

A Global Review and Network Analysis of Phytophagous Insect Interactions With Ferns and Lycophytes

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Research Article

Keywords: herbivory, host-plant selection, pteridophytes, spore feeders, network analysis

Posted Date: April 19th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-301036/v1>

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Version of Record: A version of this preprint was published at Plant Ecology on September 29th, 2021.

See the published version at <https://doi.org/10.1007/s11258-021-01187-5>.

Abstract

Ferns are the second largest lineage of vascular plants, yet our understanding of their interactions with phytophagous insects is very limited. Which insects feed on ferns? Do insects prefer specific fern taxa? Which feeding habit is the most common on ferns? Is there any evidence for coevolution between insects and ferns? Is our current knowledge on fern-insect interactions biased? To answer these questions, we analyzed 2,318 records of fern-insect interactions from 122 literature sources, based on the feeding habit of insects, fern taxa, and geographic location. We found evidence for interactions comprising 809 insect species (mainly Hemiptera, Lepidoptera, and Coleoptera) and 382 fern species (mainly Dennstaedtiaceae, Dryopteridaceae, and Pteridaceae). Leaf chewers contributed over 50% of the species, followed by sap-sucking insects (29.1%) and spore feeders (6.5%). The overall interaction analyses revealed that the entire fern-insect network had medium levels of nestedness ($NODF = 43.37$) and relatively low levels of specialization ($H2' = 0.24$). The interaction networks of fern-feeding Coleoptera were the most specialized at family ($H2' = 0.40$) and genus level ($H2' = 0.65$), whereas 6 out of 10 most specialized insect families were Lepidoptera ($d' \geq 0.44$). At the genus level, all networks had a fern-biased asymmetry. Although fern-feeding generalists were common, few cases of coevolutionary radiation have been documented. We discuss the possible biases of our dataset, which also highlight gaps to perform future research, and suggest that many more phytophagous insects on ferns remain to be discovered, especially sap-sucking, gall-forming, and spore-feeding insects on modern fern groups.

Introduction

Herbivory is the process through which plant-feeding animals assimilate carbon and other nutrients into their bodies and food chains, and approximately 18% of all plant biomass is lost to herbivory in any given terrestrial environment (Cyr and Face 1993). Evidence of insect herbivory from plant fossils dates back to the late Silurian (Labandeira 2007), but most of the insect diversity developed together with a specialization of their mouthparts and in coevolution with their host plant species (Nel et al. 2018). About 40% of the 1.067 million described insect species are known to be herbivorous (Wiens et al. 2015), with some groups (e. g. Lepidoptera, Hemiptera) predominantly so. Insects are often highly specialized plant feeders, for example, gall-formers, and frequently radiated and co-evolved with their host plants (Whitney and Glover 2013). The ubiquitous nature of insects, found in all terrestrial ecosystems (Grimaldi and Engel 2005), implies that every plant species is the food source of at least one herbivorous insect species, and even when this herbivore has not been directly observed, its presence can be inferred by observing the damage caused to the plant tissues.

Ferns, however, have been considered in the past as well-defended, herbivore-resistant plants (Brues 1920). Historically, most ferns have been assumed to be of Paleozoic origins, to possess a low nutritional value, and to be well protected by high fiber and tannin content (Mehltreter 2010). However, most of the extant fern species evolved after the angiosperms (Schneider 2016), can have similar nutrient contents in their tissues as do angiosperms (Wright et al. 2004; Richardson and Walker 2010), and do not possess the most developed defense strategies (Farias et al. 2020). After a revision of the scientific literature,

several authors found about 400 fern-feeding insect species worldwide and concluded that this record of fern-insect interactions suffers from both sampling bias and insufficient data (Balick et al. 1978; Cooper-Driver 1978; Hendrix 1980). This bias may stem from the relatively low economic importance of ferns (Markham et al. 2006) because studies on the subcosmopolitan, invasive bracken fern (*Pteridium* spp.) found a large diversity of fern-feeding insects (e.g. Wieczorek, 2009), and a review of gall-formers reported increasing numbers of these highly specialized insects on ferns (Santos et al. 2019). Finally, terrestrial (Mehltreter and Tolome 2003) and epiphytic (Mehltreter et al. 2006) ferns had leaf damage similar to that of angiosperms, with 5-15% leaf area loss (Mehltreter 2010), and even leaf-cutter ants harvest leaves from some ferns to cultivate their symbiotic fungi (Farias et al. 2018). On the other hand, it has been suggested that insects co-evolved more successfully with flowering plants because these offer a wider selection of structural elements to exploit, such as flowers, fruits, seeds, and wood, so that the insect diversity on angiosperms should be expected to be much higher than on ferns (Hendrix 1980). However, even accounting for such a structural bias, at least 1500 to 3500 fern-feeding insects would remain to be discovered (Mehltreter 2010).

This study aimed to (1) review fern-insect interactions worldwide, (2) determine the identity of fern-feeding insects their possible preferences. In addition, we investigated (3) whether some fern-feeding habits were overrepresented when compared to the overall diversity, (4) whether some fern taxa were overrepresented as hosts to phytophagous insects, and (5) whether interaction networks differed in their asymmetry, nestedness, and specialization among the three main fern-feeding insect orders at the family and genus-level. Finally, we discuss possible research-oriented, taxonomic, or geographic biases of the current data set on fern-insect interactions.

Materials And Methods

The three most comprehensive review articles (Balick et al. 1978; Gerson 1979; Hendrix 1980) were used as a starting point. A literature search on the Web of Science (Clarivate®, 2021), spanning from 1981 to the present was performed applying the search string (fern* or pteridophyt*) AND (insect* or herbivore*) NOT (fossil). To this list, we added relevant references from the Annual Review of Pteridological Research (ARPR, 1994-2018) obtaining a total of 122 literature references (Appendix 1). Any reported interaction from non-phytophagous insect orders (e.g., Mecoptera, Psocoptera, and Odonata) were considered circumstantial (e.g., resting behavior or predators) and excluded from our analyses. For each reported fern-insect interaction, we retrieved the following data: fern and insect species, feeding habit (leaf-chewers and miners, gall inducers, stem and/or rachis borers, spore-feeders, rhizome feeders, and stem and/or leaf sap-suckers, modified from Balick et al. 1978) and the country/continent of interaction. We also included any new interactions found in cited literature or other entomological books. These data were captured and organized in a Microsoft Access database that was specifically developed for this purpose.

In this database, insects (excl. other arthropods such as mites) were cataloged and ordered according to the phylogeny of the *Tree of Life Web Project* (2002) and fern taxa (including lycophytes) following PPG I

(2016). All scientific names were verified and updated accordingly. Records of unidentified taxa were excluded from analyses at those taxonomic levels but retained for analysis at higher levels.

To determine significant differences between the numbers of observed and expected interactions of (1) fern families and (2) insect orders, we performed a chi-square test, assuming a random association between phytophagous insects and vascular plant species. The expected number of fern-feeding insects was estimated by multiplying the number of known herbivorous insect species in each insect order (according to Wiens et al., 2015 summing up 423,569 spp.) by the relative percentage of fern and lycophyte species (3.86%, 11,916 spp.; Schuettpelz et al., 2016) within all vascular plants (308,374 spp.) worldwide (Christenhusz and Byng 2016). Expected numbers of fern insects were calculated by multiplying the total number of fern-feeding insects by the relative species percentage of each fern family (according to PPG I, 2016).

