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Cite this article: Park AW, Cressler CE, Dallas TA, Farrell MJ, Huang S, Pedersen AB, Varney RM. 2025 Costs of parasite generalism revealed by abundance patterns across mammalian hosts. *Proc. R. Soc. B* **292**: 20251157.
https://doi.org/10.1098/rspb.2025.1157

Received: 2 May 2025
Accepted: 25 September 2025

Subject Category:
Ecology

Subject Areas:
ecology, evolution

Keywords:
generalist parasite, costs of generalism, parasite fitness, parasite host range

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Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare.c.8075084.

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Costs of parasite generalism revealed by abundance patterns across mammalian hosts

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Most parasites are able to infect several host species, yet generalism is anticipated to be a costly strategy. Parasite abundance provides an important indicator of fitness because it is promoted by longevity and fecundity, which are correlated with a parasite's basic reproductive number. Using a global database of parasitic helminths of terrestrial mammals, we show that the abundance of parasitic helminths is phylogenetically structured across helminth species. High parasite abundance can be achieved through three separate components: infecting abundant host species, having a high infection success (prevalence) or achieving high parasite abundance withinhost individuals (infection intensity). Both phylogenetically specialist and generalist strategies can reach high abundances but through different strategies. Relatively specialist parasites achieve higher abundance than generalists on their principal host species but rely on host relatedness to infect multiple species. For generalist parasites, geographic overlap with and diet similarity to principal host species are better predictors of parasite abundance than host relatedness. This study characterizes constraints on parasite host range and provides novel context to evaluate the potential for parasites to establish in new host species.

1. Introduction

Across parasite species, there are enormous differences in their infection patterns [1–8]. Extreme specialists may infect only one host species, relying on efficient exploitation of the host to achieve high fitness [9]. At the other extreme, some generalist parasites rely on a community of host species for persistence, with each host species insufficient to sustain the parasite by itself [10]. Other parasites may attain relatively high or low fitness on principal and auxiliary host species, respectively [11], where a principal host species is that with which the parasite has the highest fitness and auxiliary hosts represent the remainder of the parasite's host range. The theory behind a trade-off hypothesis suggests that parasites may evolve specialist or generalist strategies (i.e. a degree of host specificity), based on the balance between the many costs and benefits of those strategies including variation in host availability, parasite longevity and fecundity, the efficiency of intra- and interspecific transmission and the probability of host death from infection [12]. At the cost of eschewing infection opportunities among many host species, a parasite's specialized adaptation to the ecology and physiology of a restricted set of host species should improve its total abundance via increased prevalence and average infection intensity, respectively, concerning the proportion of hosts infected in a population and the number of parasites per infected host individual [13]. To maximize fitness, parasites may be more likely to adapt to host species that represent reliable resources, which may either be of large body size and lifespan [14] or high population density [15]. Generalist parasites are anticipated to attain lower prevalence and intensity than specialists in the same host species because they may pay costs of contending with defence mechanisms of multiple, biologically distinct host species [16,17]. However, generalists can potentially benefit from more numerous or more stable host resources at the community level [17], so that their total abundance across all hosts may still be high. A further potential cost to generalist parasites comes in the form of non-host resistance [18], in which failure to infect species distantly related to principal hosts can arise as an incidental by-product of specialization on principal hosts.

Empirically, the relationship between parasite specificity and fitness may be explored through the lens of parasite abundance, which, thanks to the development of global-scale databases of parasite infections, is now feasible to estimate from its component parts: host abundance, parasite prevalence and parasite intensity [19]. In free-living plant and animal species, population size is known to correlate with fitness [20,21] because variation in abundance is strongly controlled by differences in fecundity and survivorship [22]. Additionally, large populations may reflect higher fitness due to both stronger selection via relatively large effective population sizes preventing the fixation of deleterious alleles and the introduction of novel, beneficial alleles [23]. Parasitic organisms similarly attain population sizes governed by their fecundity and survivorship, although additional processes including density-dependent transmission, overdispersion in host populations and constraints on abundance caused by parasite-induced host mortality can complicate the relationship between fitness and parasite abundance [24,25]. Like free-living species, parasites also experience fitness benefits from relatively large effective population size [26]. Consequently, estimated parasite abundance supported by a host species (hereafter, parasite abundance) reflects adaptation to a given host [27]. In cases where host abundance is known only at large spatial scales, for example, the entire host geographical range, then it is prudent to replace host abundance with host density to give a related estimate of parasite abundance. This avoids the strong assumption that parasite prevalence and intensity estimates measured locally extend throughout the geographical range of the host, which may not apply due to ecological and evolutionary differences in both host and parasite species at large spatial scales.

