trochilidae) are the primary avian pollinators of orchids. Although only about 3% of orchid species are hummingbird pollinated, this still represents almost 1,000 known species (Siegel 2011). Some genera that have documented hummingbird pollinators include *Cattleya, Elleanthus, Rodriguezia,* and *Stenorrhynchos* (Singer & Sazima 2000; Nunes et al. 2015; Caballero-Villalobos et al. 2017; Pansarin et al. 2018). These include species that are epiphytic as well as terrestrial. Orchids that rely on hummingbirds for pollination are brightly coloured and normally do not have a fragrance. Many of the orchids pollinated by hummingbirds produce pollinia that are darker in colour and nondescript. While typical orchid pollinia is a bright yellow colour, pollinia from orchids pollinated by hummingbirds are often some shade of gray, blue, or dark brown (Dressler 1971). It is thought that this is so when the pollinia attaches to the beak, the bird is less likely to remove it by cleaning when it sees a sharp colour contrast on its beak (Dressler 1971, Siegel 2011). An additional avian pollinator of orchids are sunbirds (Family Nectariniidae). They have been documented exclusively from South African terrestrial orchids, as pollinators of *Disa chrysostachya*, *D. satyriposis*, *Satyrium carneum*, *S. coriifolium*, *S. monadenum*, *S. princeps*, *S. rhodanthum*, *S. sceptrum* (Johnson 1996; Johnson & Brown 2004; Johnson et al. 2011; van der Niet et al. 2015). In the case of these sunbirds, they perch on stems of the plant while feeding on its nectar. The pollinia may become attached either to the beak or feet of the bird during this process.

POLLINATOR TAXA- MAMMALS

While extremely uncommon, there has been one documented case of mammalian pollination in the Orchidaceae. Six populations of the terrestrial orchid *Cymbidium serratum* were studied in China by Wang et al. (2008). Researchers found that the wild mountain mouse *Rattus fulvescens* (Rodentia:

Muridae) was successfully removing pollinia from orchids, as well as depositing it onto other flowers. During the visits, these mice would feed on the labellum of the flower, leading to pollinia removal (Wang et al. 2008).

ORCHID-POLLINATOR RELATIONSHIP SPECIFICITY

The advantage for orchids that have specialized relationships with a single species, is that it often results in more efficient pollen transfer than those species with multiple generalist pollinators. Specialization causes more direct transfer from one flower to another, while reducing the chance that the pollinia will be dropped or transferred to the wrong species (Scopece et al. 2010). Darwin's orchid, *Angraecum sesquipedale*, and an orchid native to south Florida, the ghost orchid, *Dendrophylax lindenii*, both require a small group of hawkmoth pollinators (Lepidoptera: Sphingidae). Hawkmoths have a long proboscis, and these orchids have a long nectar spur that the moth is able to use to reach the nectar (Kritsky 1991). Orchids may also attach pollen to a specific location on the pollinator's body, ensuring that even if the pollinator visits another species, the pollinia likely will not be transferred until it revisits an orchid of the same species (Scopece et al. 2010).

Some orchids may have a more generalist relationship with pollinators, as opposed to a specialized relationship. For example, while *Gymnadenia odoratissima* is pollinated by Lepidoptera, there are at least 12 families and 26 species of recorded pollinators (Sun et al. 2014). Johnson & Hobbhahan (2010) recorded five different species from four orders of insects (Coleoptera, Diptera, Hymenoptera, and Lepidoptera) capable of pollinating *Disa fragrans*. There is potential for the specificity of these relationships to vary based on the growth of the orchid species. The growth of the orchid, epiphytic or terrestrial, could impact how many different pollinator taxa are likely to visit the flowers and serve as pollinators. For example, some taxa may be less likely to visit a flower if it is an epiphyte growing in a dense area of branches.