Because fern defense syndromes are supposedly better adapted against leaf-chewers (Mehltreter et al. 2010; Farias et al. 2020), we expected an overrepresentation of sap-sucking Hemiptera and higher degrees of insect specialization in leaf-chewing insect orders Coleoptera and Lepidoptera (larvae), which cannot easily evade the chemical defenses of ferns. Consequently, we analyzed the nestedness, asymmetry, and specialization of interaction networks between the three dominant insect orders, generated interaction graphs, and calculated nestedness via NODF2, according to Almeida-Neto et al. (2008) with the 2.15 Bipartite package (Dormann et al. 2008) for R (ver. 2.3.2, R Development Core Team 2008). A higher nestedness implies an increasing number of interactions but few or even no group-specific interactions, i.e. insect specialists mainly interact with plant generalists and vice-versa (Bascompte et al. 2003; Bascompte et al. 2006). A nested network was considered where the NODF value observed for our network (NODF_{total}) was higher than predicted by the null model Ce (NODF(Ce)), with 1,000 randomizations for each network. The null model Ce corresponds to null model II of Bascompte et al. (2003). It assumes that the probability of an occurring interaction is proportional to the average number of interactions of both trophic levels (Bascompte et al. 2003). Network asymmetry was calculated according to Blüthgen et al. (2007), where $W = (I-F)/(I+F)$ with I (number of insects) and F (number of fern species). Positive values indicate a higher number of insects and negative values a higher number of ferns. To determine the level of group specialization, we calculated d' (Blüthgen et al., 2006). Higher d' values for each taxon within a trophic level indicate higher specialization, and that those taxa are more related to each other than to "outgroups" when compared with random or non-specialized patterns.

Results

Taxonomic distribution of fern hosts

Ferns and lycophytes of all 16 orders and 36 out of 43 families have been reported as hosts of 7 orders of herbivorous insects (Table 1). Although most fern families were exploited by insects, they varied considerably in the number of species interactions. For example, the family Dennstaedtiaceae, which

includes the well-studied bracken fern (*Pteridium* spp.), accounted for 16.3% of all reported interactions and was overrepresented when compared to a random distribution (Fig. 1). Other fern families with an overrepresentation of insect interactions were Equisetaceae, Salviniaceae, Onocleaceae, and Nephrolepidaceae. On the other hand, species-rich fern families with fewer insect interactions than expected were Dryopteridaceae (2115 fern spp., 12.0% of interactions), Polypodiaceae (1652, 5.8%), Thelypteridaceae (1034, 4.9%), and Cyatheaceae (643, 2.3%; Fig. 1). In contrast, for other species-rich fern families such as Pteridaceae (1211 spp.), Aspleniaceae (730), and Athyriaceae (650), observed and expected numbers of interactions did not differ significantly from a random distribution. Finally, families such as Lomariopsidaceae, Psilotaceae, and Saccolomataceae presented only one record each.

Taxonomic distribution of fern-feeding insects and their feeding habit

The orders Hemiptera, Hymenoptera, and Thysanoptera were over-represented on ferns, whereas Lepidoptera, Coleoptera, Diptera, and Orthoptera were under-represented (Fig. 1) when compared to a random distribution of all phytophagous species on all vascular plants. The most significant deviation from random distribution was observed for Hemiptera, which accounted for 36.6% (606/1462) of all fern-insect interactions (Table 1) and 29.1% of fern-insect species (236 spp.) but constitute only 18.8% (79,701 spp.) of all herbivorous insects (423,569 spp.; Wiens et al., 2015). Coleoptera, however, presented only 10.7% of fern-insect interactions (Table 1) and 15.4% of fern-insect species (125 spp.), but are the most species-rich insect group with 23.9% (101,268 spp.) herbivorous species (Wiens et al. 2015). Another insect order that was under-represented was Orthoptera. This order contains 22,400 phytophagous species, but only 1.1% of all fern-insect interactions and 1.5% of all fern-feeding insect species (12 spp.; Fig. 2).

Although most fern-insects were leaf-chewers (55.0%), sap-sucking insects (29.1%) were overrepresented with more than 50% above the expected number (19.0% of all herbivorous insect species; Table 2). Unique substrates of ferns such as spores were less commonly exploited (6.5%), mainly by Stathmopodidae (Lepidoptera) and Miridae (Hemiptera). Two feeding habits that have been commonly reported as highly specialized, gall-inducers and leaf-miners comprised 6% (Table 2). Gall inducers were comprised primarily of Cecidomyiidae (Diptera) whereas leaf miners came mainly from Agromyzidae and Anthomyiidae (Diptera). Underground organs such as rhizomes and roots were rarely ingested (0.7%) by four Hepialidae, one Noctuidae (Lepidoptera), and one Pseudococcidae (Hemiptera; Table 2).

Predominant insect families on ferns

Species of 14 families of Coleoptera utilize ferns as a food source, but two families account for most fern-feeders: Chrysomelidae and Curculionidae, exploit together 15 fern families as food (Fig. 3). The latter family was the only one found on Aspleniaceae, Blechnaceae, Dryopteridaceae, and Marsileaceae,

whereas Chrysomelidae was the only beetle family reported on Dicksoniaceae, Gleicheniaceae, Saccolomataceae, and Thelypteridaceae. Finally, Elateridae were found exclusively on Lygodiaceae, and Cerambycidae and Scirtidae (reported as Helodidae, Balick et al., 1978), on Dennstaedtiaceae, the best-studied fern family (Fig. 3). This last record, however, is still awaiting confirmation of herbivory.

For Lepidoptera, we found evidence of 293 fern-feeding species across 16 butterfly and moth families. Most interactions have been reported for Noctuidae, Pyralidae, Geometridae, Tortricidae, Crambidae, and Stathmopodidae (Fig. 4). It should be noted that Erebidae was only recently separated from Noctuidae (Zahiri et al. 2011) and so it is likely that some older records of Noctuidae refer to species now placed in Erebidae. Nearly all fern families were exploited by several families of Lepidoptera, except Salviniaceae for which only Pyralidae have been reported thus far.

Seventeen families of Hemiptera contained fern-feeding species. Most records belonged to Aphididae, Miridae, Diaspididae, and Coccidae (Fig. 5). Most fern families were exploited by several families of Hemiptera with exception of Psilotaceae, Marattiaceae, Anemiaceae, Lomariopsidaceae, and Oleandraceae, each with a single record (Fig. 5).

Specialization of fern-feeding insects

The interaction network analysis showed that insect families had very different levels of specialization. Within Lepidoptera, we found the highest levels of insect specialization on ferns (e.g., Nymphalidae; Table 3). Six out of 10 families with the highest d' values belonged to Lepidoptera, but only two to Hemiptera. At the generic level, 31.2% (109 out of 349) had d' values ≥ 0.5 indicating some degree of specialization (Table 3).

