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Pathogenic Fungi in Ferns and Angiosperms: A Comparative Study

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Abstract.—This study used existing databases to test the hypothesis that fern species harbor fewer pathogen species than angiosperm species. Analysis was limited to fungal pathogens because of their visibility and to herbaceous perennial dicots (forbs) because they have a similar growth form to ferns. From complete listings in the United States Department of Agriculture plant-fungal database, the number of pathogen species recorded on 200 randomly chosen ferns and herbaceous perennial dicot species were assessed. To control for differences in study effort, the number of citations to these species in the Web of Science was determined. The results showed that the major predictor of the number of fungal pathogen species known to occur on a plant species was study effort, but after controlling for this, the likelihood of a fern species being recorded as having a fungal pathogen species was much less than that for a forb. When pathogens were present, there were approximately 50% fewer pathogen species recorded on fern species than on forb species. This pattern is present even though fern species were cited on average more often than forb species, and it is consistent with impressions in the literature from studies in other parts of the world. Testable hypotheses to explain this difference are evaluated in the context of evolutionary processes leading to variation for pathogen incidence in different phylogenetic lineages, but the physiological or molecular processes that determine the higher resistance of ferns to fungal pathogens remain unknown.

Key Words.—disease resistance, parasite species richness, Uredinales, Ustilaginales, Microbotryales

This study set out to test the simple hypothesis that ferns harbor fewer fungal pathogens than flowering plants. This hypothesis was initially driven by my own casual natural history observations and readings, suggesting that pathogens are rare in both ferns (Page, 2002) and mosses (Berkeley, 1862; Davey and Currah, 2006). This is especially surprising as ferns and mosses often grow in dense mono-specific stands in moist, shaded areas where infection, especially by fungi, might be expected to be common. Similar conjectures have been made by other authors (Saxena and Harinder, 2004), and while it is generally accepted that the most common fungal pathogens of the ferns are the rust fungi (Uredinales), smut fungi (Ustilaginales, Microbotryales) have been considered to be rare or absent (Helfer, 2006; Oberwinkler, 1994). This can also be inferred by the absence of ferns as hosts in comprehensive monographs on smut fungi (Vanky, 1994; Woods *et al.,* 2018).

Whether ferns have fewer pathogens than flowering plants is a question that is not just a matter of curiosity but impinges on understanding fern evolution, their ecology, and may be important from an applied perspective. There is increasing recognition that pathogens play an important role in the ecology and evolution of natural populations of plants and animals (Gilbert, 2002), influencing their extinction risk (DeCastro and Bolker, 2005), their nutrient

cycling and food web structure (Lafferty, Dobson, and Kuris, 2006), as well as other processes such the evolution of sex (Lively, 2010) or speciation (Bomblies and Weigel, 2007). However, in ferns the major focus has been on their phylogenetic relationships, chromosome evolution, and mycorrhizae or endophytes as fungal symbiotic partners (Pressel *et al.*, 2016; Read *et al.*, 2000). There have been some previous reviews of fungal pathogens on ferns both in the US and worldwide (Helfer, 2006; Stevenson, 1945), but they have been brief and focused on documenting the major types of pathogens recorded on ferns, and have not involved a quantitative assessment of this diversity in a comparison with other types of plant.

Comparative studies of pathogen occurrence can be problematic, not only because of their taxonomic and ecological diversity, but also because data on pathogens in natural populations (as opposed to humans, crops, and domesticated animals) is still sparse and fragmentary. It is now widely appreciated that a major source of 'noise' in analyzing such data is that the number of pathogens recorded on a particular host species is highly correlated with the study effort devoted to that species (Antonovics and Hayden, 2020; Williams, Antonovics, and Rolff, 2011) and this is a characteristic feature of all disease databases (Nunn and Altizer, 2006; Walther *et al.*, 1995).

In this study, I narrow the question to the specific consideration of fungal pathogens of ferns in the United States. Fungal pathogens generally produce highly visible lesions, and are readily identifiable at least to genus based on sporangial and spore characteristics; viral and bacterial pathogens are generally far more cryptic and even less well understood taxonomically. There are substantial data on the world-wide occurrence of fungal pathogens on ferns and higher plants in the USDA databases. These data (and earlier related sources) have been used in previous assessments of the occurrence of fungal pathogens on ferns both in the US and worldwide (Helfer, 2006; Stevenson, 1945).

After correcting for study effort, the results show that fungal pathogens are less likely to be recorded as present on fern species relative to herbaceous perennial angiosperms, and that if found, fewer pathogen species are present. I discuss possible reasons for this difference, and its implications.

Materials and Methods

I narrowed the data to only consider fungal pathogens found on dicot herbaceous perennials (*i.e.*, forbs), a growth habit largely reflecting the life-form of most ferns. Shrubs and trees were excluded, not only because of their different life form, but because in the USDA plant-fungal data base it is often not clear whether the fungi that are recorded are attacking woody tissue, and therefore largely saprophytic rather than parasitic; the earlier editions of the USDA database explicitly included pathogens found on wood-products. The list of potential host plants was obtained from the PLANTS database made available by the Natural Resources Conservation Service of the USDA (https://plants.sc.egov.usda.gov/java/). The list of fern species was obtained by using

the Advanced Search Download tab, with the options 'PLANTS Floristic Area or Not=North America' and 'Category=Fern'. The broad option 'North America' was used because some trial searches indicated that the sub-option 'Lower 48 U.S. States' did not return some expected species. Checking the box 'Download text file without formatted display' allowed download of the species list, from which hybrid ferns were excluded, leaving 370 species.