MATERIALS AND METHODS

The literature used in this review consisted of 324 references, including published journal articles and books. Literature was found using JSTOR, Google Scholar, Stetson University library, and University of Florida library. Online search terms included: Orchidaceae, orchid, pollen, pollination, pollinator, fertilization, autogamy, epiphytic, and terrestrial. These references were cataloged, and any instance of taxa successfully pollinating an orchid species was included. The references cited in these papers were reviewed for additional sources that may not have been web listed. Successful pollination was deemed the adherence of pollinia onto the organism, and does not include visitors that did not remove pollinia. All orchids were recorded to the species level, and the lowest taxonomic ranking including order, family, genus, and species of each pollinating organism were documented when possible. A total of 157 orchid genera and 439 species are included in this review. Additional information that was recorded included the country from which the recorded pollination event occurred, and whether the orchid species involved was epiphytic or terrestrial. Analyses were varied out in R 4.0.5 (R Core Team 2017) and Microsoft Excel. The R package 'bipartite' is used to visualize and describe patterns in ecological webs consisting of two levels. Using this package, the orchids were split into two groups for analysis- epiphytic and terrestrial. For every orchid genus in each growth category, the number of documented pollinator species from each major taxon were recorded. These taxa included Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Orthoptera, and Thysanoptera from the class Insecta, as well as Apodiformes and Passeriformes from the class Aves, and Rodentia from the class Mammalia. These webs will serve two major purposes: (1) to show the interactions between orchid genera and the diversity of pollinator taxa, and (2) to visually represent the strength of relationships between orchid-pollinator genera. A global abundance map was created with R using the libraries tidyverse, ggplot2, reader, maps, and viridis to show the total number of orchid-pollinator interactions documented in each country from the literature used in this review.

Microsoft Excel was used for T-Tests to compare the number of epiphytic vs. terrestrial orchid genera pollinated by each of the following four taxa: Coleoptera, Diptera, Hymenoptera, and Lepidoptera. This method was also used to statistically compare the average number of

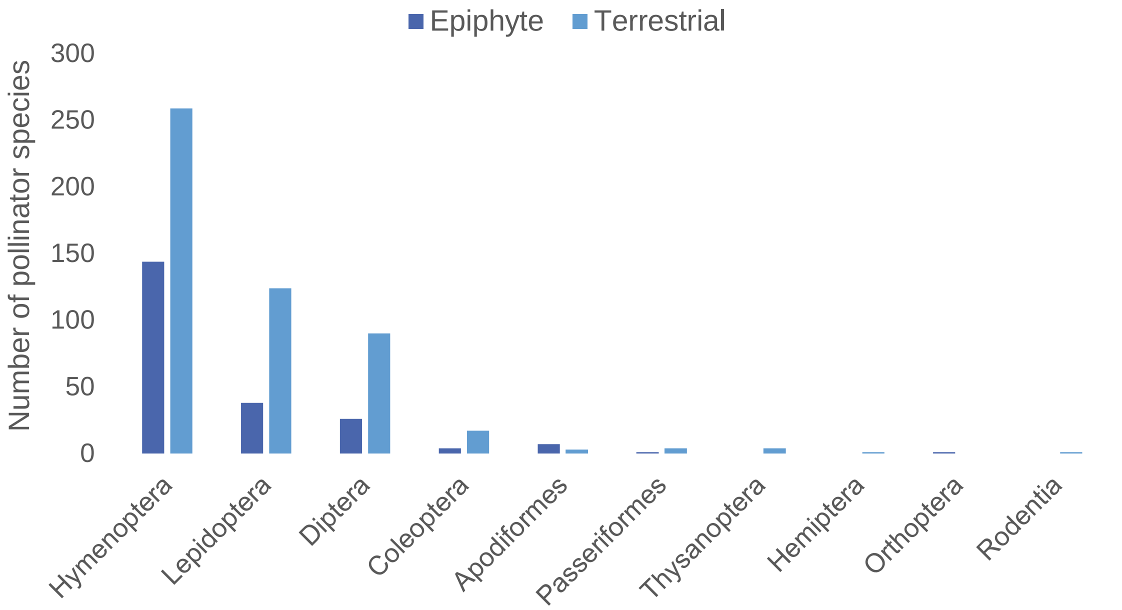

Figure 1. The total number of pollinator species of each order. For example, there were 144 species of Hymenoptera pollinating epiphytic orchids, and 259 species of Hymenoptera pollinating terrestrial orchids. A full list of the numbers for each order can be found in Table 1.

pollinator taxa from epiphytic orchid genera compared to terrestrial orchid genera. The genera numbers were used instead of species as they were comparable numbers of each, opposed to a large difference in sample size between the total number of species.

