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Parasite and pathogen effects on ecosystem processes: A quantitative review

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Abstract. Pathogens and parasites (henceforth "pathogens") can make up a large percentage of the biomass found in ecosystems, and therefore, their impacts on ecosystem processes should be prominent. Pathogens influence ecosystem processes by affecting the abundance or phenotype of hosts and through direct contributions to ecosystem production. However, there has been little quantitative synthesis of the relative effect sizes of these impacts on ecosystem processes. This study presents a systematic review and meta-analysis of pathogen effects on primary production, secondary production, and biogeochemical cycles. We find that the effects of pathogens on ecosystem processes were greater where pathogens influenced host or community abundance or biomass than when they influenced phenotypes. Pathogen impacts on primary production were larger than on secondary production or biogeochemical cycles. By contrast, we detected no general differences in effect sizes across host or pathogen taxon or ecosystem type (terrestrial vs. aquatic). While we have found potential evidence of publication bias against negative results, a well-known issue in meta-analyses, our work nonetheless shows that the available literature underrepresents some taxa and geographic regions. To better understand the extent and magnitude of pathogen impacts on ecosystem processes, future research is needed in four areas. First, research is needed on the most understudied systems, including bacteria and viruses, as well as tropical ecosystems. A second priority is research seeking to understand how key components of ecosystem variation, including age (time of ecological continuity), productivity, and species diversity and composition, may interact to mediate pathogen impacts. Third, we suggest expanding on work examining how pathogen effects are influenced by climate change, species introductions, deforestation, and other human impacts. Fourth, we expect that host coinfection influences ecosystem processes in ways that cannot always be predicted based on studies of single infections. To enable others to build on this work, we make available the data we extracted from the literature, with the code for computing effect sizes.

Key words: biogeochemical cycles; meta-analysis; parasite; pathogen; primary production; secondary production.

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Introduction

Pathogens and parasites (henceforth "pathogens") are often important controls on host populations and thereby have the potential to affect ecosystem processes, including primary production, secondary production, biogeochemical cycles, disturbance regimes, and physical structure (Price et al. 1986, Dumbauld et al. 2011, Garnas et al. 2011, Cobb et al. 2012, Sato et al. 2012, Avila et al. 2016, Simler et al. 2018). The impact of pathogen–host interactions on ecosystem processes can rival those of other trophic interactions (Zhang et al. 2015). In some cases, pathogen impacts are dramatic and readily apparent, as for example in east African savannas when the rinderpest virus severely reduced populations of wildebeest, consequently altering primary production and carbon stocks (Holdo et al. 2009). In other cases, pathogens exert important but less apparent impacts. Despite increasing attention to identifying ecosystem effects of parasites or pathogens (Preston et al. 2016, Sures et al. 2017, Frainer et al. 2018), to our knowledge, these effects have not been quantified across taxa, ecosystems, and ecosystem processes. Quantitative syntheses are needed to estimate relative impacts and prioritize research directions.

How does the pathway of pathogen impact influence the magnitude of effects on ecosystem processes? To explore this question, and inspired by the mechanisms described in a recent review (Preston et al. 2016), we present a conceptual model (Fig. 1) in which pathogens influence ecosystem processes through three pathways. The first pathway is via change in abundance or biomass of hosts, or of species interacting with the host or with the pathogen. Changes in abundance or biomass, which can occur due to effects on demography or individual growth, may change ecosystem processes. Across six studies in benthic sediments, for example, virus-caused mortality of prokaryotes released between 0.1% and 10% of the organic carbon supporting heterotrophic bacteria (Pinto et al. 2013). Pathogenic carbon consumption by the fungus *Rhytisma polare* reduced ecosystem carbon by 20% in Arctic tundra (Masumoto et al. 2018). In a second pathway, pathogens cause changes in phenotype, including manipulation of hosts and of species interacting with hosts (Poulin 2013). Nematomorph parasites, for instance, induced infected cricket hosts to enter streams, where crickets comprised 60% of the energy consumed annually by trout (Sato et al. 2011); reduced predation pressure on benthic aquatic invertebrates, in turn, increased leaf litter decomposition by 30% (Sato et al. 2012). The third pathway is a direct one, in which the biomass production of the pathogen itself is an important component of ecosystem secondary production (Thieltges et al. 2008), and may support existing or new consumers (Watson et al. 2011). Across 18 trematode species in benthic ecosystems, for example, annual production of cercariae (larval trematodes) was in some cases comparable to that of free-living invertebrates (Thieltges et al. 2008). Litter from hemiparasitic mistletoe (*Amyema miquelii*) increased litterfall by up to 189% in Australian eucalypt forest (March and Watson 2007). While there are relatively few systems for which these effects have been investigated, the impacts have been major. Pathogens effects may therefore be important to how ecosystems work, yet they remain largely unexamined.

