A global review and network analysis of phytophagous insect interactions with ferns and lycophytes

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Abstract  Ferns and lycophytes are the second and third largest lineages of vascular plants, yet our understanding of their interactions with phytophagous insects is very limited. In this study, we reviewed herbivorous insects, their feeding habits and host preferences on these two plant groups, searched for any evidence of coevolution, and discussed possible biases of our current knowledge on fern–insect interactions. We analyzed 2318 records of fern–insect interactions from 122 literature sources, based on the feeding habit of insects, fern taxa, and geographic location. We report interactions comprising 809 insect species (mainly Hemiptera, Lepidoptera, and Coleoptera) and 382 fern species (mainly Dennstaedtiaceae, Dryopteridaceae, and Pteridaceae). Leaf-chewers comprised 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 network was not significantly nested and had relatively low levels of specialization ($H_2^0 = 0.24$). The interaction networks of Coleoptera were the most specialized at family ($H_2^0 = 0.40$) and genus level ($H_2^0 = 0.65$), whereas six out of 10 most specialized insect families were Lepidoptera ($d^0 = 0.44$). At the genus level, all networks had a plant-biased asymmetry. Although insect specialists were common, few cases of coevolutionary radiation have been documented. We discuss the possible biases of our dataset, which also highlight gaps to fill in future research and suggest that many more fern-feeding insects remain to be discovered, especially sap-sucking, gall-forming, and spore-feeding insects on modern fern groups.

Keywords  Herbivory · Host-plant selection · Pteridophytes · Spore feeders · Network analysis

Introduction

Herbivory is the process through which plant-feeding animals assimilate carbon and other nutrients into their bodies, 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 that have frequently radiated and co-evolved with their host plants (Whitney and Glover 2013). The ubiquitous nature of insects in all terrestrial ecosystems (Grimaldi and Engel 2005) and the common observation of insect-damaged plant tissues imply that every plant species may serve as a food source of at least one herbivorous insect species.

Ferns and lycophytes, however, have been considered in the past as well-defended, herbivore-resistant plants (Brues 1920). Historically, most species 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). While lycophytes are of ancient origins, most of the extant fern species evolved after the split of seed plants and ferns (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, such as herbivore-induced defenses (Schoonhoven et al. 2005; Farias et al. 2020). The last reviews on fern–insect interactions reported about 400 fern-feeding insect species worldwide and concluded that their findings suffer from both sampling bias and insufficient data (Balick et al. 1978; Gerson 1979; Hendrix 1980). This bias may stem from the relatively low economic importance of most ferns (Markham et al. 2006) because in-depth studies of the common invasive bracken fern (Pteridium spp.) found a large diversity of fern-feeding insects (e.g., Wieczorek 2009). An updated review of gall-formers also reported increasing numbers of these highly specialized insects on ferns (Santos et al. 2019). Finally, leaves of terrestrial (Mehltreter and Tolome 2003) as well as epiphytic (Mehltreter et al. 2006) ferns and angiosperms suffer similar damages of 5–15% (Mehltreter 2010) indicating no major differences between the major vascular plant lineages. 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 diversity of herbivorous insects on angiosperms should be expected to be much higher than on ferns and lycophytes (Hendrix 1980). However, even accounting for such a structural bias, at least 1500 to 3500 fern-feeding insects likely remain undiscovered (Mehltreter 2010).

This study aimed to (1) review fern (and lycophyte)–insect interactions worldwide and (2) determine which herbivorous insects feed on ferns and may have developed feeding preferences on specific fern taxa. In addition, we investigated (3) whether some fern-feeding habits were overrepresented when compared to the global insect herbivore 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. The network analyses also allow the comparison with other studies and changes in network compositions after integration of future discoveries and resume the complex relationships instead of simple tabular listings used in previous reviews (such as Balick et al. 1978). 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 pteridophyte*) 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). Additional records came from entomological books and literature not included in previous reviews. Any reported interaction from non-phytophagous insect orders (e.g., Mecoptera and Odonata) was considered circumstantial (e.g., resting behavior or predators) and excluded from our
analyses. For each reported fern– and lycophyte–insect interaction, we retrieved the following data: plant 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.