The list of Angiosperms was obtained by Advanced Search in the same database, using the options 'PLANTS Floristic Area or Not=North America', 'Category=Dicot' and 'Duration=perennial' with the adjacent 'display' box checked, and 'Growth Habit=Forb/herb' with the adjacent 'display' box checked. As above, the list was downloaded and only those species with a perennial designation plus a forb/herb designation were included (species with double classifications such as biennial/perennial, shrub/forb were excluded). A total of 5,431 species were returned. Throughout, the option 'Scientific Name, include=Accepted Names Only' was used, and no attempt was made to revise any taxonomy.

From each of these lists, 200 species of ferns and 200 species of forbs were chosen at random, and without regard to any other species characteristics. These two sets of fern and perennial species were then assessed for 'study effort' by finding the number of search results in the Web of Science database (http://apps.webofknowledge.com/WOS_GeneralSearch_input.do?product=WOS&search_mode=GeneralSearch&SID=8DO4ciNdr11xcSx5AVL&preferencesSaved=), using the option "Select a database=All databases'. The species binomial was entered without quotes and under 'Topic' with no restriction as to geography, and spanning the years 1864-2019. Study effort on a species was simply the number of times that species had been cited as a 'Topic'. The search results returned publications that have the species name in the title, abstract, or key words. The Web of Science does not always take into account nomenclatural changes/synonyms in species names, and all species names entries were as in the USDA plants database.

To assess the number of fungal pathogen species recorded on each host species (sometimes termed the 'parasite species richness'; Nunn *et al.*, 2003), the USDA Agricultural Research Service database was used (https://nt.ars-grin.gov/fungaldatabases/fungushost/fungushost.cfm) under the tab 'Fungus-Host'. The searches were restricted to 'Available Localities=United States-All'. Following display of the pathogens recorded for each fern and perennial herb species, the total number (if any) were counted after removal of displayed synonyms and of pathogens with only a genus name but for which previously a genus and species name had also been given.

The statistical analysis was carried out in two steps using the R package (R Core Team, 2018). In the first step, to assess if the frequency with which at least one pathogen species was detected depended on the study effort, a logistic regression of presence (1) and absence (0) of a pathogen on a species vs. number of citations for that species was estimated. Using the function 'glm', a test for an interaction was carried out with the model (number of pathogens) $\sim$ (type) * (number of citations), with a binomial link, and where type = fern or

herb and number of citations (x) was log10 (x+1) transformed (a few species had zero citations in the Web of Science even though listed in the USDA database). As the interaction term was not significant, I tested for an effect of host type and if number of citations affected the likelihood that a pathogen would be recorded using the model (number of pathogens) ~ (type) + (number of citations)

The second step was applied only to those host species where one or more pathogen species had been recorded. To assess if the number of pathogens detected differed among host types (fern or herb), the same model as above was used, except with a Gaussian link (assuming normally distributed error) and using log10 (x) transformed numbers for pathogen and host species because there were no zero values.

Results

The probability of detecting a pathogen on a host increased significantly ($P<0.0001$) with the number of citations to that host; the interaction term in the logistic regression was not significant ($p<0.58$) indicating no difference between ferns and forbs in the slope of the regressions on a logistic scale. Pathogens were recorded as occurring significantly less frequently ($P=0.018$) on fern species than forb species after controlling for the search effort on each plant species (Fig. 1). The difference in means of the logistic regression was 0.678 (97.5% confidence intervals=0.764-1.43). Because logistic regression involves log transformation of the ratio of presence/absence, this difference is difficult to interpret straightforwardly, but inspection of Fig. 1 shows that at citation numbers of 100, pathogens are recorded on about half as many ferns as forbs.

In terms of total numbers for the 200 species of each type, there were 21,335 citations for ferns and 32 had at least one pathogen, whereas for herbs there were 14,095 citations and 41 had at least one pathogen. The slope of the relationship between pathogen occurrence and number of citations was 1.091 (0.25-97.5% confidence intervals=0.764-1.43), indicating that the log odds ratio of detecting a pathogen in the database increased by one for approximately every log10 number of citations.

Given that one or more pathogens were present, the number of pathogens found also increased significantly ($P<0.0005$) with the number of citations. The slope of the relationship between number of pathogens and number of citations was 0.198, indicating that for every ten-fold increase in the number of citations, there was a 1.57-fold (57%) increase in the number of pathogen species recorded. The interaction term was non-significant ($P<0.97$) indicating no difference between forbs and ferns in the slope of the regressions (on a log-log scale).

There were significantly ($P=0.0082$) fewer pathogens on ferns than on forbs (Fig. 2). The least square means when back transformed, indicated that there were 2.40 (confidence interval 1.73-3.33) pathogens predicted per citation in ferns and 4.28 (confidence interval 3.02-6.05) per citation in herbaceous dicots.