We address three questions about pathogens and ecosystem processes that arise from our conceptual model. First, how does the magnitude of pathogen effects vary between pathogen and host taxa, ecosystem types, and the specific ecosystem process of interest? To address this question, we present a meta-analysis of pathogen effects on ecosystem processes—primary and secondary production and biogeochemical cycling.

Second, are the effects of pathogens on ecosystem processes stronger along some mechanistic pathways compared to others? To address this question, we conducted a meta-analysis of how pathogen effect sizes differ among the pathways described in our conceptual model (Fig. 1). This meta-analysis is a step toward identifying the contexts in which measured effects are large, and conversely those in which pathogens seem to be inconsequential to ecosystem processes.

Third, do studies of pathogen effects on ecosystem processes adequately reflect their occurrence and importance in nature? To answer this question, we present a systematic review of

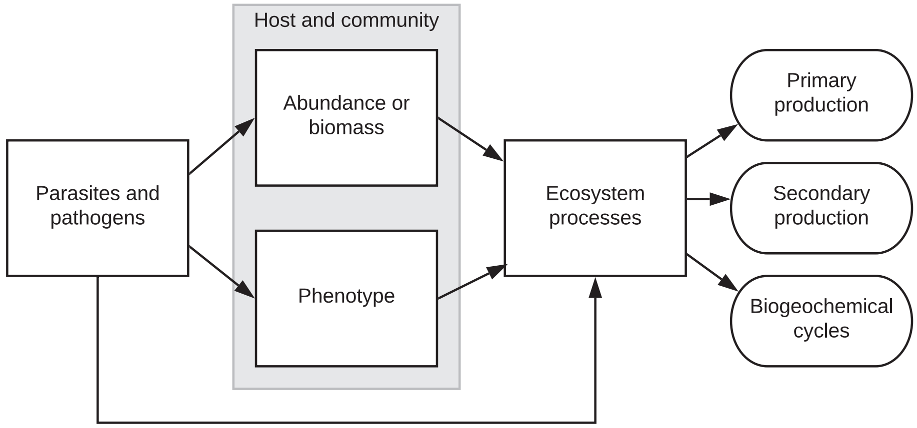

Fig. 1. Conceptual diagram of pathways by which pathogens or parasites can influence ecosystem processes. The diagram does not include all causal links, for example, the potential for feedbacks from ecosystem structure and function back to pathogens or parasites.

the ecological literature, quantifying the frequencies of taxa, pathways, ecosystem processes, and ecosystem types represented in peer-reviewed literature. The results identify knowledge gaps and point to priorities for future research to improve our understanding of pathogen impacts on ecosystems. By publishing the data we collected and the code we used for computing effect sizes, we also provide a foundation for more quantitative syntheses in the future.

Materials and Methods

Search strategy and selection criteria

Our systematic literature review followed the preferred reporting items for systematic review and meta-analysis protocols (PRISMA-P; Moher et al. 2015). The search strategy, adapted from that used in a recent review on this topic (Preston et al. 2016), required a title or abstract to contain terms related to pathogens and to primary or secondary production or biogeochemical cycles (Appendix S1). The search was performed in Web of Science on 17 July 2018 and extended back to 2007. Screening and review steps, including details on inclusion criteria and the numbers of articles at each step, are described in Appendix S2: Fig. S1. We included studies only if they contained quantitative data on pathogens in relation to ecosystem processes. We intentionally avoided using the terms “yield” and “crop” because the large body of literature on specific crop–pathogen interactions would have strongly biased our survey toward interactions involving a small set of crop hosts, generally under intensive management, with limited relevance to complex natural communities. Measures of primary and secondary production included biomass or biovolume; secondary production also included energy flow between trophic levels. Biogeochemical cycles included the elemental composition of living and non-living ecosystem components, fluxes of elements or water, and rates of decomposition. We define primary production as creation of biomass by primary producers (autotrophs) and secondary production as creation of biomass by secondary producers (heterotrophs).