In this database (Fuentes-Jacques et al. 2021), 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 (2016). In the remainder of the text, we use the terms fern-feeding or fern–insect interactions always referring to lycophytes as well. 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) plant families and (2) insect orders, we performed a Chi-square test, assuming that each of the 308,374 vascular plant species (Christenhusz and Byng 2016) has the same chance to be randomly exploited by the 423,569 herbivorous insect species (according to Wiens et al. 2015). Based on this average of 1.37 phytophagous insects per vascular plant species, we expected 16,367 insects to feed on the 11,916 species of ferns and lycophytes (3.86% of vascular plants; PPG I 2016). For each phytophagous insect family/order and fern/lycophyte family, the number of expected fern– and lycophyte–insect associations can be calculated according to the number of species in each family/order.

Because fern defense syndromes are supposedly better adapted against leaf-chewers (Mehltreter et al. 2010; Farias et al. 2020), we expected within the three most dominant insect orders (Hemiptera, Coleoptera, and Lepidoptera) 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 and generated interaction graphs. We calculated nestedness via NODF2, according to Almeida-Neto et al. (2008) with the 2.15 Bipartite package (Dormann et al. 2008) for R (ver. 4.0.2, R Core Team 2021). A higher nestedness implies an increasing number of interactions but few or even no group-specific interactions (i.e., specialist insects mainly interact with generalist plants and vice-versa; Bascompte et al. 2003, 2006). A network was considered significantly nested when the NODF value observed for our network (NODF_total) was higher than predicted by the null model Ce (NODF(Ce)), with 1000 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. Connectance \( (C = L/(I \times F)) \) is defined as the number of observed links (L) divided by the number of all possible interactions between both trophic levels \( (I \times F) \); Blüthgen et al. 2008). Higher connectance values describe networks where many insect species interact with a large number of ferns. To determine the level of group specialization, we calculated \( d' \) and \( H_2' \) (Blüthgen et al. 2006). While \( d' \) measures the specialization within a network, \( H_2' \) is an indicator of specialization across an entire network. Both values range on a scale between 0 and 1, where higher values describe a higher degree of specialization (Blüthgen et al. 2006).

Results

Taxonomic distribution of fern and lycophyte hosts

In our bibliographic review, we found evidence for 809 insect species that were recorded to feed on ferns and lycophytes. If all known phytophagous insect species would feed equally on all vascular plant species (mean of 1.37 insects per plant), we would expect that ferns and lycophytes are the food source of at least 16,000 insect species. Thus, our current dataset would document only 5% of the expected total. In our study, ferns and lycophytes of all 14 orders and 39 out of 51 families have been reported as hosts of seven orders of herbivorous insects (Table 1). Although most
Table 1 Number of species interactions per phytophagous insect order and fern and lycophyte family