Recent research suggests that our understanding of patterns of host-parasite associations may be improved by considering both the phylogenetic and ecological distances among potential host species [28]. Evolutionary ecological forces could lead to patterns of parasite abundance changing with phylogenetic distance from a principal host species due to evolved resistance and parasite specialization [18]. In addition, ecological opportunity for infection may counterbalance or even outweigh phylogenetic barriers to infection [5,28], so that predictors describing ecological similarity and transmission opportunity such as dietary preference and geographic range size [29] may better explain patterns of parasite abundance. In addition, host body size is a general indicator of the metabolic rate [30] and is associated with animal behaviours (e.g. foraging ranges and thus exposure to parasites) and life histories, including the pace of life [31], a suite of traits that can influence investment in immunity [32]. Consequently, considering similarity in both phylogenetic and ecological dimensions can help better identify and understand the costs and benefits of specialization and generalization.

Studies aimed at characterizing and explaining variation in parasite abundance as a function of specificity are limited in number. Across parasites of freshwater fishes, both endo- and ectoparasites exhibit a tendency to trade off abundance with host range; parasites infecting a greater number of host species typically attain lower prevalence and intensity per host species compared to parasites infecting fewer species [16]. The abundance of ectoparasitic fleas of small rodents shows the opposite pattern; generalist parasites attain higher abundance than specialist counterparts, which is posited to be related to a higher mean and lower variance of the number of host individuals [17]. A study of helminths infecting birds found evidence that specialist nematodes attain higher abundance than generalist nematodes, whereas trematodes show the opposite pattern, and cestodes show no significant relationship between specificity and abundance [33]. These equivocal findings across systems invite a macroecological study synthesizing parasite abundance data across multiple host and parasite species and integrating the phylogenetic and ecological perspective to better understand how specialist and generalist infection strategies fare in terms of maintaining parasite populations.

Here, we evaluate the extent to which parasite host range incurs costs in abundance and the primary factors that underlie such costs. Mammalian hosts are a promising group to test for a relationship between parasite abundance and specificity as the parasites of carnivores, ungulates and primates (orders: Carnivora, Cetartiodactyla, Perissodactyla and Primates) are well-documented in the Global Mammal Parasite Database (GMPD) and include data on parasite prevalence and intensity [34], while average host population densities are also readily available [35]. This allows investigation into which of the three components (host density, parasite prevalence and parasite intensity) primarily drives parasite abundance across host species. Additionally, hosts are well described in terms of their average adult body mass [35], geographical ranges [36] and diet [37], facilitating investigation into which ecological traits may explain similarities in parasite infection patterns across species in addition to well-established phylogenetic relationships [38]. Specifically, we might expect phylogenetically specialist parasites (i.e. those infecting phylogenetically clustered host species) to obtain relatively similar, high levels of abundance in association with the shared evolutionary history and overall biological similarity among their host species and that parasite abundance may decline with phylogenetic distance from the principal host. Accordingly, we include previously calculated values of parasite phylogenetic specificity [8] as a predictor variable. In contrast, generalists may have low abundance due to the trade-off hypothesis [16,17] or infect principal host species that support relatively high abundance and infect auxiliary hosts opportunistically, providing low parasite abundance due to non-host resistance [18]. Furthermore, if such opportunistic infections are a result of circumstance, we may expect generalist parasite abundance patterns to be explained by factors such as shared geographic range or diet between principal and auxiliary hosts. Overall, by comparing host species in terms of parasite abundance, we can tease apart the roles of host relatedness and ecological similarity in explaining parasite abundance and its distribution across hosts.