RESULTS

Of the 439 orchid species included in this review (in 157 total genera), 165 are epiphytes (74 genera), while 274 are terrestrial (83 genera). The epiphytic species were pollinated by a minimum of 221 different animal species, and the terrestrial orchids were pollinated by a minimum of 503 different species (Fig. 1, Tab. 1). When comparing the genera that four major taxa (Hymenoptera, Lepidoptera, Diptera, and Coleoptera) pollinate, there were significant differences between two of the orders. While there was no statistically significant difference in the number of epiphytic vs terrestrial orchid genera that Diptera (P = 0.14) or Lepidoptera pollinate (P = 0.20), there was a significant difference between the number that Coleoptera and Hymenoptera pollinate (P = 0.0005 and P = 0.008, respectively). In both cases, there were significantly more terrestrial orchid genera pollinated than epiphytic (Fig. 2). We see this trend in the bipartite webs created as well, with more diversity in the connecting bars of the terrestrial web than epiphytic (Fig. 3 and Fig. 4).

In both webs, the thickest bars between pollinator order and orchid genus are found in the Lepidoptera. This suggests that the species within those genera have a more specialized orchid-pollinator relationship, as opposed to being

Table 1. The number of species in each order found to pollinate epiphytic and terrestrial orchids.

	Epiphytic Orchids	Terrestrial Orchids
Hymenoptera	144	259
Lepidoptera	38	124
Diptera	26	90
Coleoptera	4	17
Apodiformes	7	3
Passeriformes	1	4
Thysanoptera	0	4
Hemiptera	0	1
Orthoptera	1	0
Rodentia	0	1
Total	221	503

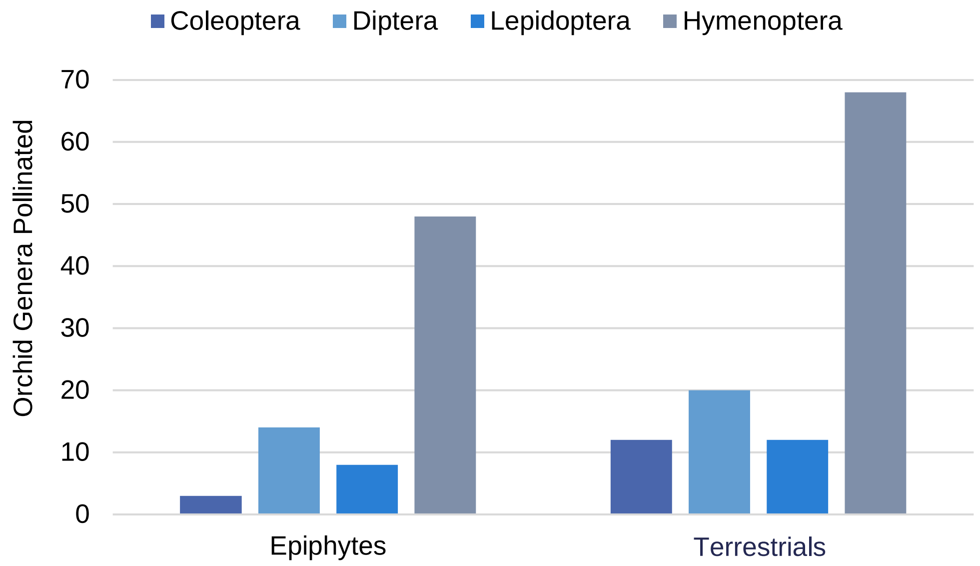

Figure 2. The total number of orchid genera (epiphytic and terrestrial) that are pollinated by each of the four major orchid pollinating insect orders. The Coleoptera and Hymenoptera display significantly different results between epiphytic and terrestrial orchid genera (*P* = 0.00046 and *P* = 0.0079).

pollinated by a more generalist taxa. The webs also suggest that terrestrial orchids tend to be more generalist pollinated, as indicated by the higher number of overlapping bars.

Terrestrial orchids tended to be pollinated by slightly more pollinator taxa than epiphytic orchids (1.45 ± 0.1 SEM vs. 1.15 ± 0.06 SEM taxa, $P = 0.011$, Fig. 5).

Orchid pollinator records were geographically biased (Fig. 6). A total of 50 countries were included, ranging from as few as one study per country up to 77 studies to date in Brazil. Pollination records included 112 publications from 1930-1999, and 215 publications from 2000-2022, indicating an increasing trend in orchid pollination research.