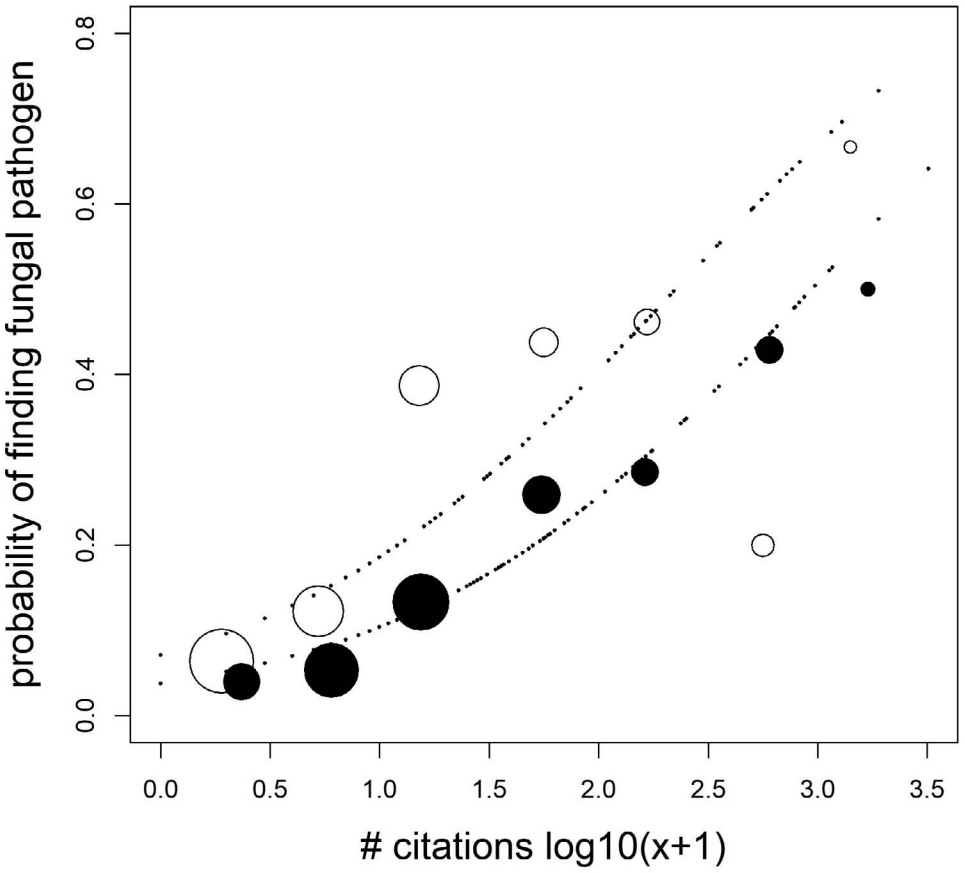

FIG. 1. The relationship between probability of detecting a fungal pathogen and number of citations to the host, back transformed from a linear logistic regression fit (see text). The points are predicted values from the logistic regression (upper series are herbaceous perennials). Open circles show observed probabilities, for forbs, and closed circles show probabilities for ferns when data are grouped into classes of 0-0.5, etc. on a log10 scale. Diameter of the dot is proportional to the number of citations in each of the classes.

In terms of actual numbers, for the 32 fern species with pathogens, there were 9,278 citations and 98 unique pathogen-host species combinations, whereas for herbs there were 6,353 citations and 203 unique pathogen-host species combinations.

I examined if there was evidence of phylogenetic signal in the data by comparing fungal incidence in monophyletic clades as determined by Pryer *et al*. 2004, and by Pteridophyte Phylogeny Group (2016). Because the occurrence of fungi was very sporadic (only 32 of the 200 fern species had records of any fungi, with uneven clade sampling), I used generalized linear models, again using log10(x+1) number of citations as a covariate, but assuming the number of fungi recorded were Poisson distributed (SAS Proc GLMMIX, model

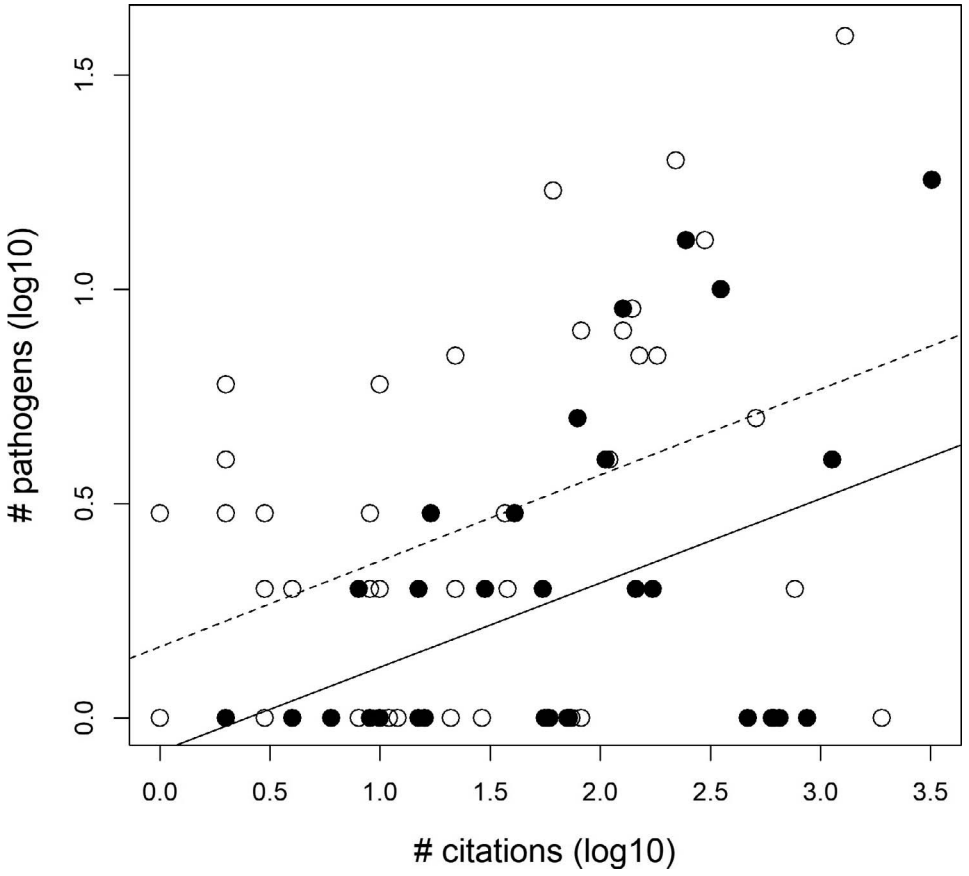

FIG. 2. The relationship between number of fungal pathogens detected on a host species and number of citations to that host (both on log10 scale). Black dots = ferns and open circles=forbs. Lines are linear regressions, solid=ferns, dashed = forbs.

fungi=citations order family(order), and correcting for overdispersion; SAS Institute 2016). The effect of orders ($F_{4,15}$=1.75, P <0.191) was not significant, but the effect of families was highly significant ($F_{15,179}$=2.25, P <0.0063). There were two sub-orders of the Polypodiales with more than one family in each, namely Aspleniinae and Polypodiinae, and a nested analysis of variance for an effect of sub-order and family showed no effect of suborder but also significant variation among families ($F_{9,89}$=2.29, P <0.023) within sub-order. However, variation among families in proportion of species with at least one record was not significant (P<0.70, using logit link). Genus effects within families were not significant.