| Family          | Insect order | Total |
|-----------------|--------------|-------|
|                 | Coleoptera   | Diptera | Hemiptera | Hymenoptera | Lepidoptera | Orthoptera | Thysanoptera |
| Lycophods       |              |        |           |             |             |            |              |
| 1. Lycopodiaceae|              | 3      | 5         | 16          | 330         | 11         | 23          |
| 2. Isoetaceae   | 1            | 4      | 4         | 16          | 1           | 1          | 23          |
| 3. Selaginellaceae| 2           | 4      | 16        | 1           | 1          | 23          |
| Ferns           |              |        |           |             |             |            |              |
| 4. Anemiaceae   |              | 3      | 3         | 16          | 1           | 1          | 23          |
| 5. Aspleniaceae | 12           | 5      | 33        | 18          | 2           | 70         |
| 6. Athyriaceae  | 10           | 38     | 12        | 15          | 15          | 75         |
| 7. Blechnaceae  | 6            | 6      | 1         | 12          | 12          | 13         |
| 8. Cibotiaceae  | 1            | 2      | 8         | 13          | 13          | 11         |
| 9. Cyatheaceae  | 12           | 2      | 8         | 1           | 12          | 34         |
| 10. Cystopteridaceae| 1        | 2      | 8         | 1           | 12          | 34         |
| 11. Davalliaceae| 1            | 1      | 1         | 1           | 1           | 10         |
| 12. Dennstaedtiaceae| 20      | 17     | 49        | 29          | 119         | 2          |
| 13. Dicksoniaceae| 3           | 4      | 3         | 1           | 3           |
| 14. Diplaziopsidaceae| 2      |        |           |             |             | 2          |
| 15. Dryopteridaceae| 9          | 12     | 80        | 13          | 1           | 176        |
| 16. Equisetaceae| 18           | 3      | 15        | 16          | 3           | 55         |
| 17. Gleicheniaceae| 1           | 11     | 7         | 2           | 22         |
| 18. Hymenophyllaceae| 2          | 3      |           |             |             | 5          |
| 19. Lindaeaceae |              | 1      | 1         | 1           | 1          |
| 20. Lomariopsidaceae| 1           | 1      |           |             |             | 1          |
| 21. Lygodiaeae |              | 2      | 2         | 13          | 17         |
| 22. Marattiaceae| 2            | 1      | 1         | 2           | 6          |
| 23. Marsileaeae | 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          | 22         |
| 28. Plagiogyriaceae| 3           |        | 1         |             | 4          |
| 29. Polypodiaceae| 4           | 11     | 38        | 2           | 24         |
| 30. Psilotaceae |              | 1      |           |             | 1          |
| 31. Pteridaceae | 8            | 76     | 48        | 1           | 4          |
| 32. Saccolomataceae| 1           |        |           |             | 1          |
| 33. Salviniaeae | 10           | 5      |           | 23          | 3           |
| 34. Tectariaceae| 7            |        |           | 3           | 10         |
| 35. Thelypteridaceae| 4       | 1      | 39        | 15          | 14         |
| 36. Woodsiaceae | 3            |        | 1         |             | 4          |
| 37. Unidentified| 47           | 2      | 104       | 1           | 20         |
| Total           | 157          | 85     | 606       | 101         | 470        |

Maximum values for each fern and lycophyte family are highlighted in bold
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 a significant overrepresentation of insect interactions were for instance 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. 2). The most significant deviation between observed and expected numbers was found in Hemiptera, which accounted for 36.6% (606/1462) of all fern–insect interactions (Table 1) and 29.1% of fern-feeding 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-feeding 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-feeding insects were leaf-chewers (55.0%), sap-sucking insects (29.1%) were over 50% more common than the expected number (19.0% of all herbivorous insect species; Table 2). Unique structural elements of ferns such as spores were less commonly exploited (6.5%), mainly by Stathomprobidae (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). Subterranean plant organs such as rhizomes and roots were only attacked (0.7%) by herbivorous insects from four

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**Fig. 1** Observed and expected number of phytophagous insects for each fern and lycophyte family. The area of each rectangle is proportional to the number of species. Colors indicate families with significantly over- (blue) or under-represented (red) numbers of insects (Pearson residuals of Chi-square test, \( \chi^2 = 2630.4, df = 35, p < 2.22e-16 \))
Hepialidae, one Noctuidae (Lepidoptera), and one Pseudococcidae (Hemiptera; Table 2).

Predominant insect families on ferns

Species of 14 families of Coleoptera use ferns as a food source, but two families account for most fern-feeders: Chrysomelidae and Curculionidae, which exploit together 15 fern families as food (Fig. 3C). 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, click beetles (Fam. Elateridae) were found exclusively on the climbing fern family Lygodiaceae, and longhorn beetles (Cerambycidae) on the bracken fern family Dennstaedtiaceae. Marsh beetles (Scirtidae, reported as Helodidae, Balick et al. 1978) were also found on bracken ferns, the best-studied fern family of our dataset (Fig. 3C) but it remains unclear if they actually feed on them.

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. 3B). Nearly, all fern families were exploited by several families of Lepidoptera, except Salvinia for which only Pyralidae have been reported so far.

Seventeen families of Hemiptera contained fern-feeding species. Most records belonged to Aphididae, Miridae, Diaspididae, and Coccidae (Fig. 3A). Most fern families were exploited by several families of Hemiptera with exception of Psilotaceae, Marattiaceae, Anemiaceae, Lomariopsidaceae, and Oleanodraccaceae, each with a single record (Fig. 3A).