Discussion

With approximately 30,000 species of orchids, there is still much to learn about orchids and their pollinators. Of the species included in this review, approximately 55% were pollinated by Hymenoptera, 20% by Diptera, 16% by Lepidoptera, 4% by Coleoptera, and 3.5% by Apodiformes and Passeriformes (1.5% and 2%, respectively). The remaining were single records of pollination by Hemiptera, Orthoptera, Thysanoptera, and Rodentia. There was a difference between only two pollinator taxa when comparing the 74 epiphytic and 83 terrestrial orchid genera, with significantly more Hymenoptera and Diptera pollinating terrestrial genera than epiphytic. Though the numerical difference was small, terrestrial genera were found to be pollinated by significantly more taxa than epiphytic orchids ($P = 0.011$), suggesting that they use a more generalist pollination strategy. This is also supported by our Bipartite graphs, which had more interactions for terrestrial orchids than epiphytic. Not only was there a significant difference in the number of higher taxonomic groups, there were over 500 documented species pollinating terrestrial orchids compared to only about 220 species that pollinate epiphytes.

It is possible that terrestrial orchids had significantly higher pollinator diversity than epiphytes due to accessibility of the flowers. While some individuals may be growing on lower branches and tree trunks, others may be growing in more densely branched locations, making some pollinators less likely to visit those species. Additionally, some taxa may be less likely to be visiting flowers that are growing on higher tree branches.

In a review specifically of some orchids in the subtribe Oncidiinae, the literature supported the idea that these orchids rely on pollinators for seed production, and are not autogamous (self-fertilizing). The genera in this subtribe include