Because there is evidence that ferns have few smut fungi (see Introduction) I also specifically searched the USDA plant-fungal database for 'Basidiomycota-Smuts' (Ustilaginales and Microbotryales). No smuts were recorded among the 98 pathogen-fern combinations while 7 of the 203 pathogen-forb combinations

included smuts; Fisher's exact test showed that this difference only approached statistical significance (P=0.102). Excluding smuts had a negligible effect on the statistical conclusions above.

Discussion

My results clearly show that fewer fungal pathogen species have been recorded on fern species than on dicot herbaceous perennials in the United States. I used taxonomy-based random sampling of species as the simplest approach, without regard to phylogeny and without regard to host or pathogen traits. Importantly, like many other analyses of host-pathogen data bases (see Introduction), the major determinant of a pathogen species being recorded on a host species was study effort, as estimated from the number of citations to it in the literature. This applied to presence and absence of any pathogens on a host, as well as number of pathogens per host. While the analysis of the hosts and their pathogens was restricted to the United States, the metric of how well a species had been studied was not restricted geographically; nevertheless, study effort was still the major predictor of pathogen occurrence. My results certainly contradict Stevenson (1945), who wrote that "these interesting and often delicate plants [*i.e.*, ferns] are as much subject to attack by parasitic fungi as are the higher plants." Although he used similar information from a precursor of the current USDA data base, his analysis was not quantitative.

Beyond showing the methodological feasibility of such analyses, more questions are raised than answered by this study. The first question is whether the conclusion that ferns have fewer fungal pathogens than dicot herbaceous perennials is itself valid and whether this can be generalized to ferns (Polypodiopsida) and angiosperms as a whole. Previous studies have shown differences among angiosperm families in the incidence of fungal pathogens (Antonovics and Hayden, 2020). In my data, there was also evidence of heterogeneity in fungal incidence among fern families, but the data were too sparse and unbalanced in taxon representation to do any detailed phylogenetic analysis. It therefore remains an open question if the difference I found between ferns and forbs is driven by the occurrence of particular taxa in the United States or if it is more general. An analysis with additional data from other regions would address this question, but prior qualitative assessments in other countries also argue that the patterns seen here may extend beyond the United States.

More than a century ago, the British mycologist Berkeley (1892, p.8) remarked that:

> "Nor are the vascular cryptogams, such as ferns, mosses, and liverworts without their own especial enemies, though these are fewer in number perhaps than in other organized beings."

Oberwinkler (1994, p.8), another outstanding mycologist, referring to plants in southern Germany, wrote (translated from German):

> "Powdery and downy mildews don't occur on ferns, nor do smut fungi, but there are several rust fungi."

In the Biological Flora of the British Isles (https://www.britishecologicalsociety.org/publications/journals/journal-of-ecology/biological-flora-database/), a series of thorough autecological reviews of species of British plants, seven fern species are considered. Five are noted as having no fungal pathogens, and *Dryopteris carthusiana* (Vill.) H. P. Fuchs as having only one. *Pteridium aquilinum* (L.) Kuhn, bracken, a well-studied species of economic importance because of its invasiveness and toxicity to cattle, is listed as having three pathogens on the prothalli, and seven on the adults, but Marrs and Watt (2006) conclude, "In short, *Pteridium*, like most ferns, is remarkably resistant to disease." Helfer (2006), in his review of worldwide pteridophyte pathogens in the USDA database, noted that rusts were absent in *Equisetum*, and that there was only one record from the lycophytes. None of the 20 most common genera of pathogens were smuts, downy, or powdery mildews. Hopefully the present study will stimulate studies of fungal and other pathogens of ferns beyond the United States to see if these patterns are robust to more thorough taxon sampling, especially in the tropics, and the extent to which they are dependent also on the type of fungal pathogen being considered.

The possibility that the observed pattern is the result of biases in the sampling prior to entry into the databases also cannot be excluded. For example, researchers on ferns may be less trained in or may have less interest in detecting fungal pathogens than researchers on herbaceous plants. Alternately, pathogens on ferns may be less visible than those on herbaceous perennials. However, these explanations are unlikely, as fern biologists have a 'strong-eye' for details of frond morphology and therefore would be expected to notice pathogen lesions if they were present. Moreover, analysis of the citation data showed that the average number of citations per species was significantly greater for ferns than for forbs (Fig. 3). The reason may be that in the United States there are far fewer fern species (370 in my listing) than forb species (5,428) and this, combined with a dedicated 'constituency' of fern biologists, has resulted in ferns being sampled more thoroughly than herbaceous perennials. The absence of any significant differences between ferns and forbs in the slopes of the regressions of pathogen occurrence vs. study effort indicates that the probability of detection 'per increase in study effort' is also similar in the two categories, albeit there is a large variation about these regressions.