Specialization of fern-feeding insects

The interaction network analysis of our dataset, which did not include possible interactions of fern-feeding insects with other vascular plants, showed that insect families had very different levels of specialization on ferns and lycophytes as host plants alone. Within Lepidoptera, we found the highest levels of insect specialization on ferns (e.g., Nymphalidae; Table 3) and six out of 10 families had the highest $d'$ values. At the generic level, 31.2% (109 out of 349) had $d'$ values $\geq 0.5$ indicating some degree of specialization (Table 3). In the overall network, specialization was highest for Coleoptera at both family and genus level with $H'_2$ values of 0.40 and 0.65, respectively (Table 4), because most Coleoptera were feeding on the fern families Dennstaedtiaceae, Dryopteridaceae, Pteridaceae, and Polypodiaceae (Fig. 3B–C). In contrast, Hemiptera had the lowest levels of specialization (i.e., lowest $H'_2$ values) of the three studied insect orders at the overall network level. Connectance values of the networks were $\leq 0.21$, indicating a low number of existing links between both trophic levels, herbivorous insects and ferns/lycophytes. None of the networks was significantly nested at the family level because all NODF2 values (Table 4) were below the
Table 2  Relative frequency of 809 fern-feeding insects grouped by feeding habit and insect order

| 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               | –                      | –                | 0.1                 | –                        |
| Hemiptera    | 6.9              | –               | 0.5               | 0.1                    | 0.1              | –                   | –                        |
| Hymenoptera  | 13.5             | 0.1             | 1.2               | 0.5                    | 2.2              | 0.6                 | –                        |
| Coleoptera   | 13.5             | 0.9             | 0.4               | 1.2                    | 2.2              | 0.6                 | –                        |
| Lepidoptera  | 6.9              | –               | 0.5               | 0.1                    | –                | –                   | –                        |
| Total        | 55.0             | 3.0             | 3.1               | 2.6                    | 6.5              | 0.7                 | 29.1                     |

The most important feeding habits for each insect order are formatted in bold.

Fig. 3 Species-interaction networks between families of three prevailing insect orders (left) and ferns and lycophytes (right): A Hemiptera (169 spp.), B Lepidoptera (274 spp.), and C Coleoptera (80 spp.). Insect families are ordered following the Tree of Life Web Project (2002) and fern families ordered following PPG I (2016). Abbreviations of fern families correspond to the first three letters of each family (in Table 1). The thickness of connecting lines and tiles is proportional to the number of interacting species (within parentheses). Interactions with unidentified ferns were discarded.
Web asymmetry also differed considerably depending on the analyzed taxonomic level. Insect genera in the network 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%), the Americas (32.2%), and Europe (26.1%; Fig. 4). In the Americas, the distribution of records is highly biased with 82.2% of the records from N-America, 7.5% from C-America (incl. Mexico and the Caribbean Islands), and 10.3% from S-America. The remaining interactions were from Oceania (7.6%) and Africa (1.8%; Fig. 4). Reports of fern-

Table 3 Ten fern-feeding insect families (A) and genera (B) with highest $d^0$ values

| Insect families | Insect genera |
|----------------|---------------|
| Nymphalidae = 0.83 (Lep) | Caribovia = 1.00 (Hem) |
| Gryllidae = 0.78 (Ort) | Eoparargyactus = 1.00 (Lep) |
| Cydnidae = 0.58 (Hem) | Eudonia = 1.00 (Lep) |
| Pergidae = 0.58 (Hym) | Paradetis = 1.00 (Lep) |
| Cryptophagidae = 0.56 (Col) | Xenotrichaea = 1.00 (Lep) |
| Tischeriidae = 0.53 (Lep) | Paratrigonidium = 0.87 (Ort) |
| Crambidae = 0.48 (Lep) | Ripersia = 0.87 (Hem) |
| Cixiidae = 0.45 (Hem) | Tongeia = 0.87 (Lep) |
| Aleyrodidae = 0.44 (Hem) | Catoptria = 0.87 (Lep) |
| Tropiduchidae = 0.44 (Hem) | Agromyza = 0.87 (Dip) |