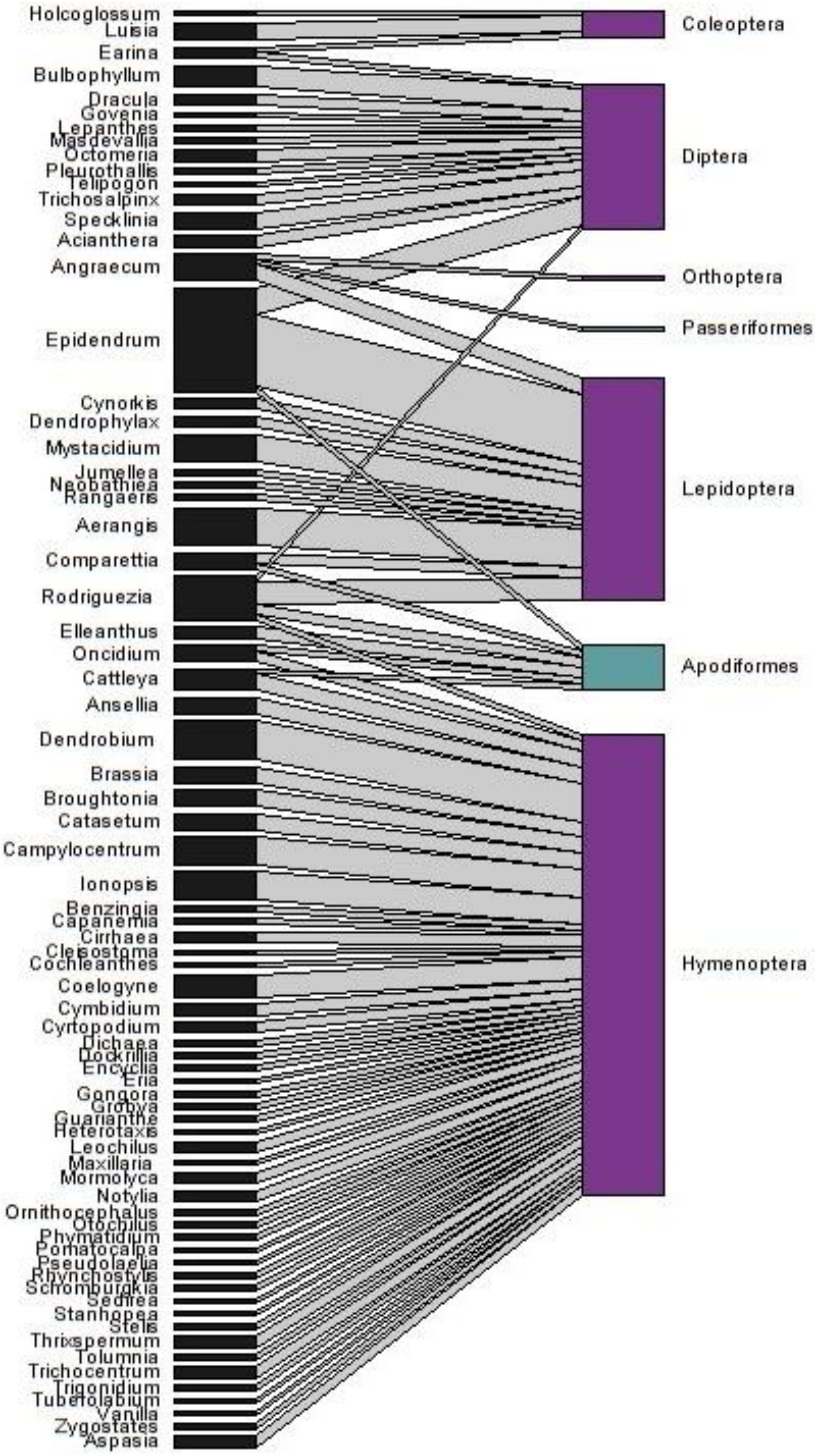

Figure 3. Bipartite interaction web of epiphytic orchid genera (left) and the taxa that have been observed as pollinators (right). Each bar represents at least one instance of a pollinator interaction between the two taxa. The thicker the connecting bars are between the two groups, the more documented instances of pollination by a species in that genus have occurred. The order of the taxa was arranged by R to show the fewest number of overlapping bars. Taxa with purple bars represent insects, while taxa with blue bars represent birds.