The differing relative commercial relevance of ferns and flowering plants is also an unlikely contributory factor to their contrasting number of pathogens. Although crops have more pathogens than non-crop species (although not on a per citation basis; Antonovics and Hayden, 2020), no crops were present among the herbaceous perennial species. However, there were two horticulturally important species among the ferns, namely, *Nephrolepis exaltata* (L.) Schott, Boston fern, and *Cyrtomium falcatum* (L. f.) C. Presl, the holly fern; they had the highest proportion of pathogens per citation (13/245 and 9/127,

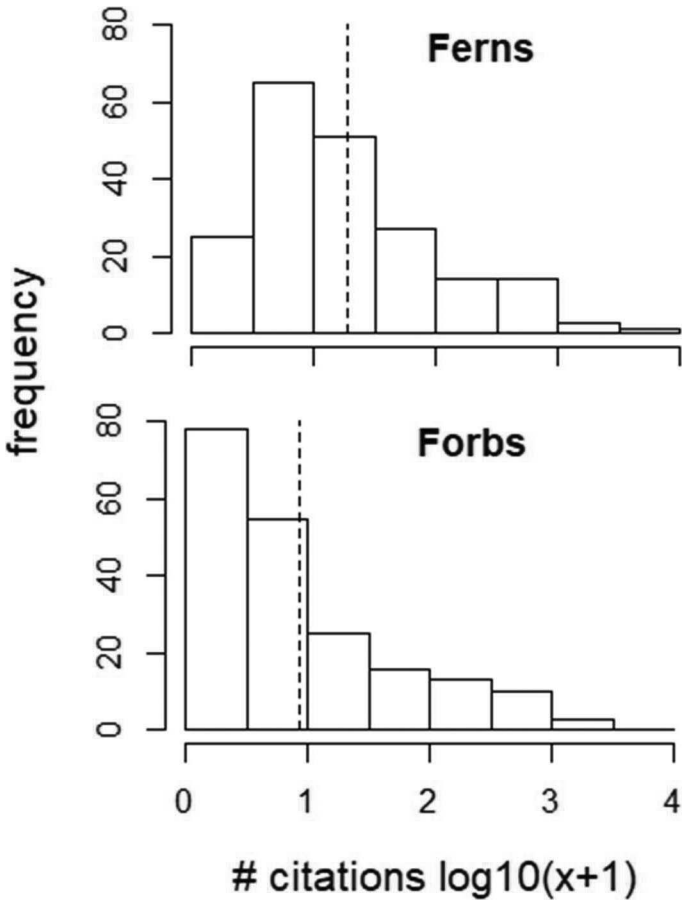

FIG. 3. Frequency of a given number of citations in the Web of Science for ferns and forbs. Dashed vertical lines indicate means. Number of citations are grouped on a log10 scale. The difference between the means is highly significant ($P<0.001$) both by heterogeneity chi-squared on classes in the histograms (=41.5, df=7) and by a t-test on log10(x+1).

respectively). The four most frequently cited ferns in my study sample were *Pteridium aquilinum* (3214 times), *Dryopteris filix-mas* (L.) Schott (1898), *Azolla filiculoides* Lam. (1167) and *Athyrium filix-femina* (L.) Roth (1133), while the most frequently cited forbs were *Silene vulgaris* (Moench) Garcke (1896), *Asclepias syriaca* L. (1295), *Lotus pedunculatus* Cav. (1156), and *Inula britannica* L. (827). The latter, a weedy species, was only introduced into the US in 1999 (Lehtonen, Schall, and Wager-Pagé, 2009).

It is possible to ask why ferns have fewer pathogens than forbs from either a direct mechanistic viewpoint (whether physiological or ecological) or from an evolutionary perspective (what are the evolutionary origins of the observed patterns). At present it is not known if ferns have different resistance mechanisms relative to angiosperms. Both ferns and angiosperms likely use

secondary compounds with anti-fungal properties as well as mechanisms based on more specific molecular recognition. Ferns have a broad range of secondary compounds, and although some of these are both unique and well-characterized chemically, this is usually not in the context of an interest in their susceptibility to pathogens. For example, the comprehensive review of acylphloroglucinol compounds in Dryopteridaceae (Socolsky, Hernandez, and Bardon, 2012) describes their anti-helminthic, anti-tumor, molluscicidal, and antibacterial properties but does not mention tests of anti-fungal activity. Other reviews (Vetter, 2018) mention that many secondary compounds have anti-fungal "properties" or "activity" but their role in defense against natural pathogens is rarely considered. Page (2002) discusses the diverse chemical armament of ferns mostly in the context of herbivory, but also notes that ferns survive regimes under which "most flowering plant seedlings would readily 'damp-off' through rapid fungal attack". However, he does not describe experimental work explicitly demonstrating this or suggest a specific mechanism.

Regarding molecular mechanisms, phylogenetic studies have shown that NBS-LRR genes, implemented in the resistance of angiosperms to fungal, oomycete, and bacterial challenge, had their origins prior to the evolution of land plants (Shao *et al.*, 2019). It has also been found that the *Azolla* genome has all the components of the jasmonic and salicylic acid pathways involved in pathogen and herbivore defense in angiosperms (de Vries *et al.*, 2017). A study of a subset of the LRR resistance genes (with the toll interleukin-1 receptor) in a range of plants (Sun *et al.*, 2013), showed that whereas numerous genes were present in dicots, only one copy of one type was present in *Selaginella moellendorffii* Hieron., the only 'fern' for which a sequence was available. Their conclusion that "more information from other species of pteridophytes is needed" was not surprising. There are therefore simply insufficient studies to know if ferns have unique disease resistance mechanisms at the molecular level.