In the overall network, specialization was highest at the genus level (Tables 4, 5), especially in Coleoptera, whereas the highest nestedness (NODF2) was observed at the family level, where most of the interactions occurred with fern families Dennstaedtiaceae, Dryopteridaceae, Pteridaceae, and Polypodiaceae (Figs. 3, 4). Web asymmetry also differed considerably depending on the analyzed taxonomic level. Insect genera were far more diverse than fern genera (positive web asymmetry). On the other hand, the web asymmetries within each insect order were negative at the family level (Table 4) with more fern families than insect families.

Geographic distribution of fern-insect interactions

Most fern-insect interactions have been observed in Asia (32.4%), America (32.2%), and Europe (26.1%). The remaining interactions were reported from Oceania (7.6%) and Africa (1.8%; Fig. 6). Reports of fern-feeding Lepidoptera and Coleoptera came mainly from America, whereas Hemiptera have been registered far more in Europe and Asia. From Oceania, there are several reports of Lepidoptera, Hemiptera, and

Coleoptera, whereas from Africa the low number of fern-insect interactions indicates a possible lack of data (Fig. 6).

Discussion

We found bibliographic evidence for 809 fern-feeding insect species, nearly twice as much as the 420 species reported in the last compilation by Balick et al. (1978). Even with this reported increase in the number of interactions, we assume that the study of fern-insect interactions is still in its beginnings. Currently, we know of 423,569 phytophagous insect species (Wiens et al. 2015) feeding on 308,374 vascular plant species (Christenhusz & Byng, 2016) of which 3.86% are ferns (PPG I, 2016). Based only on our current knowledge, we would expect that each vascular plant is attacked by an average of 1.37 insect species and that at least 16,000 insect species may feed on ferns alone. Even if we assume that flowering plants may attract more insect species, because of their larger diversity of morphological and reproductive structures (Balick et al. 1978; Hendrix 1980; Mehltreter 2010), many more fern-feeding insects remain to be discovered.

Recent time-calibrated phylogenies suggest that the first ferns and insects had already evolved during the Silurian (431 mya, Testo & Sundue, 2016) and Ordovician (479 mya; Misof et al., 2014). According to these studies, leptosporangiate ferns originated 357 mya and the order Polypodiales (modern ferns) 290 mya (Testo and Sundue 2016), whereas flying insects (Pterygota) evolved as early as 406 mya. Because of the old phylogenetic origin of ferns and their long evolutionary coexistence with insects, Brues (1920) was surprised by the few reported fern species serving as host plants for insects, expecting exactly the opposite pattern. However, since Schneider et al. (2004) it became clear that 90% of extant fern lineages are comprised of groups of much more recent phylogenetic origin (e.g., Polypodiales), and may have evolved even later in the shade of angiosperm evolution. In recent contributions, several authors have found examples of fern-insect coevolution occurring in some insect groups with different feeding habits such as spore-feeding microlepidoptera (Oecophoridae, Sawamura et al., 2009), sap-sucking-bugs (Miridae, Konstantinov & Knyshov, 2015), and leaf-chewing sawflies (Symphyta Isaka & Sato, 2014, 2015; Schneider, 2016). Host plant switching from older fern taxa or angiosperms to more modern fern groups must have occurred before such newer adaptive radiations. Because of the co-occurrence of host plant switching and coevolutionary radiation, we did not find a clear pattern in our network analyses between the evolutionary age of fern hosts and their phytophagous insect groups. For instance, in Coleoptera only Chrysomelidae and Curculionidae were well represented as fern-feeders, feeding on a wide range of 11 and 9 fern families, respectively (Fig. 3). This result suggests that these fern-feeders are generalists with a wide spectrum of host plants or specialists that have radiated after host plant switching. Each insect group must be analyzed to decide which explanation is valid. In Lepidoptera (Fig. 4), a similar case can be made with Noctuidae and Stathmopodidae. However, in the latter family, we frequently find more specialized spore-feeders (Sawamura et al. 2009), indicating a possible case of host plant switching and further specialization. Hemiptera, Aphididae, and Miridae were the most common fern-feeders (Fig. 5). Whereas most aphids are known to be generalists (Ali and Agrawal 2012), for Miridae it has been shown that coevolution has been occurring on ferns (Konstantinov and Knyshov 2015). Finally, for insect

families of the three orders with few reported fern-feeders, more data are needed to draw any further conclusions about their degree of specialization.

In our network analyses, we found several patterns that point to the specialization of interactions at different taxonomic levels. For example, the relatively high nestedness values at the family level indicated the specialization of fern-feeding insects and their host plants, which has also been reported in previous studies (Jensen and Holman 2000; Konstantinov and Knyshov 2015). Nestedness was partly influenced by fern and insect families with abundant records of interactions. In these cases, the elevated nestedness (NODF2) represented a higher frequency of insects feeding on a single fern family. Specializations at the genus (Shen and Hsu 2020) or even species-level (O'Brien 2009) were documented as well, but require much more comprehensive case studies across the biogeographic range of host plants and phytophagous insect species to draw any final conclusions (Novotny et al. 2010). With our current knowledge on fern-insect interactions, specialization peaked at the genus level where our dataset had the highest resolution (e.g., largest number of identified taxa of ferns and insects). At the species level, where single-observations were most common, data resolution is simply insufficient to detect any specialization. Low nestedness values (NODF2) at the genus level, however, may also demonstrate that many fern-feeding insect species can exploit several host genera (Table 5). Although the conclusions from the network analyses of our data set are still very limited due to the lack of more comprehensive information, they can serve as a baseline for further research. Future studies have to consider important variables such as genetic distance between interacting species, feeding guilds (Cagnolo et al. 2011), temporal habitat dynamics such as seasonality, resource abundance (López-Carretero et al. 2014), and ecological succession. For instance, some invasive fern species such as *Pteridium* and *Lygodium* invade disturbed habitats (Akomolafe and Rahmad 2018) and Lepidoptera are some of the first herbivores to recolonize recently-disturbed habitats (Villa-Galaviz et al. 2012). Numerous studies have focused on this kind of interactions, but their outcome might not be comparable with natural undisturbed environments because in areas that are dominated by pioneer plants the connectance and nestedness of plant-insect interactions were severely diminished (Araújo 2016; Ximenes Pinho et al. 2017), as observed at the genus and species level in our study.