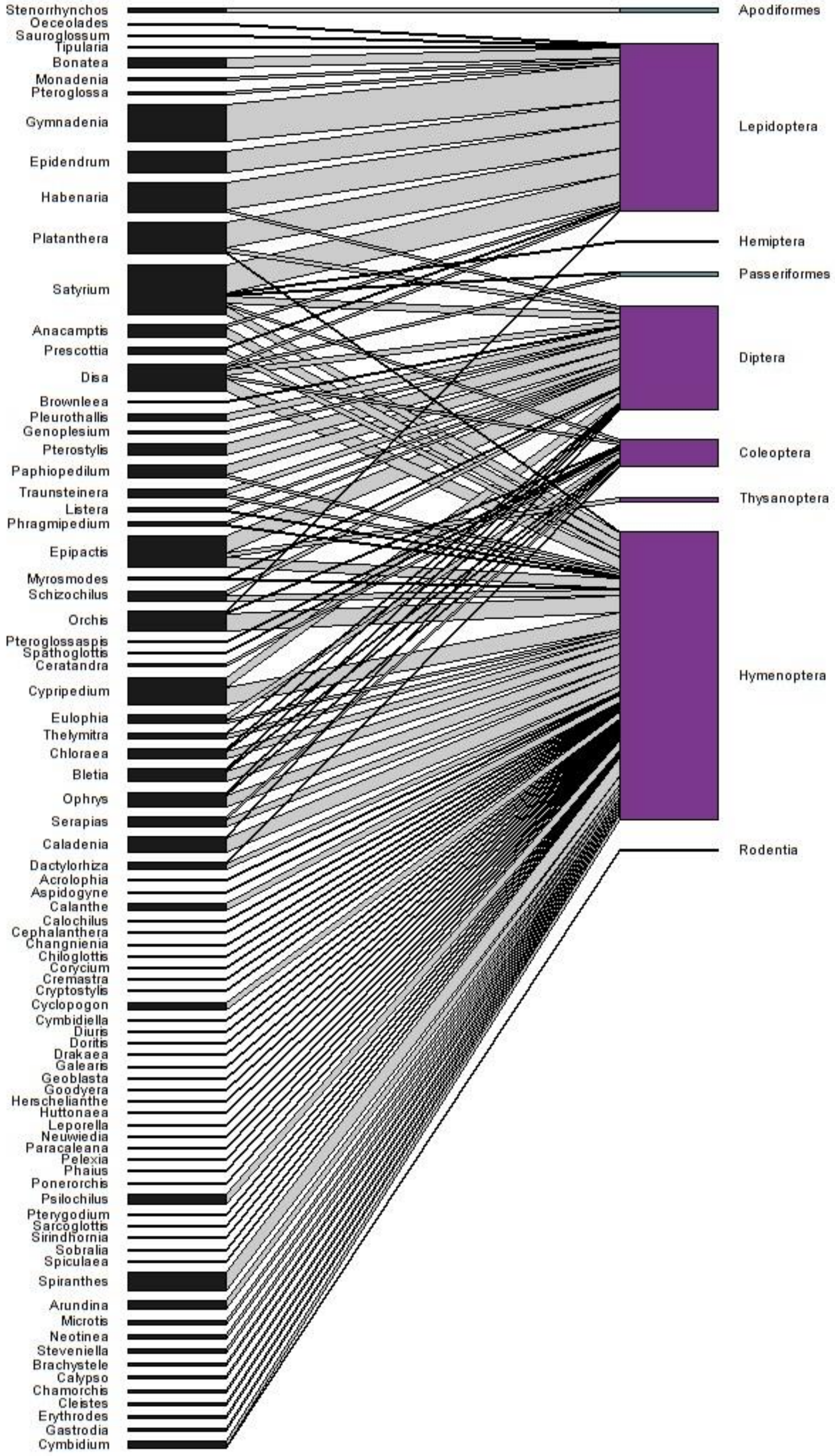

Figure 4. Bipartite interaction web of terrestrial orchid genera (left) and the taxa that have been observed as pollinators (right). Each bar represents at least one instance of a pollinator interaction between the two taxa. The thicker the connecting bars are between the two groups, the more documented instances of pollination by a species in that genus have occurred. The order of the taxa was arranged by R to show the fewest number of overlapping bars. Taxa with purple bars represent insects, while taxa with blue bars represent birds.

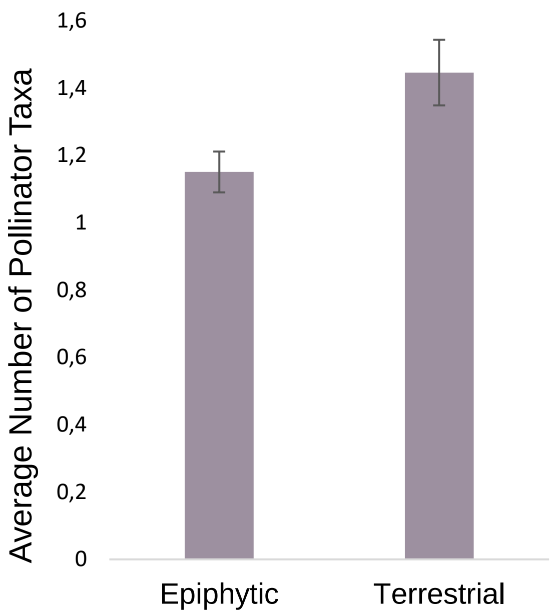

Figure 5. The average number of pollinator taxa (to the Order level) documented to pollinate epiphytic and terrestrial orchids. The terrestrial orchid genera were pollinated by significantly more taxa (1.45 ± 0.1) than the epiphytic genera (1.15±0.06) (*P* = 0.011) Error bars represent the standard error of the mean.

both epiphytic and terrestrial species. Of the species included, they found that nearly 70% were entirely self-incompatible, and would require some type of pollinator for seed set (Castro & Singer 2019). Additionally, some orchids that are assumed to be autogamous may significantly benefit from pollinator visitation. In south Florida, the terrestrial species *Eulophia alta* was reported as autogamous; however, it was later determined that spontaneous autogamy was uncommon, with only about 7% of flowers studied producing seed capsules (Johnson et al. 2009). While some orchids may be considered autogamous because they are self-compatible, it may also be true that the presence of a pollinator will increase their chance at reproductive success, and would also help to improve genetic diversity within the population. In some cases, the same orchid species will use different pollinators in different locations depending on what species are present. If terrestrial orchids do have a wider range of generalist pollinating taxa, they may utilize this to their advantage to increase seed set across a wider range of locations. As factors like climate change can alter the ranges of some of these plants and pollinators, there may be differences in their reproductive capabilities with new species in an area. This may also have the opposite effect, in which a pollinator for a specific species may have a lower tolerance for change, causing a loss in pollinator taxa. Orchids that have more generalist pollinator relationships may be able to better withstand a loss in some taxa while still attaining reproductive success.