Data collection

For each quantitative study, we extracted data on the kingdom of the host and of the pathogen; pathways by which the pathogen affected ecosystem processes (abundance, phenotype, direct, and/or undetermined); ecosystem type (terrestrial vs. aquatic); location; and biome. In some cases, pathogen or host taxa could be classified as prokaryotic or eukaryotic, but not classified to kingdom. Sometimes, it was not possible to distinguish whether the effects of a pathogen on ecosystem processes were via the abundance or phenotype pathways; for example, if soil elemental concentrations were measured in forest plots invaded vs. uninvaded by a fungus pathogenic to trees (Lovett et al. 2010), any effects may have been due to an unknown combination of changes in host or community abundance, and changes in phenotype of infected plants. In such cases, we indicated that the pathway was undetermined.

For each paper in the systematic review, we also sought to extract measures of the effects of the pathogen on ecosystem processes. We described effect sizes using the standardized mean difference, Cohen's d, in one of two ways: either infected vs. not infected, or in relation to infection prevalence or intensity (Borenstein et al. 2009, Koricheva et al. 2013). We included only data that could be extracted from the main text and tables of an article, excluding supplementary materials and graphs that required digitizing. Effects were excluded where information was insufficient to calculate d, for example, if variance was unreported and could not be computed, or controls were lacking. We included effects related to the abundance, phenotype, and undetermined pathways.

Statistical analysis

Studies presented a range of data types, including means and variances of ecosystem functions for infected vs. control groups, correlation coefficients relating infection to ecosystem function, and results of one-way ANOVAs, among others. Using equations relating test statistics, we converted a range of data types to Cohen's d (Appendix S3). We analyzed the natural log of the absolute value of d, adding a small value (1×10^{-6}) to each effect size to enable log transformation of all values. All analyses were done in R version 3.4.4 (R Core Team 2020).

We evaluated how effect sizes were influenced by a number of factors, including the taxa of pathogen and host, ecosystem type, the ecosystem process, and effect pathway. Separate linear mixed models were constructed to address each predictor; separate models were used, rather than combining multiple predictors in one model, to accommodate small sample sizes. Each model contained one fixed effect (e.g., pathway), and study was treated as a random effect. Models were fitted using function lme in R package nlme. Weights were set to the inverse of the sampling variance in Cohen's d. Least-squares means were calculated, and pairwise comparisons were made to determine which groups significantly differed from each other (using functions emmeans and CLD in package emmeans). We presented results after back-transformation from the log to linear scale, applying standard correction factors to avoid bias caused by transformation (Baskerville 1972). For the meta-analysis on pathogen taxa, non-fungal microbial taxa were reclassified into one group of other microbes, because the sample sizes for the constituent taxa were too small to analyze separately. The meta-analysis on host taxa was limited to plant and animal hosts, the two most common taxa.

We evaluated the relationship between effect sizes and sampling variances in effect sizes using visual inspection of a funnel plot and by computing a Kendall's rank correlation test; significant correlation may arise due to publication bias or other sources of variation (e.g., in study populations or methods) (Koricheva et al. 2013). This analysis used the original values for Cohen's d, rather than the absolute values. Publication bias, which is often present in meta-analyses (Koricheva et al. 2013), occurs when the effect sizes used in a meta-analysis result in conclusions different from those that would have been reached had the meta-analysis included every appropriate statistical test conducted. Publication bias can come about in several ways, including when effect size influences the probability of publication (e.g., due to selective reporting or decisions of editors), when effect size of a particular variable influences its inclusion in a publication, or when effect size influences whether a publication is included in a meta-analysis (e.g., due to publication language). Correlation between effect size and sampling variance may result from publication bias or from heterogeneity across studies in methods, taxa or ecosystems, duration, or sample sizes (Koricheva et al. 2013). Given the diversity of host–pathogen systems examined in our study, it would be reasonable to expect this heterogeneity to contribute to a correlation between effect size and variance.

We determined association frequencies among particular taxa, pathways, and ecosystem processes. Chi-square tests evaluated associations between pathogen and host taxa, and between these taxa and ecosystem types (terrestrial vs. aquatic), pathways, and ecosystem processes. We used function chisq.test in the R stats package, with simulated P values to accommodate low expected counts for some combinations.