Insect orders within parentheses (Col: Coleoptera, Dip: Diptera, Hem: Hemiptera, Hym: Hymenoptera; Lep: Lepidoptera, Ort: Orthoptera)

Table 4 Network-level interaction metrics for three insect orders between insects and ferns/lycophytes at two taxonomic levels

| Taxonomic level/Insect order | $H^2$ | Connectance | NODF2 | Insects | Ferns/Lycophytes | Web asymmetry |
|-----------------------------|-------|-------------|-------|---------|-----------------|---------------|
| Family level                |       |             |       |         |                 |               |
| 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         |
| Genus level                 |       |             |       |         |                 |               |
| 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          |

NODF2 values were not significant ($P > 0.05$)

Fig. 4 Geographic distribution of observed fern–insect interactions (on log scale) indicating possible biases
feeding Lepidoptera and Coleoptera came mainly from the Americas, 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 commonly observed lack of data (Fig. 4).

Discussion

Number of fern/lycophyte–insect interactions

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/lycophyte–insect interactions is still in its beginning. If the currently known 423,569 phytophagous insect species (Wiens et al. 2015) would be equally distributed on 308,374 vascular plant species (Christenhusz and Byng 2016) of which 3.86% are ferns and lycophytes (PPG I 2016), we would expect that each vascular plant species is attacked by an average of 1.37 insect species and that at least 16,000 insect species may feed on ferns and lycophytes 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.

Host-plant specialization and adaptive radiations

Recent time-calibrated phylogenies suggest that the first ferns and insects had already evolved during the Silurian (431 mya, Testo and Sundue 2016) and Ordovician (479 mya; Misof et al. 2014), respectively. 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 has become 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 shadow 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 and Knyshev 2015), and leaf-chewing sawflies (Symphyta, Isaka and Sato 2014, 2015; Schneider 2016). Historic host plant switching from ancestral angiosperm and fern taxa to more recently diverged fern lineages must have occurred before such newer adaptive radiations.

Several fern-feeding insect families were able to exploit many fern families of different evolutionary age and biochemical setup. For instance, Chrysomelidae (Coleoptera), which evolved in the Upper Cretaceous (Gómez-Zurita et al. 2007), can feed on a wide range of fern families (Fig. 3C), including Equisetaceae, Pteridaceae, and Polypodiaceae, which evolved in the Silurian, Jurassic, and Cretaceous, respectively (Testo and Sundue 2016). Some chrysomelids are specialists (e.g., six species of Hippuriphila) feeding only on biochemically exceptional Equisetaceae, because these ferns contain high concentrations of Si (Poinar 2014), whereas other species such as Schenkligia bhaumiki is a generalist feeder on at least four fern families including Pteridaceae and Polypodiaceae (Patra and Bera 2007). Consequently, the interaction networks (e.g., Fig. 3C) for a single insect family can result from a mixture of generalist and specialist fern-feeding insect species. Each insect group must be analyzed to decide which kind of feeding prevails. In Lepidoptera (Fig. 3B), a similar case can be made with Stathmopodidae, which comprise many species that are feeding specifically on fern spores (Sawamura et al. 2009), but not necessarily toward a specific fern genus or family (Park et al. 2018; Shen and Hsu 2020; Wang et al. 2020). Several species of Stathmopoda have been recorded on a single fern species (e.g., Stathmopoda elyella on the mangrove fern Acrostichum aureum) and other species (e.g., Stathmopoda aenea) have been encountered on members of several fern families indicating their lower degree of specialization and capacity to host plant switching (Balick et al. 1978). Because spore-feeding taxa are nested among several angiosperm-feeders, they must have switched several
times from angiosperms to ferns (Muggleston 1989; Sugiura and Yamazaki 2004; Wang et al. 2020). In Noctuidae, *Hydraecia micacea* have been only found on Equisetaceae (Poinar 2014) and *Callopistria juventina* on fern species of nine families (Balick et al. 1978). In Hemiptera, Aphididae, and Miridae were the most common fern-feeders (Fig. 3A). 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. In the overall network, Coleoptera were the most specialized insect order at family and genus level (highest $H^2$ values), followed by Lepidoptera and Hemiptera, and within the individual networks, Lepidoptera were the most specialized (highest $d^*$ values). Our result for Coleoptera was somewhat surprising because, in other studies, Lepidoptera and Hemiptera have been reported to possess much higher levels of food plant specialization with over 60% of species feeding on a single genus, whereas in Coleoptera, only 35% were specialized (Chapman 1982). On the other hand, only a few studies have detected adaptive radiation of herbivorous insects in ferns and those were from Hemiptera (Konstantinov and Knyshov 2015) and Coleoptera (Poinar 2014). Because very few specializations at the genus (Shen and Hsu 2020) or even species-level (O’Brien 2009) were well documented, much more comprehensive case studies across the biogeographic range of host plants and phytophagous insect species are required to draw any final conclusions on the levels of specialization (Novotny et al. 2010).