2. Methods

(a) Parasite abundance

Abundance data for helminth parasites infecting free-ranging, land species of carnivores, primates and ungulates (orders: Carnivora, Cetartiodactyla, Perissodactyla and Primates) were obtained from the GMPD 2.0 [34]. These data were combined with estimates of average body mass and host population density data for mammal host species from the PanTHERIA database [35]. The data were further filtered to include only studies in which parasite intensity was estimated using adult worm counts (recorded in the GMPD as: 'ParasiteCount', 'Average number of parasites per animal', 'Count', 'individual worms', or 'number of individual'), excluding other measures such as faecal egg counts. Records were dropped if the parasite was not identified to species level, if either prevalence or intensity data were not reported, if the parasite did not infect at least two host species, if the host was an intermediate rather than definitive host species to the parasite or if the definitive hosts in the GMPD were atypical (electronic supplementary material, table S1). The resulting dataset contained 1112 records comprising 106 parasite species in 43 host species. Parasites infecting only one host species were inspected for host population density, prevalence, intensity and parasite abundance for comparison with the same measurements of multi-host parasites in association with their optimal host species, i.e. their maximum values (electronic supplementary material, figure S1).

For the multi-host parasites, upon grouping by host and parasite species, average prevalence was calculated as a weighted mean using the number of host individuals from which each prevalence value was estimated, and average intensity was calculated as an arithmetic mean. Estimated parasite abundance per host species was then calculated as the product of host population density, average parasite prevalence and average parasite intensity, following methods proposed previously [19]. While host abundance, not host density, is the formal component of parasite abundance, infection is measured at a local scale in the GMPD, and this varies across studies. Because spatial extrapolation of prevalence and intensity throughout the host range is inappropriate, average host density was used in place of host abundance as a metric that is invariant across spatial scales, providing relative measures of parasite abundance. In addition to raw measures of parasite abundance, standard effect sizes for parasite prevalence and intensity per host-parasite combination were calculated as $(x - \mu)/\mathrm{SD}$, where x is the average measure for a host-parasite interaction, μ is the average measure for the parasite, and SD is the standard deviation of the recorded measure for the parasite. Similar standard effect sizes were calculated for host population density and parasite abundance, with the latter calculated from untransformed components rather than from standard effect size components. Collectively, these standard effect sizes allow comparison across parasite species, which can vary dramatically due to different parasite life histories and host species regional pools.

A comparison of total abundance (summed across all observed host species) was made among parasite species, along with their host species-specific abundance and evenness in abundance across host species. Evenness was calculated as the per host species decrease in relative abundance (log transformed), obtained via linear regression, for each parasite species with their hosts ordered from highest (principal) to lowest parasite abundance. Subsequent analysis comparing evenness across parasite species was performed using phylogenetically controlled linear regression. Lastly, the comparison of parasite abundance between pairs of species was attained using the difference in the standard effect sizes for parasite abundance.

(b) Phylogenetic signal in parasite abundance

As there is currently no helminth phylogeny that includes branch length estimates spanning all of our focal parasite species ($n = 106$), we reconstructed a working phylogeny based on parasite taxonomy using the ape::as.phylo function in R [39], with unit branch length segments between ranks of kingdom, phylum, class, order, family, genus and species. Parasite species had their abundance estimate combined with the tree using the phylobase::phylo4d function in R [40], from which a phylogenetic signal in abundance could be tested for directly using Abouheif's C-mean test (R function adephylo::abouheif.moran by [41]) which does not rely on branch length estimates [42]. The taxonomic tree was also used to control for phylogenetic covariance in statistical models, detailed in §2d below. Equivalent analyses were also conducted on a subset of parasite species ($n = 69$) for which we were able to build a molecular phylogeny using sequence information for the cytochrome oxidase I (COI, COX1) gene to verify that results were qualitatively identical across taxonomic and phylogenetic tree approaches (detailed methods and results presented in the electronic supplementary material).