There have also been discussions on why certain phylogenetic lineages may have more pathogen species than others. One hypothesis is that the long-term persistence of pathogens in a lineage is dependent on frequent host shifts among closely related species (Nunn *et al.*, 2004; Thines, 2019). A prediction of this hypothesis is that pathogen species diversity should be higher in lineages that are more diverse, and this was observed by Huang *et al.* (2014) in a study of parasite species richness in carnivores. This should be a very testable hypothesis in ferns given large variation in lineage diversity within the group and evidence for family level variation in pathogen occurrence within the Polypodiales. Another possibility that has been suggested is that older lineages have fewer pathogens because they have had a longer period to evolve effective resistance. Thus, in a study of immune responses and disease incidence in extant species of corals, Pinzon *et al.* (2014) found that species that diverged more than 200 mya had fewer pathogens and stronger constitutive immune functions (measured in a variety of ways) than more recently diverged species. A difficulty with this hypothesis when applied to any one pair of lineages (*e.g.*

ferns vs. angiosperms) is that any two lineages always have the same "age" and therefore would have been exposed to pathogens for identical time periods. However, given that pathogens are often quite lineage specific (Antonovics *et al.,* 2012), a clade retaining ancestral traits may have been exposed to their specialized pathogens longer than a more recently derived clade that acquired new pathogens after divergence. The quite general expectation is therefore that lineages retaining more ancestral traits should have fewer pathogens than derived lineages, and this would be consistent with the present findings.

Unfortunately, these various hypotheses are difficult to distinguish by the single pairwise presented here, but the evidence of family variation in pathogen incidence, even with limited sampling, suggests a broader and more comprehensive analysis of pathogen incidence in ferns in the context of phylogeny may be very fruitful. Other studies have compared the diversity of pathogens on hosts differing in a variety of characteristics: endangered vs. non-endangered (Altizer, Nunn, and Lindefors, 2007), dioecious vs. hermaphrodite (Williams, Antonovics, and Rolff, 2011), rare vs. common: Gibson, Mena-Ali, and Hood, 2010), long vs. short lived (Lindenfors *et al.*, 2007), and invasive vs. non-invasive (Mitchell and Power, 2003). For ferns, this is potentially a rich area for future study, especially as comprehensive databases are being established for trait characteristics in land-plants generally (McGill *et al.*, 2006) and in fungal species (Aguilar-Trigueros *et al.*, 2015). This study has shown that the sporadic nature of the data on pathogen incidence is a major factor making this more difficult, yet this can be overcome by assessment of 'study effort'. I hope the present study provides useful methodological pointers to stimulate future comparative work on ferns and their pathogens at a rigorous quantitative level, as well as encouraging research on fern-pathogen interactions at many levels.

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Appendix

1. List of fern species used in the study, and in parentheses the number of citations and number of pathogen species recorded for each. Species names are not italicized, and authority names are as in the USDA plant database (see text).

Adiantum capillus-veneris (791,0); Adiantum caudatum (84,0); Adiantum hispidulum (38,0); Adiantum jordanii (6,1); Adiantum melanoleucum (2,0); Adiantum viridimontanum (7,0); Arachniodes simplicior (6,0); Argyrochosma dealbata (1,0); Argyrochosma incana (3,0); Argyrochosma jonesii (1,0); Argyrochosma limitanea (1,0); Argyrochosma microphylla (1,0); Aspidotis californica (2,0); Aspidotis carlotta-halliae (2,0); Aspidotis densa (5,0); Asplenium abscissum (5,0); Asplenium adiantum-nigrum (163,0); Asplenium adulterinum (35,0); Asplenium cristatum (9,0); Asplenium dalhousiae (27,0); Asplenium heterochroum (6,0); Asplenium monanthes (26,0); Asplenium montanum (35,0); Asplenium pinnatifidum (24,0); Asplenium plenum (3,0); Asplenium resiliens (11,0); Asplenium rhizophyllum (22,0); Asplenium ruta-muraria (824,0); Asplenium scolopendrium (783,0); Asplenium trichomanes (974,0); Asplenium trichomanes-ramosum (10,0); Asplenium tutwilerae (1,0); Asplenium verecundum (1,0); Asplenium vespertinum (2,0); Astrolepis windhamii (2,0); Athyrium americanum (4,1); Athyrium filix-femina (1133,4); Azolla filiculoides (1167,0); Azolla microphylla (251,0); Blechnum occidentale (49,0); Blechnum spicant (175,0); Bommeria hispida (15,0); Botrychium alaskense (4,0); Botrychium boreale (27,0); Botrychium crenulatum (9,0); Botrychium echo (4,0); Botrychium gallicomontanum (9,0); Botrychium jenmanii (4,0); Botrychium lineare (7,0); Botrychium lunaria (442,0); Botrychium matricariifolium (84,0); Botrychium minganense (24,0);