There are several limitations even with our current, most updated dataset on fern–insect interactions. One limitation is its lack of completeness because we conclude that we may have only documented about 5% of the expected fern-feeding insect diversity (809 observed of over 16,000 estimated insect species). Second, the dataset was focused on ferns as host plants and did not include seed plants as possible hosts of the registered fern-feeding insects. Consequently, we cannot exclude that numerous insect species in our dataset that were recorded on a single or few fern species are not necessarily specialized on these host plants alone but may also feed on seed plants and may be recognized as generalist species in the future. Network parameters on specialization will change if all host plants of the considered phytophagous insects in our study would be included. On the other side, this limitation should not be expected in any of the fern-feeding insects that have already been studied in detail and which have radiated on ferns (e.g., Sawamura et al. 2009; Poinar 2014). Third, in our global data set, many species interactions cannot occur because of their restricted geographic distribution. However, we assume that this limitation has only a minor effect on our network parameters at higher taxonomic levels. For instance, 35 of the 36 fern families have a pantropical or cosmopolitan distribution and can interact with all regionally available insects. 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, we observed low levels of connectance, supposedly because our dataset was built on a set of geographically widely dispersed studies and could be considered as an artifact of bibliographic studies. However, a low connectance can also be the consequence of disturbance and considerably diminish the connectance of a plant–insect interaction network (Aráujo 2016; Ximénes Pinho et al. 2017).

Feeding habits of insects on ferns and lycophytes

Our study confirmed that fern-feeding insects present a wide array of feeding habits, although most are leaf-chewers and sap-suckers, and that some groups such as gall-formers are highly specialized, whereas others such as spore-feeders can present specialists and generalists. These results coincide with the idea that 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). For instance, external leaf-chewers that devour entire leaves (such as larvae of many Coleoptera and...
Lepidoptera) 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 physiologically 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). On the other hand, 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 are practically useless and easily evaded by sap-sucking herbivores (Mehltreter 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 vigorous regrowth (Mehltreter 2010; Mehltreter and 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.

Possible biases of the dataset

Despite our exhaustive review, 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 may be 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. (Dennstaedtiaceae), Salvinia spp. (Salviniaceae), and Lygodium spp. (Lygodiaceae) constitute 16.8% of all records but are focused only on these three fern genera (see Fig. 1; Table 1). 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 Platycerium) 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. A relatively complete sampling of fern–insect interactions under such circumstances should be much easier to achieve and may
allow us to hypothesize on the relative proportions and preferences of fern-feeding insects in less studied tropical climates, although temperate species richness is much lower than in the tropics. For instance, North American reports (USA and Canada) contributed 27.1% of fern-feeding 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 and 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. 4). 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 florals, 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.

To avoid or at least reduce research biases of fern–insect interaction studies as we have faced in this study, we conclude that we need future research projects that (1) are focused simultaneously on both the insect and the plant and include the best level of taxonomic identification, (2) include all possible plant hosts for the investigated insects, (3) cover native plant species in their natural habitat rather than focus only on invasive or ornamental plant species under greenhouse or laboratory conditions, and (4) cover several geographic areas at the same time by joining collaborative networks of researchers.

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Data availability  All used references are given in appendix 1 as a supplementary file. The data set is available online https://doi.org/10.6084/m9.figshare.16606580.

Declarations

Conflict of interest  The authors declare no conflicts of interest nor competing interests.

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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