(c) Predictors of parasite abundance

Parasite generalism was considered from three perspectives: number of host species (within the GMPD), the phylogenetic relatedness of host species (i.e. phylogenetic host specificity) and the geographic range of the parasite. Phylogenetic host specificity for a parasite species was calculated as the standard effect size of the mean pairwise phylogenetic distance among hosts using an established mammal phylogeny [38], with more negative values indicating phylogenetically specialist parasites; infecting host species more closely related than expected by chance [8]. Although more recent mammal phylogenies have

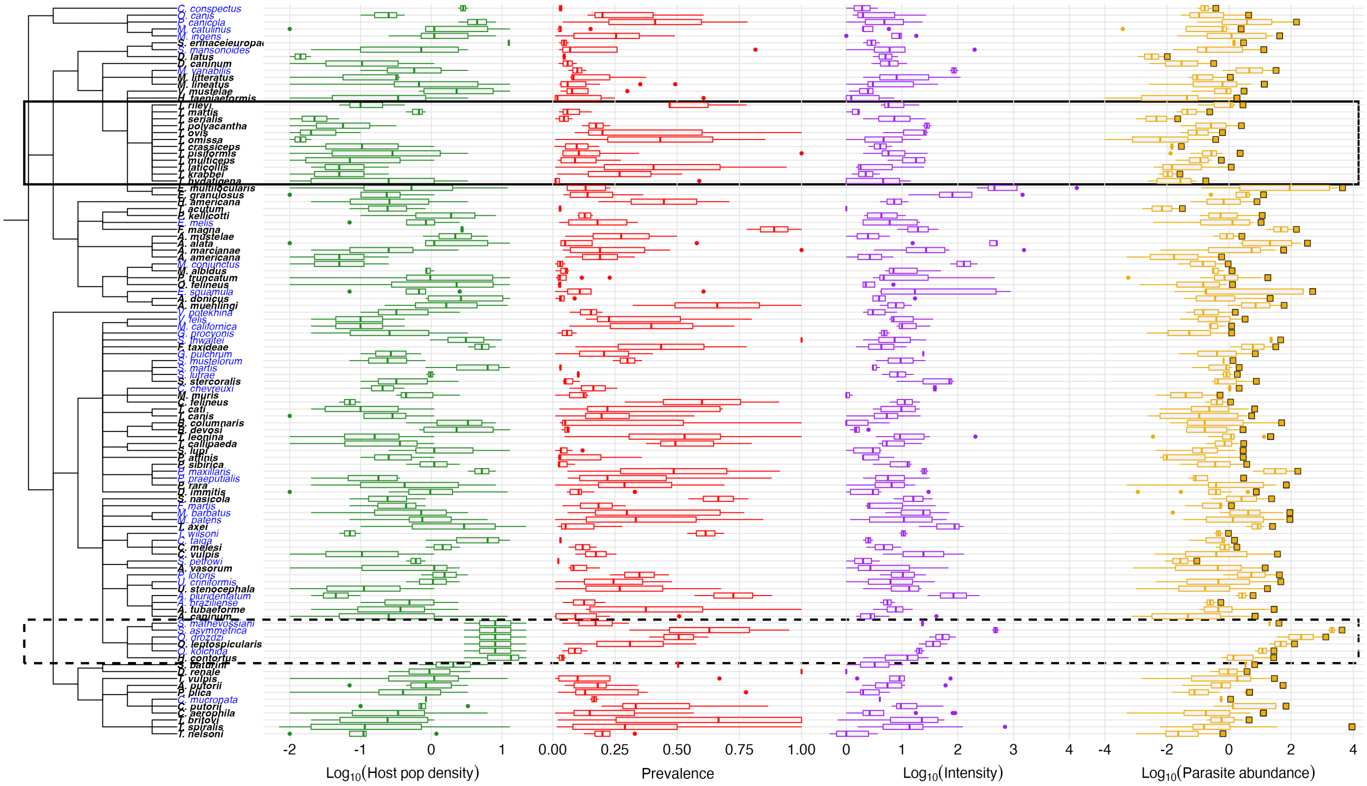

Figure 1. Taxonomic tree of parasitic helminths with corresponding box-and-whisker plots showing their range of host population density (green), estimated prevalence (red), intensity (purple) and abundance (gold) across their host range. The filled gold squares (far right) represent the total estimated parasite abundance (i.e. summed across all host species). Large rectangles highlight parasite clades referred to in the text as exhibiting low (solid) and high (dashed) parasite abundance. Parasite species names in black were retained in the phylogenetic analyses (electronic supplementary material).

been published, this version was used because it matched the mammal taxonomy in the GMPD. Following recent approaches [43], the geographical extent of a parasite was defined as the number of ecoregions in which it occurs, using georeferences of infections in GMPD and terrestrial ecoregion shapefiles [44], under an equal area projection.