The few studies that have focused on fern-insect interactions can provide us with direct insights into the different degrees of specialization in fern-feeding insects. O'Brien (2009) described a new beetle species, *Notioides sporocarpicus*, feeding on the sporocarps of *Marsilea mollis*, an aquatic fern. Although this curculionid can feed on other plant species as well, its specific diet and behavior of pupating within the sporocarp point to an ongoing higher specialization. On the other hand, because of their unique diet, spore-feeding Stathmopodidae could be assumed to possess a high degree of host specialization, but in fact, the specialization is focused on fern spores as a whole, not towards a specific fern genus or family (Park et al. 2018; Shen and Hsu 2020; Wang et al. 2020). More importantly, the spore-feeding taxa are nested among several angiosperm-feeders, indicating several events of host plant switching (Muggleston 1989; Sugiura and Yamazaki 2004; Wang et al. 2020). Finally, other studies indicate cases of adaptive radiation and coevolution of fern-insects after host plant switching. Over 90% of the sawfly genera (Hymenoptera, Symphyta) feed only on one of the major clades of vascular plants: conifers, monocots,

eudicots, or ferns (Schneider 2016). Two of the three clades of fern-feeding genera (Heptamelidae and Selandriineae) may have switched from angiosperms to ferns, because they have evolved after the evolution of angiosperms, and the subfamily Selandriinae diverged at the same time as their host plants in the monocots and ferns (Isaka and Sato 2014; Isaka and Sato 2015). In fern-feeding aphids, 15 of 16 species belong to a monophyletic clade that has evolved after host plant switching (Jensen and Holman 2000), and in Miridae (Hemiptera) 9 out of 12 species form a monophyletic clade of fern-feeders (Konstantinov and Knyshov 2015).

The previous examples have shown that fern-insect coevolution has occurred in insect clades with different feeding habits. This seems counterintuitive at the first sight because ferns defend themselves with an array of ecological, biochemical, and morphological traits (Farias et al. 2020) to which insects have to adapt when selecting their host plants (Thorsteinson 1960). For instance, Orthoptera feed mainly on grasses (Joern 1979) and one would expect that fern species to which they have switched might have similar defense syndromes as their original host plants. More important than a generalized preference for a taxonomic plant group, diversification and specialization differ according to the feeding habit and plant organ exploited by the herbivore (Novotny et al. 2010). External leaf chewers such as Coleoptera and Lepidoptera, besides being the most common type of herbivore, tend to be more generalists (Novotny et al. 2010) because they are confronted with a whole array of chemical defenses since leaves are the most chemically complex plant organ, responding physiochemically not only to the amount of ambient light (Sedio et al. 2017) but also altering their biochemical makeup when exposed to herbivore damage (Hay and Brown 1992).

Sap-feeders (i.e. Hemiptera) occupy all ends of the specialist-generalist spectrum, showing only a negative correlation between body size and host-specificity (Novotny and Basset 1999). The low specialization score of sap-feeders found in our study may be due to the abundance of Aphididae (43.5% of all sap-feeders), a family composed primarily of generalist insects that induce low-levels of chemical defense responses in target plants (Ali and Agrawal 2012). Ferns possess a large array of mechanical and general chemical defenses such as fibers and tannins, which are directed against leaf-chewing insects but practically useless and easily evaded by sap-sucking herbivores (Mehlreter, 2010). Under greenhouse conditions aphids often thrive and can be abundant on ferns, indicating that ferns are not as toxic as sometimes suggested. Indeed, ferns often do not invest in metabolically expensive chemical defenses but rather respond to leaf damage with stronger growth (Mehlreter, 2010; Mehlreter & García-Franco, 2008). For sap-feeding insects this kind of herbivore tolerance by ferns is beneficial (Zvereva et al. 2010), because they do not have to deal with toxic responses to their attack. However, to our knowledge, no studies have been undertaken to investigate the chemical responses of ferns to sap-sucking insects. Despite our exhaustive revision, we still assume that some of the results might be prone to research-oriented and/or geographic biases, especially when compared to the more comprehensive data available for angiosperm-feeding insects. Following Hendrix (1980), we assume the following possible biases: (1) one-sided research approaches that focus either on botanic or entomological studies, (2) specific applied research interests such as the search for biological control organisms against invasive ferns, (3) the interest of horticulturists to control pests of ornamental ferns, and (4) geographic

biases because of the concentration of research institutes in countries with temperate climates while ferns and insects are more diverse in tropical countries where less research is performed.

The first bias is the consequence of a one-sided research emphasis, focused on only one part of the interaction. For instance, pteridologists tend to focus their research on the fern species and may investigate leaf damage, but often fail to identify the involved insect species (Patra and Bera 2007; Santos et al. 2019). Conversely, and far more frequently, entomological literature describes the insect part of the interaction in great detail, but does not pay much attention to the fern host (Mukhopadhyay and Thapa 1994; Isaka and Sato 2015). Clearly, information is left out in these one-sided research projects and maybe even useless for the exploration of fern-insect interactions. The second bias can result from a few intensively studied, specific subjects. This approach often provides very detailed information on ferns and insects. However, the search for biological control organisms against weedy, invasive fern species such as *Pteridium* spp., *Salvinia* spp. and *Lygodium* spp. constitute 16.8% of all records but are focussed only on these three fern genera. Moreover, biological control of *Lygodium* spp. was also quickly restricted to the most promising control organisms, insects in six genera of crambid moths. The same is true for the third bias, the great horticultural interest in identifying and fighting common greenhouse pests on cultivated ferns *ex-situ* (e.g., *Dryopteris filix-mas*). Balick et al. (1978) found a disproportionate number of hemipteran herbivores in greenhouses (17 out of 20 records). In our study, 382 out of 443 insect records on popular cultivated ferns (*Adiantum*, *Asplenium*, *Davallia*, *Dryopteris*, *Nephrolepis*, and *Platyserium*) were either Hemiptera, Lepidoptera, or Thysanoptera. For the UK, we retrieved 100 insect records on 67 fern species. However, when non-native ferns were removed (i.e., cultivars or naturalized species), only 18 insect species records on 31 fern species remained, a reduction of 82% and 54%, respectively. A fourth, geographic bias might be the consequence of more complete plant and insect collections of some countries in temperate climates, but with much less diverse flora and fauna. In some way, this bias can also be considered an advantage. A relatively complete sampling of fern-insect interactions under such circumstances should be much easier to achieve and may allow us to draw more detailed conclusions about the relative proportions of fern insects and their feeding preferences in temperate climates, although these numbers underestimate the global diversity of fern insects. For instance, North American reports (USA and Canada) contributed 27.1% of fern-insect records, although this region has only 557 fern species (Moran and Labiak 2015). In contrast, Latin America comprised only 5.2% of the interaction records but encompasses an estimated 4000-5000 fern species. Consequently, fern-rich countries such as Colombia (1689 spp., Bernal et al., 2016), Ecuador (1475 spp., Jørgensen & León-Yáñez, 1999), and Brazil (1403 spp., Flora Do Brasil 2020, 2021) must be undersampled. Furthermore, we found a large number of fern-feeding Hemiptera but a much smaller number of Lepidoptera for Asia than for the Americas (Fig. 6). Because the fern diversity of Asia is as high or even higher than of the Americas (Morin et al. 2015), there is no reason to expect such pronounced differences, unless entire insect groups have only radiated in the Neotropics, which seems unlikely. Finally, with our much-improved knowledge on fern floras, entomologists should find it easier to identify ferns as host plants and interdisciplinary research such as on fern-insect interactions should benefit from this botanical progress.

Declarations

Acknowledgments

We thank Elda Catalina Flores-Galván for her assistance in data capture.

Funding: Research was funded by the Instituto de Ecología A.C. (projects 20030-10796 to KM and 20030–10128 to VHO). JFJ thanks CONACyT for his doctorate scholarship (no. 589325).