Results

Pathogen impacts were evident across our three conceptual pathways but only for two of the three ecosystem processes examined (Fig. 2A,B). The abundance and undetermined pathways by which pathogens influence ecosystem processes had similar effect sizes and both were greater than the phenotype pathway (Fig. 2A). Pathogens had stronger effects on primary production than on secondary production or biogeochemical cycles (Fig. 2B). There were no differences in effect sizes based on ecosystem type (Appendix S2: Fig. S2, Table S1), pathogen taxon (Appendix S2: Fig. S3, Table S2), or host taxon (Appendix S2: Fig. S4, Table S3). A significant correlation between effect size and sampling variance ($Z = 3.63$, $P = 0.0003$) indicates possible publication bias or other sources of heterogeneity across studies (e.g., differences in host–pathogen systems or methods, as discussed above; Fig. 2C). From 2,169 citations returned by the literature search, 46 studies (2% of all citations) met the criteria for inclusion in meta-analysis, and 128 studies (6%) were included in the systematic review. Eighty-two studies included in the systematic review were excluded from the meta-analysis because they lacked controls (14 studies) or because data were unavailable or incomplete. Data extracted from studies are available, as well as R code used for computing effect sizes (Fischhoff et al. 2018).

While evidence from the available literature showed that pathogens can have large effects on ecosystem processes, it was also clear that this literature has considered only a small subset of the diversity of pathogens, hosts, and ecosystems. Studies of pathogen effects on ecosystem processes have been conducted in only a handful of all the possible combinations of taxa, ecosystems, pathways, processes, and geographies (Figs. 3 and 4; Appendix S2: Fig. S5, Table S4). The four most frequently studied combinations, representing 26% of 72 total combinations seen across all studies, all involved plant hosts in terrestrial ecosystems infected by either parasitic plants (18% of observed combinations) or fungal pathogens (8%). Of the 72 observed combinations, 11 combinations accounted for 50% of the studies. Certain combinations known to occur in nature, for example, plant hosts with viral pathogens in terrestrial ecosystems (Malmstrom and Alexander 2016), were not found in the available literature as defined by our search strategy. These patterns reflect, in part, associations between host and pathogen taxa ($\chi^2 = 144.91$, $P = 0.0005$; Fig. 3).

Pathogen and host taxa depended on ecosystem type (pathogen $\chi^2 = 47.74$, $P = 0.0005$; host $\chi^2 = 88.26$, $P = 0.0005$; Appendix S2: Fig. S6). Certain pathogen and host taxa were overrepresented among studies of particular ecosystem processes; for example, parasitic animals and animal hosts were overrepresented for secondary production (pathogen $\chi^2 = 25.34$, $P = 0.002$; host $\chi^2 = 43.73$, $P = 0.0005$; Appendix S2: Figs. S7, S8). Pathway and pathogen taxon were also significantly associated ($\chi^2 = 41.71$, $P = 0.0015$; Fig. 4; Appendix S2: Fig. S9). However, the pathways by which pathogens influenced ecosystem process were independent of host taxa ($\chi^2 = 14.04$, $P = 0.28$; Appendix S2: Fig. S10).

Certain geographies, biomes, and pathogens were underrepresented in the literature. Most studies were in the northern temperate zone, with only 25% of studies conducted below 27.6° latitude (Appendix S2: Fig. S11). Half of the studies (64) were located in temperate broadleaf, mixed, or coniferous forests (Appendix S2: Table S5), while some terrestrial biomes (e.g., tropical and subtropical dry or coniferous forests, flooded grasslands, mangroves) were not represented in any studies. Viruses (9% of studies) and bacteria (4%) were underrepresented relative to their diversity and abundance in nature. There are, for example, an estimated 320,000 undiscovered viruses in mammals (Anthony et al. 2013), compared to approximately 4,200 known species of haustorial parasitic plants (Nickrent 2002). Yet, those parasitic plants represented 20% of studies in our review.

The overall results of the meta-analysis were influenced by the preponderance of studies examining pathogen effects on primary production, for which the host abundance pathway predominated. We hypothesized that the importance of the host abundance (including biomass) pathway by which pathogens affect ecosystem processes would differ for plant vs. non-plant hosts. To test