Parasite abundance supported by different pairs of host species was compared in relation to host species phylogenetic distance, geographic overlap and ecological similarity based on body size and diet. The phylogenetic distance between host pairs was calculated using the same published phylogeny of mammals used to calculate parasite specificity [38]. Differences in average host body mass were obtained from the PanTHERIA database [35]. Geographic overlap of host species was measured as area from mammal geography range maps [36] in an equal area projection using the Simple Features (sf) package in R [45]. Diet similarity between pairs of species was estimated using EltonTraits 1.0 [37] which includes the proportion of species' diets that belong to each of 10 categories. Vectors of these proportions were assessed for similarity for each pair of host species using the Horn–Morisita index [46].

(d) Statistical modelling

Correlations between the components of parasite abundance and abundance itself were established using Spearman rank correlation tests. Subsequently, parasite abundance and its components were related to predictor variables through a series of phylogenetic generalized linear models (PGLMs) which account for phylogenetic relatedness of parasite species, implemented via the R package 'caper' [47], in conjunction with the parasite taxonomic tree with unit branch lengths (figure 1).

The relative contribution of principal host species (defined per parasite species as those with the highest parasite abundance) to the total parasite fitness was evaluated under specialist versus generalist parasite scenarios. Because initial analyses showed a significant constraint on total parasite abundance by phylogenetic specificity, parasite species were assigned specialist or generalist status using the phylogenetic specificity score (outlined above in 'Predictors of parasite specificity'). To form a balanced number of pairwise comparisons, the mean specificity score was used as the cutoff (n = 154 for specialists with score below the mean, and n = 146 for generalists). For each resulting parasite group ('specialists' and 'generalists'), linear models relating different pairwise comparisons of hosts were constructed. Predictor variables were phylogenetic distance, diet similarity, geographic overlap and difference in body mass, and p-values were adjusted for multiple comparisons using the Holm method [48]. Regular linear models (versus phylogenetic linear models) were used because parasite species are repeated (i.e. in cases where a parasite has data relating to more than 2 host species, the principal host species can be compared with multiple auxiliary host species).

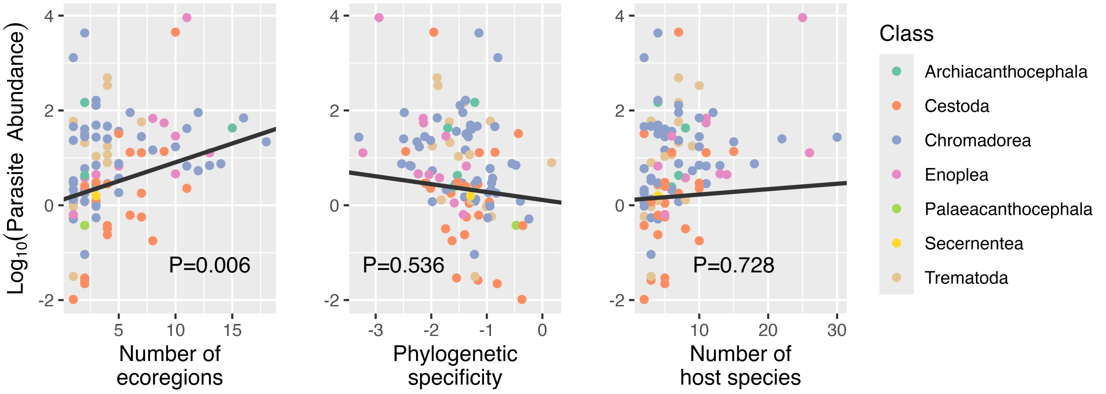

Figure 2. Estimated parasite abundance as a function of number of ecoregions in which parasite occurs, phylogenetic specificity of parasite (standard effect size with larger negative numbers indicating extreme specialism), and number of host species the parasite infects. Regression lines show marginal effects of predictor variables from a single multivariate, phylogenetically controlled linear model. Circle colour indicates parasite taxonomic class.