Botrychium mormo (14,0); Botrychium oneidense (13,0); Botrychium pallidum (9,0); Botrychium paradoxum (9,0); Botrychium pedunculosum (4,0); Botrychium pseudopinnatum (3,0); Botrychium pumicola (10,0); Botrychium simplex (69,0); Botrychium tunux (5,0); Botrychium virginianum (145,2); Campyloneurum phyllitidis (15,1); Ceratopteris richardii (337,0); Cheilanthes clevelandii (2,0); Cheilanthes cooperae (3,0); Cheilanthes covillei (1,0); Cheilanthes feei (10,0); Cheilanthes gracillima (7,0); Cheilanthes intertexta (2,0); Cheilanthes lanosa (24,0); Cheilanthes lendigera (3,0); Cheilanthes lindheimeri (6,0); Cheilanthes newberryi (3,0); Cheilanthes notholaenoides (8,0); Cheilanthes pringlei (2,1); Cheilanthes tomentosa (19,0); Cheilanthes villosa (15,0); Cheilanthes viscida (2,0); Cheilanthes wrightii (5,0); Cheiroglossa palmata (8,0); Cryptogramma sitchensis (3,0); Ctenitis submarginalis (9,0); Cyrtomium caryotideum (26,0); Cyrtomium falcatum (127,9); Cystopteris bulbifera (55,2); Cystopteris laurentiana (4,0); Cystopteris protrusa (18,0); Cystopteris tenuis (8,0); Dennstaedtia bipinnata (4,0); Dennstaedtia globulifera (12,0); Deparia petersenii (9,0); Diplazium pycnocarpon (13,0); Drynaria quercifolia (92,0); Dryopteris arguta (17,3); Dryopteris campyloptera (34,0); Dryopteris carthusiana (871,1); Dryopteris celsa (44,0); Dryopteris cinnamomea (25,0); Dryopteris filix-mas (1898,0); Dryopteris fragrans (121,0); Dryopteris intermedia (132,0); Dryopteris rossii (5,0); Gaga arizonica (0,0); Grammitis nimbata (3,0); Gymnocarpium appalachianum (4,0); Gymnocarpium disjunctum (15,0); Gymnocarpium dryopteris (652,1); Gymnocarpium jessoense (13,0); Gymnocarpium robertianum (522,0); Hymenophyllum tayloriae (4,0); Hypolepis repens (14,0); Macrothelypteris torresiana (47,0); Marsilea ancylopoda (8,0); Marsilea minuta (157,0); Marsilea mollis (12,0); Marsilea mutica (11,0); Marsilea oligospora (8,0); Marsilea quadrifolia (237,0); Matteuccia struthiopteris (469,1); Microgramma heterophylla (8,0); Nephrolepis cordifolia (149,0); Nephrolepis exaltata (245,13); Nephrolepis falcata (9,0); Neurodium lanceolatum (2,0); Notholaena aliena (3,0); Notholaena californica (8,0); Notholaena grayi (4,0); Notholaena neglecta (7,0); Odontosoria clavata (1,0); Onoclea sensibilis (353,10); Ophioglossum engelmannii (19,0); Ophioglossum nudicaule (62,0); Ophioglossum pendulum (28,0); Ophioglossum petiolatum (72,0); Ophioglossum polyphyllum (27,0); Ophioglossum vulgatum (603,1); Osmunda claytoniana (79,5); Pecluma dispersa (2,0); Pecluma ptilodon (6,0); Pellaea atropurpurea (36,0); Pellaea breweri (6,0); Pellaea bridgesii (3,0); Pellaea cordifolia (5,0); Pellaea intermedia (6,0); Pellaea lyngholmii (1,0); Pellaea mucronata (9,1); Pellaea ovata (15,0); Pellaea ternifolia (19,0); Pellaea truncata (8,0); Pentagramma triangularis (18,0); Phanerophlebia umbonata (1,0); Phlebodium aureum (56,1); Pityrogramma calomelanos (173,2); Pleopeltis astrolepis (10,0); Pleopeltis polypodioides (22,0); Polypodium calirhiza (4,0); Polypodium glycyrrhiza (59,1); Polypodium hesperium (15,1); Polypodium sibiricum (12,0); Polystichum acrostichoides (106,4); Polystichum braunii (86,0); Polystichum californicum (10,0); Polystichum dudleyi (6,0); Polystichum imbricans (13,0); Polystichum kwakiutlii (1,0); Polystichum scopulinum (5,0); Polystichum setigerum (1,0); Pteridium aquilinum (3214,18); Pteridium caudatum (72,1); Salvinia molesta (620,1);

Salvinia natans (559,0); Salvinia oblongifolia (10,0); Stenochlaena tenuifolia (8,2); Thelypteris augescens (11,0); Thelypteris dentata (53,0); Thelypteris grandis (6,0); Thelypteris hispidula (19,0); Thelypteris nevadensis (6,0); Thelypteris palustris (143,0); Thelypteris patens (12,0); Thelypteris pilosa (13,0); Thelypteris puberula (5,0); Thelypteris quelpaertensis (5,0); Thelypteris reptans (8,0); Thelypteris simulata (10,0); Trichomanes lineolatum (3,0); Vittaria appalachiana (14,0); Vittaria lineata (33,0); Woodsia alpina (62,0); Woodsia appalachiana (3,0); Woodsia glabella (30,2); Woodsia ilvensis (69,0); Woodsia obtusa (36,0); Woodsia oregana (16,1); Woodsia phillipsii (1,0); Woodwardia areolata (15,2); Woodwardia fimbriata (10,1); Woodwardia radicans (58,1); Woodwardia virginica (41,3).

2. List of herbaceous perennial dicots used in the study, and in parentheses the number of citations and number of pathogen species recorded for each. Species names are not italicized, and authority names are as in the USDA plant database (see text).