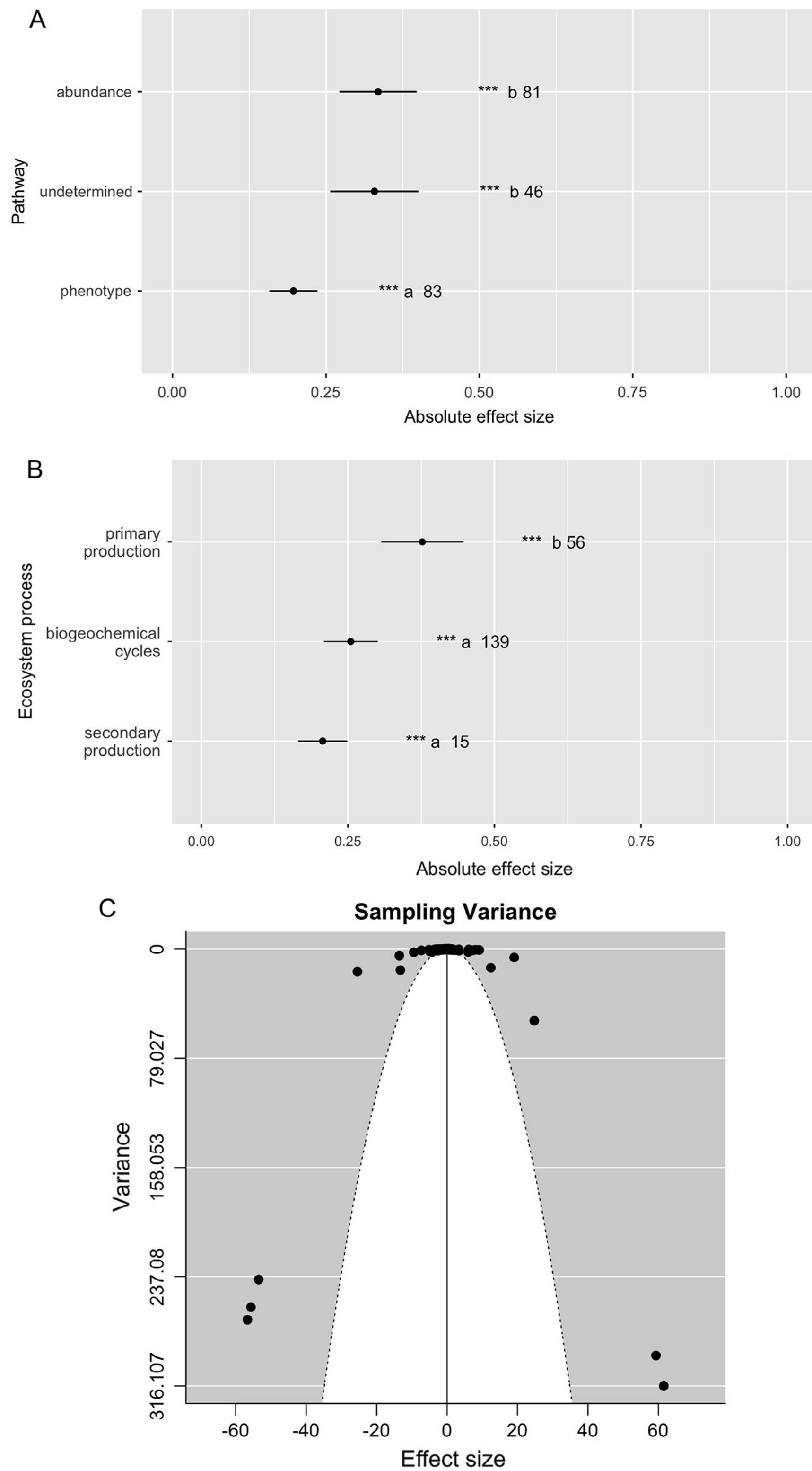

Fig. 2. (A) Absolute value of effect sizes and 95% confidence intervals for each of three pathways by which

(Fig. 2. *Continued*)

pathogens or parasites act. The same letter indicates two groups do not significantly differ in a pairwise comparison of least-squares means. Asterisks indicate significant differences from zero (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Numbers refer to sample sizes. (B) Absolute value of effect sizes and 95% confidence intervals for each of three ecosystem processes in systems influenced by pathogens or parasites. (C) Funnel plot depicting observed effect sizes (Cohen's d) vs. variance in d. Without publication bias or other sources of heterogeneity, most points would be expected to lie within the white pseudo-confidence region.