Conflicts of interest/Competing interests: The authors declare no conflicts of interest nor competing interest.

Availability of data and material (data transparency): All used references are given in appendix 1. The used data matrix will be made available on request, added as appendix 2 or uploaded to a data server in response to the editor's preference.

Code availability: N/A

Authors' contributions (optional: please review the submission guidelines from the journal whether statements are mandatory)

Consent to participate: All participants agreed to be listed as authors.

Consent for publication: All authors agreed with the content of the final version and its submission to Plant Ecology.

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Tables

Table 1. Number of species interactions per phytophagous insect order and fern and lycophyte family. Maximum values for each fern and lycophyte family are highlighted in bold.

Family	Insect order							
	Coleo- ptera	Di- ptera	Hemi- ptera	Hymeno- ptera	Lepido- ptera	Ortho- ptera	Thysano- ptera	Total
Lycopods								
1. Lycopodiaceae					3			3
2. Isoetaceae		1			4			5
3. Selaginellaceae		2	4		16		1	23
Ferns								
4. Anemiaceae			3					3
5. Aspleniaceae	12	5	33		18		2	70
6. Athyriaceae		10	38	12	15			75
7. Blechnaceae	6	4	26	2	11	0	2	51
8. Cibotiaceae			6		2	4	1	13
9. Cyatheaceae	8	5	8	1	12			34
10. Cystopteridaceae	1	2	8					11
11. Davalliaceae		1	7		1		1	10
12. Dennstaedtiaceae	20	17	49	29	119	2	3	239
13. Dicksoniaceae	3		4		3			10
14. Diplaziopsidaceae					2			2
15. Dryopteridaceae	9	12	80	13	61		1	176
16. Equisetaceae	18	3	15	16	3			55
17. Gleicheniaceae	1		11	1	7		2	22
18. Hymenophyllaceae		2	3					5
19. Lindsaeaceae				1		1		2
20. Lomariopsidaceae			1					1
21. Lygodiaceae			2	2	13			17

22. Marattiaceae		2	1	1	2			6
23. Marsileaceae	3		4	1	2			10
24. Nephrolepidaceae	2	1	15		10			28
25. Oleandraceae			2					2
26. Onocleaceae		2	8	4	15			29
27. Osmundaceae		2	2		17		1	22
28. Plagiogyriaceae			3		1			4
29. Polypodiaceae	4	11	38	2	24		7	86
30. Psilotaceae			1					1
31. Pteridaceae	8		76		48	1	4	137
32. Saccolomataceae	1							1
33. Salviniaceae	10		5		23	3		41
34. Tectariaceae			7		3			10
35. Thelypteridaceae	4	1	39	15	14			73
36. Woodsiaceae			3		1			4
37. Unidentified	47	2	104	1	20	5	2	181
Total	157	85	606	101	470	16	27	1462

Table 2. Relative frequency of 809 fern-feeding insects grouped by feeding habit and insect order. The most important feeding habits for each insect order are formatted in bold.

Insect order	Leaf chewers	Leaf miners	Gall inducers	Stem/ rachis borers	Spore feeders	Rhizome feeders	Stem/leaf sapsuckers
Orthoptera	1.5%			-	-	-	-
Thysanoptera	2.0%		0.2%	-	-	-	-
Hemiptera			0.2%	-	3.6%	0.1%	29.1%
Hymenoptera	6.9%		0.5%	0.1%	0.1%	-	-
Coleoptera	13.5%	0.1%		1.2%	0.5%	-	-
Lepidoptera	30.8%	0.9%	0.4%	1.2%	2.2%	0.6%	-
Diptera	0.4%	2.0%	1.7%		0.1%	-	-
Total	55.0%	3.0%	3.1%	2.6%	6.5%	0.7%	29.1%

Table 3. Ten fern-feeding insect families (A) and genera (B) with highest d' values

A) Insect families	B) Insect genera
Nymphalidae = 0.83	<i>Caribovia</i> = 1.00
Gryllidae = 0.78	<i>Eoparargyactis</i> = 1.00
Cydnidae = 0.58	<i>Eudonia</i> = 1.00
Pergidae = 0.58	<i>Paradetis</i> = 1.00
Cryptophagidae = 0.56	<i>Xenotrachea</i> = 1.00
Tischeriidae = 0.53	<i>Paratrigonidium</i> = 0.87
Crambidae = 0.48	<i>Ripersia</i> = 0.87
Cixiidae = 0.45	<i>Tongeia</i> = 0.87
Aleyrodidae = 0.44	<i>Catoptria</i> = 0.87
Tropiduchidae = 0.44	<i>Agromyza</i> = 0.87

Table 4. Network-level interaction metrics for three insect orders between insect families and fern families.

Insect order	H2'	Connectance	NODF2	Insect families	Fern families	Web asymmetry
Coleoptera	0.40	0.19	44.80	9	16	-0.28
Hemiptera	0.21	0.21	53.48	17	31	-0.29
Lepidoptera	0.30	0.18	46.35	24	28	-0.08
All orders	0.24	0.14	43.37	64	36	0.28

Table 5. Network-level interaction metrics for three insect orders between insect genera and fern genera.

Insect order	H2'	Connectance	NODF2	Insect genera	Fern genera	Web asymmetry
Coleoptera	0.65	0.05	3.51	41	30	0.15
Hemiptera	0.21	0.04	14.98	91	89	0.02
Lepidoptera	0.32	0.02	9.76	164	73	0.38
All orders	0.28	0.02	9.81	349	123	0.48