Abronia ammophila (6,0); Agoseris lackschewitzii (2,0); Alternanthera caracasana (10,0); Ammocodon chenopodioides (3,0); Anaphalis margaritacea (127,8); Anemone drummondii (10,2); Anemone tuberosa (74,1); Angelica breweri (1,3); Antennaria marginata (22,0); Apium nodiflorum (587,0); Apium repens (211,0); Arabis gracilipes (1,0); Arabis hastatula (1,0); Arabis macdonaldiana (2,0); Arabis oregana (3,0); Arabis subpinnatifida (2,0); Arenaria livermorensis (1,0); Arnica amplexicaulis (23,0); Arnoglossum diversifolium (2,0); Artemisia laciniata (82,1); Asclepias eriocarpa (35,0); Asclepias scaposa (1,0); Asclepias subverticillata (12,0); Asclepias syriaca (1295,39); Astragalus americanus (12,0); Astragalus leucolobus (3,0); Astragalus oophorus (2,0); Astragalus phoenix (164,0); Astragalus preussii (11,1); Astragalus ripleyi (0,0); Astragalus soxmaniorum (0,0); Astragalus subvestitus (1,0); Baptisia cinerea (2,0); Bartsia alpina (82,0); Berlandiera subacaulis (3,0); Bidens lemmonii (1,0); Boltonia apalachicolensis (1,0); Boykinia richardsonii (4,0); Callirhoe alcaeoides (2,4); Campanula aparinoides (9,3); Castilleja aquariensis (1,0); Castilleja cinerea (1,0); Castilleja elegans (6,0); Centaurea nigrescens (56,0); Chaptalia tomentosa (9,0); Cirsium clavatum (9,0); Cirsium rusbyi (1,0); Clematis integrifolia (71,1); Conioselinum mexicanum (0,0); Coreopsis grandiflora (151,7); Cymopterus minimus (1,0); Dahlia pinnata (220,20); Dalea searlsiae (8,1); Delphinium alpestre (4,0); Delphinium bakeri (0,0); Delphinium nuttallianum (82,8); Delphinium nuttallii (9,0); Desmanthus bicornutus (11,0); Dianthus carthusianorum (555,0); Draba monoensis (2,0); Draba oreibata (3,0); Dracocephalum thymiflorum (22,0); Drosera linearis (66,0); Encelia nutans (3,0); Enydra fluctuans (44,0); Epilobium luteum (29,1); Erigeron breweri (5,0); Erigeron foliosus (6,0); Eriogonum gracilipes (1,0); Eriogonum panguicense (0,0); Eryngium articulatum (1,0); Eupatorium perfoliatum (140,9); Eupatorium rotundifolium (37,3); Eurybia avita (0,0); Eurybia horrida (1,0); Eurybia merita (2,0); Filipendula vulgaris (346,0); Frasera puberulenta (1,0); Galium humifusum (23,0); Gentiana douglasiana (1,0); Gentiana rubricaulis (0,0); Geranium atropurpureum (4,0); Gratiola hispida (0,0); Grindelia decumbens (1,0); Guardiola platyphylla (3,3); Haplocarpha lyrata

(6,0); Harbouria trachypleura (3,0); Hedeoma oblongifolia (1,0); Hedysarum boreale (38,2); Helianthella microcephala (0,0); Helianthus radula (18,0); Hermbstaedtia odorata (4,0); Heterotheca camporum (6,0); Horkelia sericata (0,0); Hydrastis canadensis (509,5); Hymenoxys lapidicola (1,0); Iliamna grandiflora (1,0); Inula britannica (827,0); Ivesia pityocharis (1,0); Justicia spicigera (47,0); Lasianthaea podocephala (4,0); Lenophyllum texanum (2,0); Leontodon hispidus (674,0); Lesquerella pruinosa (0,0); Lewisia longipetala (5,0); Lewisia nevadensis (3,2); Limonium sinuatum (182,7); Lithospermum mirabile (1,0); Lobelia glandulosa (8,0); Lomatium austiniae (0,0); Lomatium farinosum (4,0); Lomatium juniperinum (1,0); Lotus pedunculatus (1156,0); Ludwigia sphaerocarpa (3,1); Lupinus culbertsonii (2,0); Matelea cynanchoides (0,0); Meehania cordata (6,0); Mentzelia texana (3,0); Mertensia arizonica (8,0); Mimulus lewisii (110,4); Mirabilis glabra (74,0); Mirabilis hirsuta (56,0); Mirabilis oxybaphoides (4,0); Mirabilis texensis (7,0); Monarda russeliana (2,0); Nymphaea tetragona (163,0); Oenothera acutissima (7,0); Oenothera latifolia (30,0); Oenothera nuttallii (9,2); Oxytropis maydelliana (21,1); Packera hyperborealis (0,0); Parnassia cirrata (1,0); Pediomelum pauperitense (2,0); Penstemon alamosensis (0,0); Penstemon albidus (4,2); Penstemon gibbensii (3,0); Penstemon labrosus (1,0); Penstemon pinorum (1,0); Penstemon saxosorum (1,0); Penstemon tenuis (3,0); Penstemon triflorus (5,0); Phacelia arizonica (6,0); Phlox amoena (10,1); Phlox stolonifera (16,0); Physostegia digitalis (5,0); Plantago rugelii (61,17); Polemonium eddyense (1,0); Potentilla drummondii (12,1); Potentilla plattensis (2,0); Potentilla reptans (498,0); Prenanthes nana (4,0); Primula laurentiana (12,0); Pseudognaphalium jaliscense (2,0); Ranunculus allenii (0,0); Ranunculus andersonii (5,0); Ranunculus flammula (764,2); Ranunculus orthorhynchus (2,3); Ranunculus recurvatus (10,6); Rapistrum perenne (12,0); Rorippa coloradensis (0,0); Rudbeckia graminifolia (3,0); Rudbeckia scabrifolia (9,0); Ruellia purshiana (3,0); Rumex pallidus (12,0); Salvia whitehousei (1,0); Satureja hortensis (722,0); Saxifraga hieraciifolia (4,0); Saxifraga tricuspidata (15,1); Schoenocrambe barnebyi (1,0); Scutellaria floridana (5,0); Scutellaria pseudoserrata (2,0); Sedum lanceolatum (31,0); Sedum mexicanum (17,0); Senecio atratus (3,0); Sidalcea covillei (1,0); Silene californica (22,2); Silene rectiramea (0,0); Silene vulgaris (1896,1); Silphium brachiatum (2,0); Silphium glutinosum (1,0); Silphium perfoliatum (299,13); Stachys bigelovii (2,0); Stachys recta (172,0); Stachys stebbinsii (1,0); Stachys sylvatica (144,0); Stellaria irrigua (3,0); Stenandrium dulce (5,0); Symphyotrichum pygmaeum (3,0); Symphytum asperum (119,0); Taenidia integerrima (2,6); Thymophylla micropoides (1,0); Trifolium ambiguum (357,0); Trifolium barnebyi (2,0); Trifolium longipes (22,7); Triosteum angustifolium (6,1); Vernonia blodgettii (2,0); Viola calcicola (5,0); Viola charlestonensis (2,0); Viola umbraticola (1,0); Wyethia helianthoides (1,1).