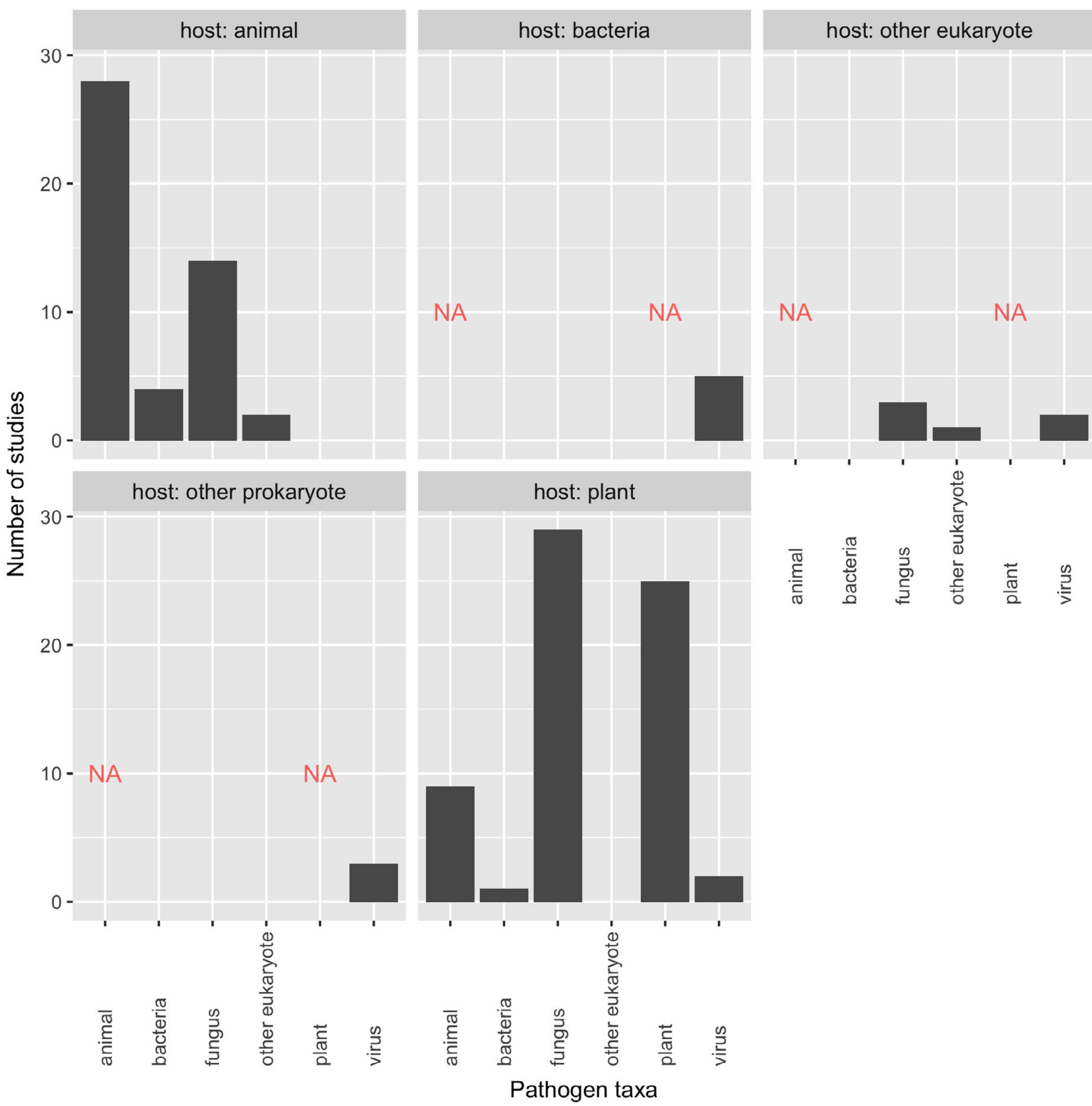

Fig. 3. Frequency of pathogen or parasite taxa examined in relation to host taxa in the literature review. Combinations which are physically implausible (e.g., a parasitic animal infecting a bacteria) are marked as NA.

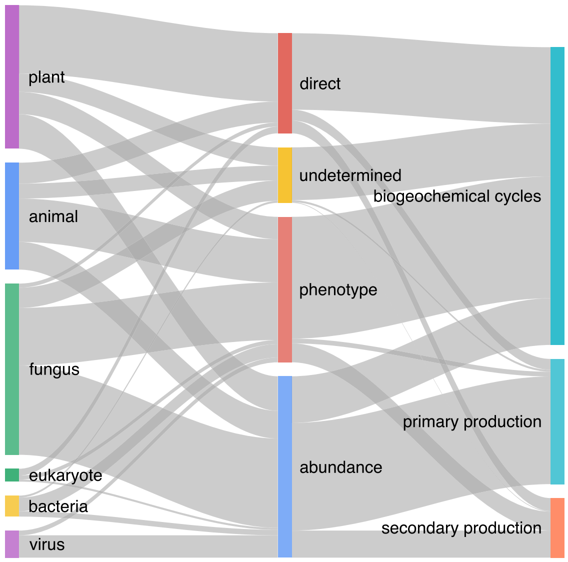

Fig. 4. Distribution of pathogens (left) among pathways (center) and distribution of pathways among ecosystem processes (right). For example, each pathogen or parasite taxon is represented in the abundance pathway, and the abundance pathway affects each ecosystem process.