Figures

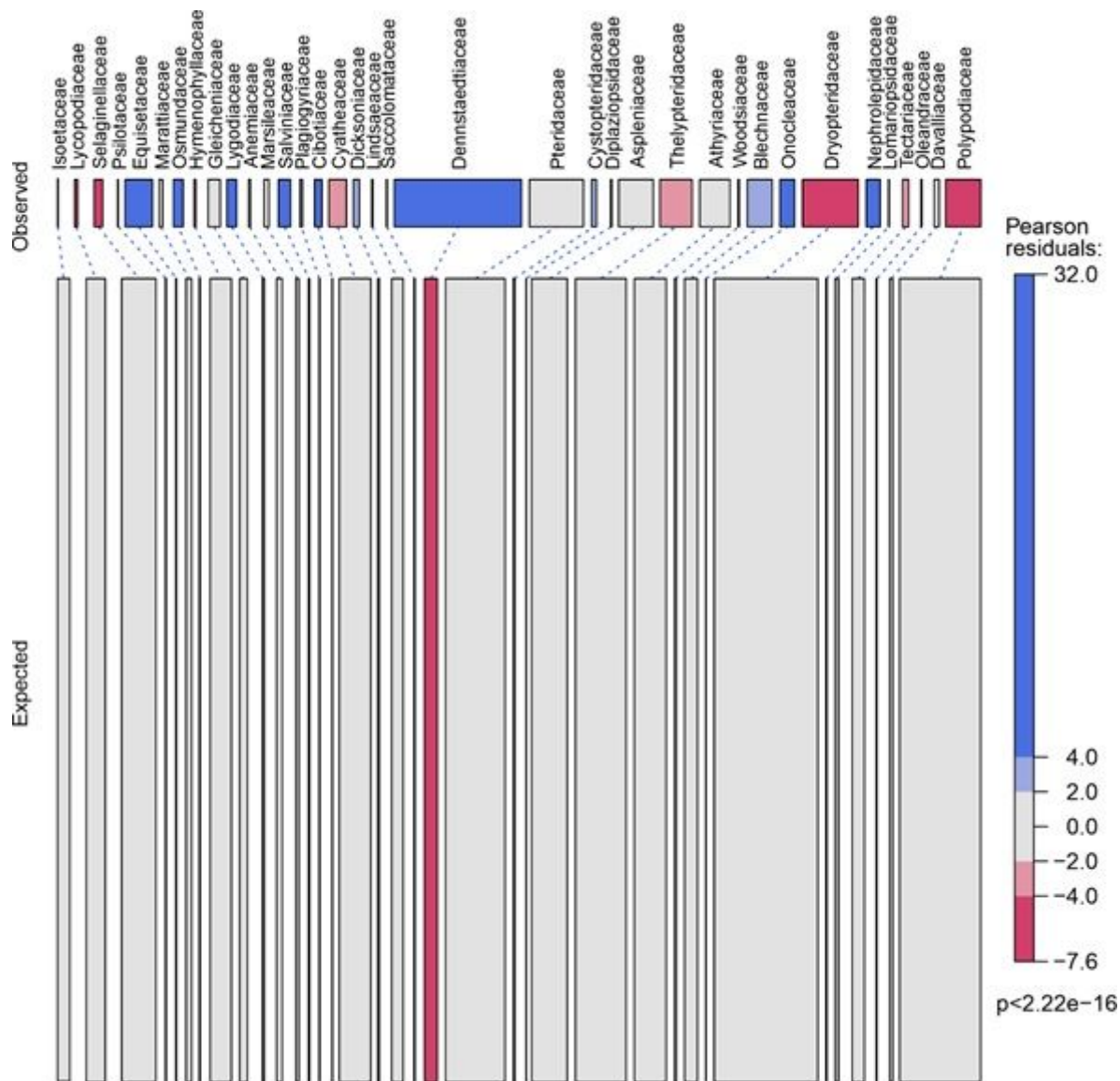


Figure 1

Observed and expected number of phytophagous insects in each fern and lycophte family. Colors indicate families with significantly over- (blue) or underrepresented (red) numbers of insects (Pearson residuals of Chi-square test).

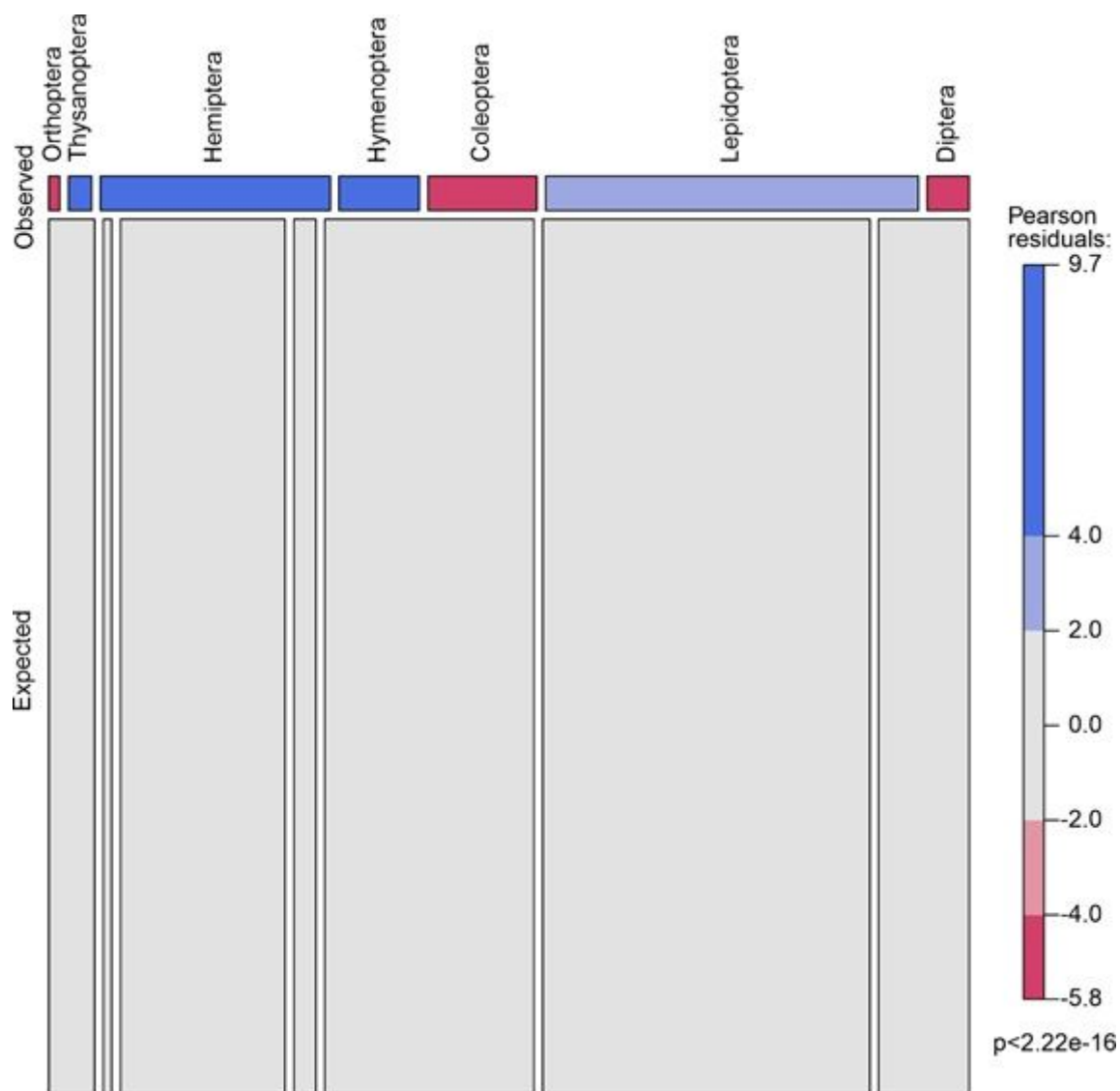


Figure 2

Observed and expected numbers of fern-feeding species by insect order. Colors indicate significantly over- (blue) and underrepresented (red) insect orders (Pearson residuals of Chi-square test).