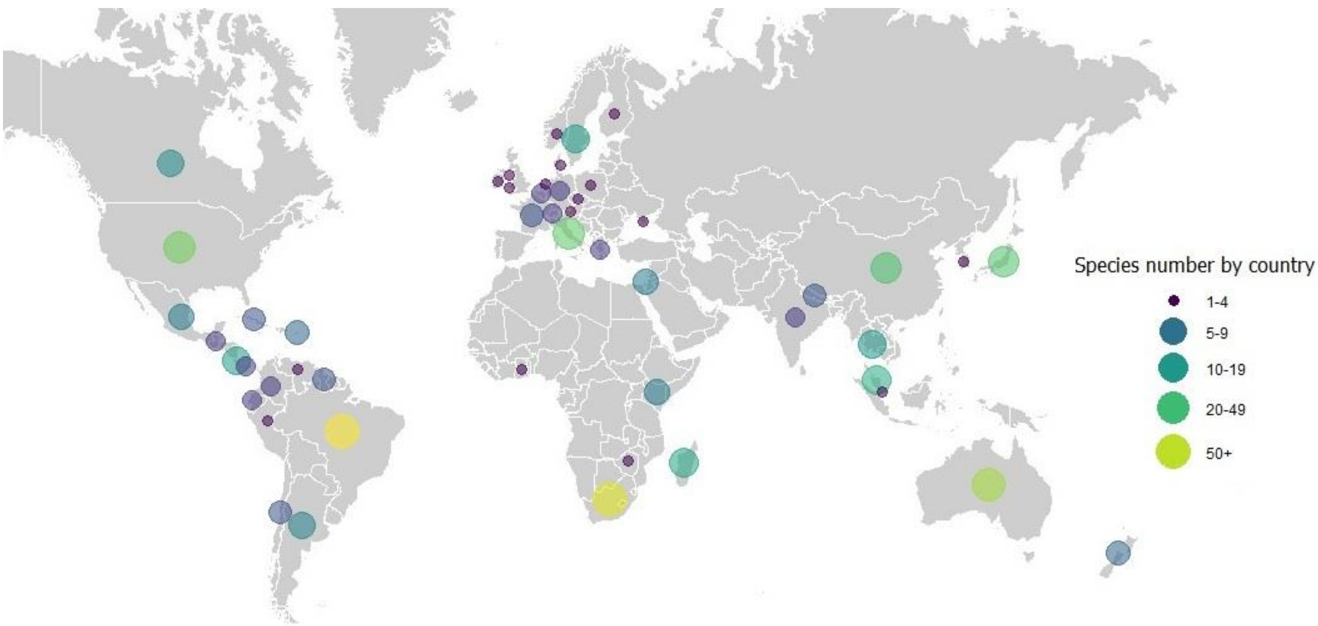

Figure 6. Global distribution map of the orchid pollination studies included in this review. The larger the circle, the more orchid species that were studied in that country.

Less than 6% of all orchid species have been assessed for the IUCN red list, and 46.5% of those that have been assessed are listed as either Critically Endangered, Endangered, or Vulnerable. Poaching, climate change, and habitat fragmentation are all some of the major threats that orchids face. Orchid hotspots of richness and rarity were studied for the epiphytic genus *Lepanthes* to determine the most effective conservation strategies. The study found that the most important factor threatening these orchids extinction was habitat loss, and in areas with high habitat loss and fragmentation, *ex situ* conservation strategies would be most effective (Crain & Tremblay 2014). The results of this study suggest that epiphytic species have a more specialized range of host taxa. For an epiphytic genus like *Lepanthes*, that loss of habitat could more strongly impact their ability to reproduce if their pollinators are negatively affected by the habitat change. Many of the orchid habitats threatened with extinction loss are in tropical regions, where they are more frequently found *in situ*. Of the orchid pollination studies used in this review, the regions with the most documented pollinator information were typically tropical and sub-tropical countries (Fig. 6).

Between the threats to orchids, their pollinators, and relatively few species having their reproductive strategies studied, this is an area of research that should continue to grow. Aspects such as their method of attraction (fragrance, colour, deception, nectar rewards, etc.), breeding systems, pollinator taxa, and reproductive success are all important factors to understanding in order to provide conservation strategies for a plant family with a large proportion of threatened and endangered species.

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix 1. Reference list of the orchid pollination studies included in this review.

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