this hypothesis, we removed studies from the dataset in which plants were hosts (54% of all studies) and repeated the analyses of pathway or ecosystem process as predictors of effect size. Excluding data on plant hosts, effect sizes for the abundance and phenotype pathways were similar (Appendix S2: Fig. S12, Table S6). Therefore, large effect sizes reported by studies of plant hosts contributed to larger effect sizes observed in the abundance pathway in the overall dataset. However, when excluding data on plant hosts, effect sizes on primary production were still larger than those on secondary production and biogeochemical cycles (Appendix S2: Fig. S13, Table S7). Thus, the large primary production effect appears to exist even without the disproportionate share of data from plant host studies.

Discussion

Pathogens play a significant role in ecosystem processes across a diverse array of host taxa and geographies. Here we demonstrate that the magnitude of pathogen impacts on ecosystem processes depends on the pathways by which pathogens act, as well as the particular ecosystem processes affected. Pathogens tend to have 1.7 times the impact (effect size) on ecosystem processes when affecting the biomass or abundance of host species or interacting species, relative to the impacts via the phenotype pathway (Fig. 1). These results provide a quantification of a previously reported pattern that more studies have reported density-mediated effects than trait-mediated effects of pathogens on ecosystem processes (Preston et al. 2016). Phenotypic changes may result in smaller effects on ecosystem processes in part because these phenotypic changes often reflect a middle ground in the coevolution of host and pathogen fitness strategies (Lefèvre et al. 2008). An important research frontier would be to assess whether the phenotypic change pathway is more important in non-plant hosts, whereas the abundance/biomass pathway is more important in plant hosts. The pattern of abundance- vs. phenotype-influenced effects of pathogens can be contrasted with that found in a meta-analysis of predator–prey interactions, where predator intimidation of prey (a phenotypic effect pathway) had a larger effect on prey resources (an ecosystem process), compared to the effects of the predator killing its prey (an abundance pathway; Preisser et al. 2005).

We also found that the published research likely covers only a subset of the likely effects of pathogens on ecosystem processes in nature, and this uneven coverage across systems is likely to have influenced the effect sizes estimated in our meta-analysis. One possible reason why plant hosts, and certain other systems, have received more research attention is that these systems were a priori considered more important by investigators. Economically or societally important interactions, for example, fungal pathogens of crop or timber plant hosts, receive more attention compared to studies of plants without these uses. A second possible explanation for the uneven representation is publication bias against negative results (i.e., other systems were studied but not reported on because no effects were found). Correlation between effect sizes and variances may indicate publication bias, although such correlation may also arise from heterogeneity in study subjects or methods (Koricheva et al. 2013). The question remains whether systems that appear less frequently, or not at all, in the literature are ones that have not yet been studied or for which negative results were observed but have not been reported.

Our results suggest that while pathogen impacts on ecosystems can indeed be large, developing a more comprehensive understanding will depend on future research across a greater range of host–pathogen systems, both in terms of taxa as well as biomes and geography. A previous review noted that, to understand ecosystem effects of pathogens, it is necessary to have data on ecosystem effects of infection on a per host basis, on infection prevalence and intensity, and on the relative importance of the host species to ecosystem processes (Preston et al. 2016). To develop a predictive framework thus requires host, pathogen, and ecosystem trait data (Schmitz 2009, Frainer et al. 2018). Our results indicate that some of these data exist in published studies, while some likely need to be gathered, through observational studies replicated across ecosystems, as well as large-scale field manipulations of pathogens, as also recommended in a recent review (Preston et al. 2016). Existing case studies vary in the information reported. However, a more complete dataset will emerge by integrating information from case studies (e.g., taxa, locations, dates) with information in complementary studies or datasets on species (Weimann et al. 2016), ecosystems, and ecosystem processes (Yuan et al. 2010). While our search required terms on both ecosystem processes *and* pathogens or parasites, additional literature searches on either ecosystem processes *or* parasites or pathogens may uncover additional studies that report effect sizes for apparently underrepresented host–pathogen systems. These literature searches would further confirm whether systems that appear to be understudied are in fact so.