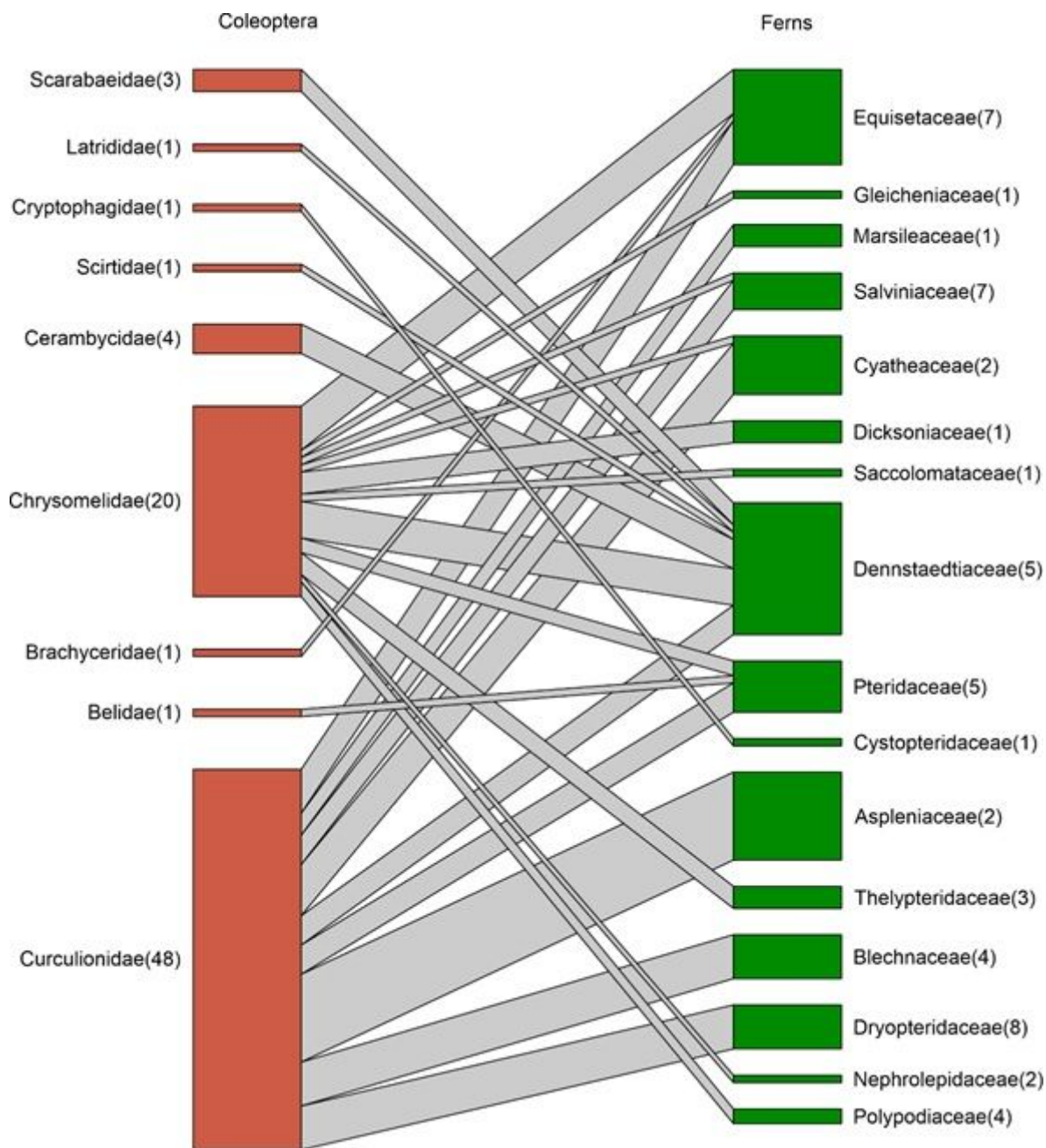


Figure 3

Species-interaction network between families of Coleoptera (80 spp., left) and ferns (54 spp., right), both in phylogenetic order from top to bottom. Species numbers are given within parentheses. Forty-five species of Coleoptera were discarded from this network because of interactions with unidentified ferns.

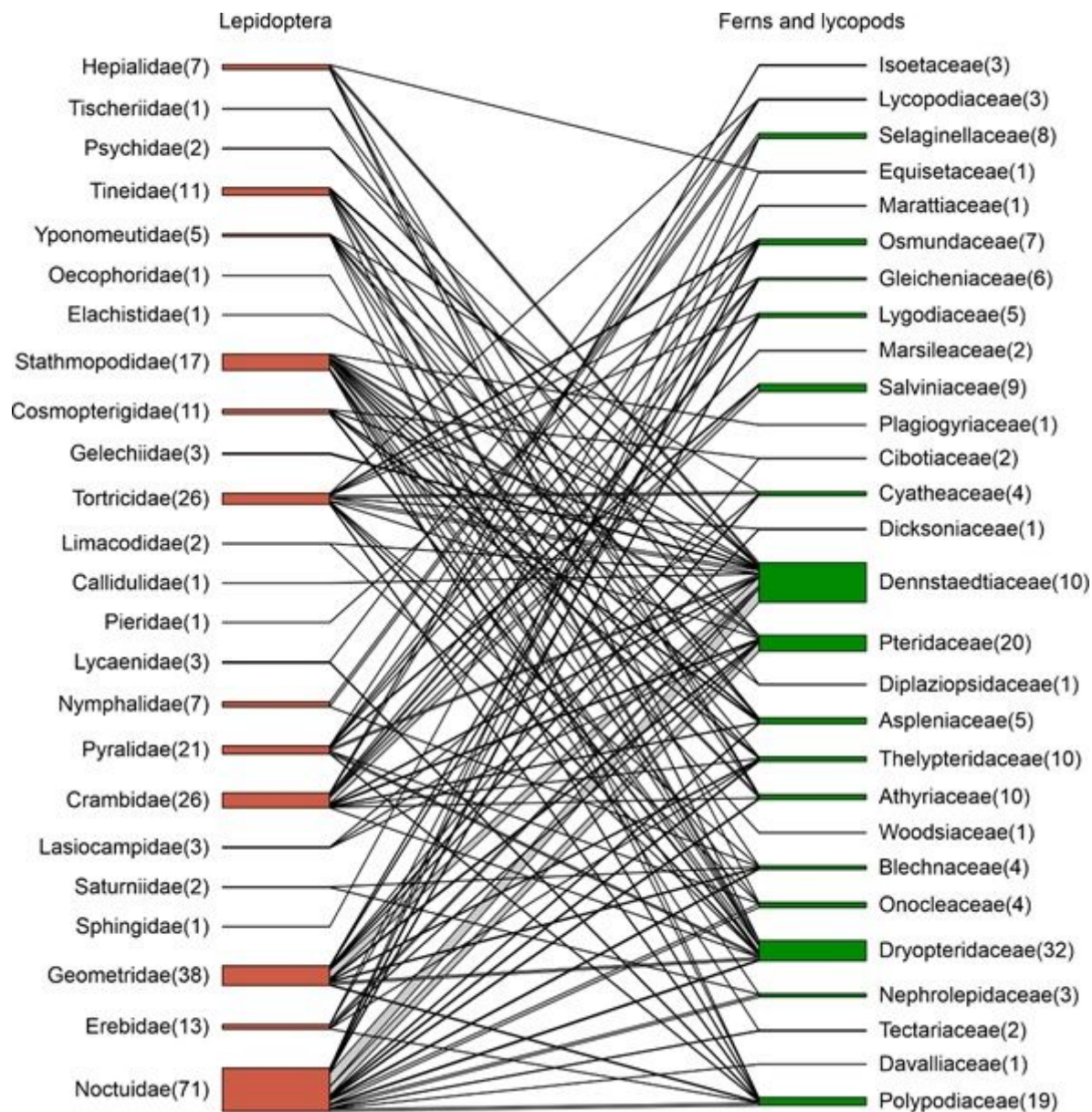


Figure 4

Species-interaction network between families of Lepidoptera (274 spp., left) and ferns and lycophytes (175 spp., right), both in phylogenetic order from top to bottom. Species numbers are given within parentheses. Nineteen species of Lepidoptera were discarded from this network because of interactions with unidentified ferns.