We close by suggesting four priorities for future study, including understudied areas in which we expect to find important effects of pathogens on ecosystem processes. First, we recommend conducting studies in host–pathogen systems that have received less attention, including bacterial and terrestrial viral pathogens, as well as in biomes and geographies that have received less attention (e.g., boreal forest, tundra, the tropics, the Southern Hemisphere). The available studies suggest there are likely to be important effects of bacteria and viruses in terrestrial (Hartley et al. 2009, Holdo et al. 2009) and aquatic (Frost et al. 2008, Pinto et al. 2013) ecosystems. The lack of studies on viruses and terrestrial plants, for instance, reflects a major research gap, as there are likely significant ecosystem impacts of these infections. A second priority is research that seeks to understand how key axes of ecosystem variation, including age (time of ecological continuity), productivity, and diversity and composition (of hosts, pathogens, and traits), may interact to mediate pathogen impacts (Maron et al. 2011, von Oheimb et al. 2014, Frainer et al. 2018). We hypothesize that pathogen effects are greater in ecosystems where the period of coevolution with pathogen has been shorter, as for example in novel urban, silvicultural, and agricultural ecosystems, or where invasive species are involved, and that disturbance and pathogens can have synergistic effects. This would be consistent with increased impacts of environmental variability in younger ecosystems such as afforested lands (von Oheimb et al. 2014, Musavi et al. 2017). Third, we suggest expanding on past work examining how pathogen effects are influenced by human actions: climate change (Butenschoen and Scheu 2014), species introductions (Metz et al. 2013) deforestation (Vittor et al. 2009), and ecosystem management, including actions in response to pathogen effects (Eviner and Likens 2008). Climate change, for example, is hypothesized to increase ecosystem effects of pathogens, which are expected to adapt to changing conditions more rapidly than hosts due to pathogens having more rapid generation times and broader thermal tolerances (Cohen et al. 2017, Frainer et al. 2018). Fourth, we expect that host coinfection influences ecosystem processes in ways that cannot always be predicted based on effects of single infections. Though understudied in general, coinfection is known to affect transmission rates (Hall-Mendelin et al. 2016), host mortality (Ezenwa and Jolles 2015), and host phenotype (Rossi et al. 2017) in various systems. For example, the tropical panic grass *Dichanthelium lanuginosum* is conferred tolerance to geothermal soils when infected by the fungus *Curvularia protuberata*, but only when the fungus is itself infected by a virus (Márquez et al. 2007).

While our study used a search strategy adapted from a previous review (Preston et al. 2016), only eight of the 46 studies from which we extracted effect size measures were included in the 39 quantitative articles identified by the previous review (Preston et al. 2016). The infrequent overlap can be attributed to three differences in search strategies. First, our search strategy excluded studies on ecosystem structure or temporal dynamics, topics that were included in the previous review. Second, our meta-analysis included studies from 2007 through 2018, whereas the previous review included studies from 1980 through 2013. Third, we included articles from all subject areas in Web of Science, whereas the search in the previous review was restricted to ecology within Web of Science.

Given their global distribution and potentially global impacts, the ecosystem effects of parasites or pathogens have received increasing attention (Preston et al. 2016, Sures et al. 2017, Frainer et al. 2018), and some ecosystem effects have recently been quantified for particular systems (Thieltges et al. 2008, Pinto et al. 2013, Zhang et al. 2015). However, we are unaware of prior attempts to quantify these effects across taxa, ecosystems, and ecosystem processes. We detected significant effects of pathogens on ecosystem processes across systems, pointing to the need to broaden the focus of disease ecology, which traditionally has emphasized pathogen effects on host individuals, populations, and communities (Eviner and Likens 2008). To this end, additional synthesis, and field studies in understudied host–pathogen systems, will contribute to building a more comprehensive understanding of pathogens as drivers of ecosystem processes. As new work is undertaken, researchers can build on the data and code accompanying this paper to address new questions. We expect pathogens will take on increasingly influential roles in ecosystems due to anthropogenic disturbances. Greater collaboration between disease ecologists and ecosystem ecologists would facilitate advances in understanding and management of ecosystems and the services they provide society.

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