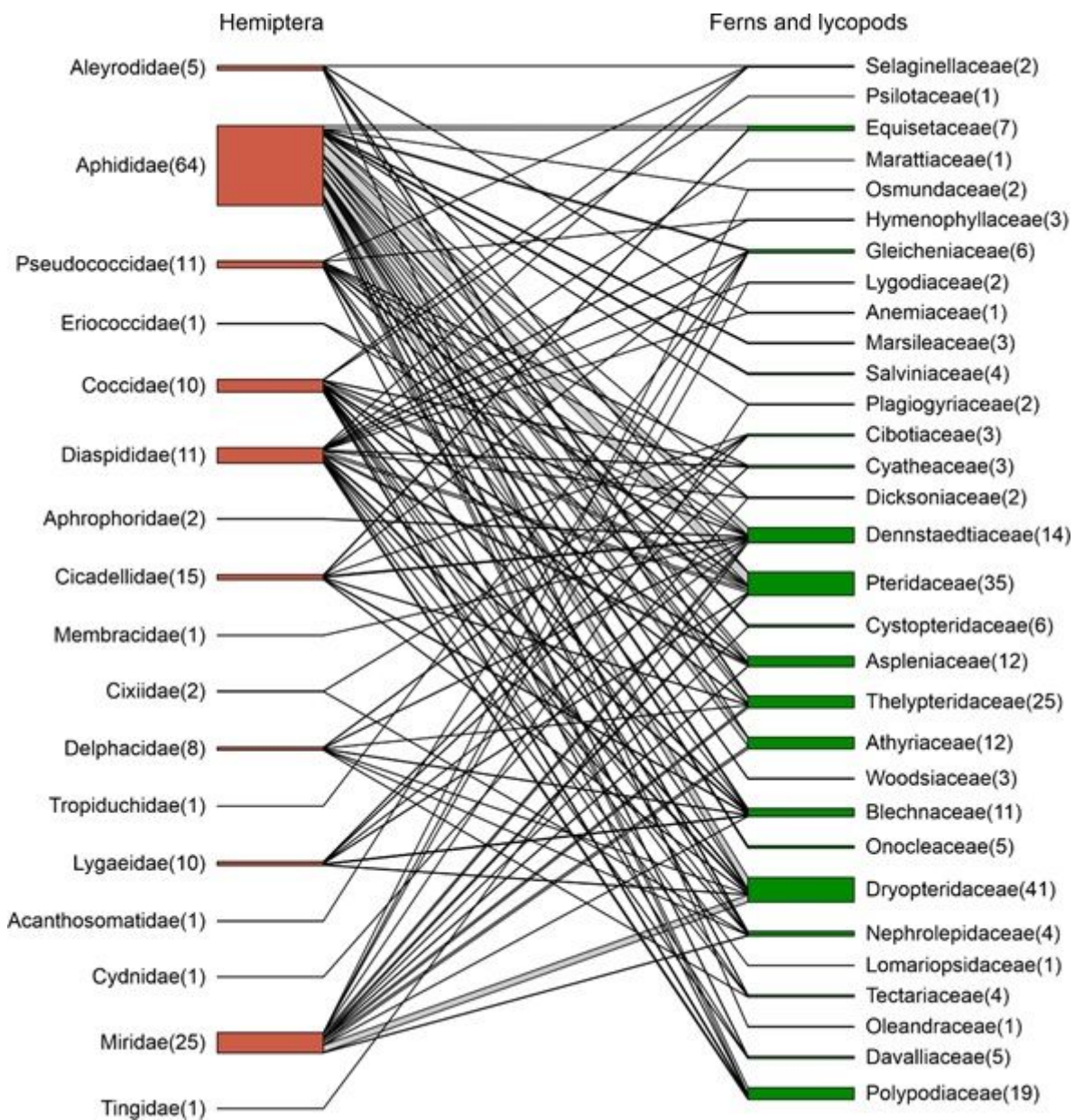


Figure 5

Species-interaction network between families of Hemiptera (169 spp., left) and ferns and lycophytes (240 spp., right), both in phylogenetic order from top to bottom. Species numbers are given within parentheses. Ninety-nine species of Hemiptera were discarded from this network because of interactions with unidentified ferns.

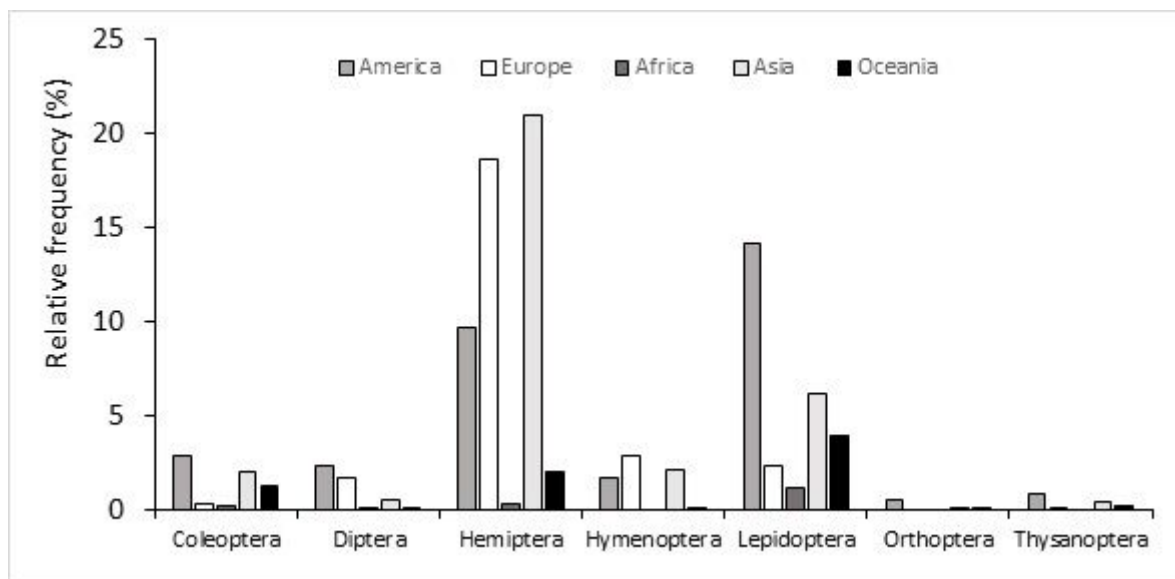


Figure 6

Geographic distribution of observed fern-insect interactions indicating possible biases.

Supplementary Files

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- [Appendix1.docx](#)