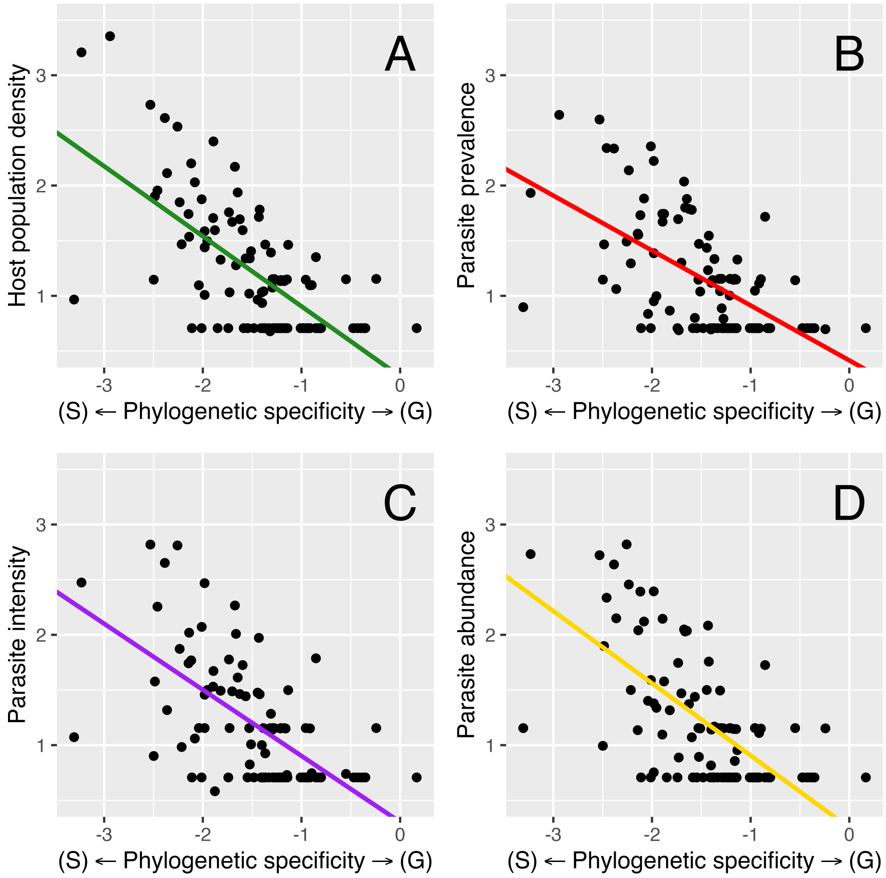

Figure 3. The relationship between phylogenetic specificity and abundance supported by a parasite's principal host. 'Principal host' is defined for each component separately: (A) host population density (green), (B) parasite prevalence (red), (C) parasite intensity (purple) and (D) integratively as total parasite abundance (gold). All measures are standardized effect sizes. (S) and (G) indicate specialist and generalist parasite species, respectively.

3. Results

(a) Overall patterns of parasite abundance

Our data show that parasite abundance has a significant phylogenetic signal (p-value = 0.001; figure 1). As illustrative examples, species in the *Haemonchidae* family (figure 1, dashed rectangle: *Haemonchus contortus*, *Ostertagia drozdi*, *O. kolchida*, *O. leptospicularis*, *Spiculopteragia asymmetrica*, *S. mathevossiani*) exhibit high total abundance whereas the *Taenia* genus contains several species with relatively low total abundance (figure 1, solid rectangle; e.g. *T. crassiceps*, *T. krabbei*, *T. serialis*).

All three components of parasite abundance in a given host species (host population density, prevalence and intensity) were positively associated with total parasite abundance (electronic supplementary material, figure S2). Among component pairs, prevalence and intensity showed the most consistent (positive) correlation, but the spread of correlation values for all component pairs underscores that parasite abundance is driven by only one or two of the three components in some cases (electronic supplementary material, figure S2).

Among the three indicators of a parasite's generalism, high total parasite abundance was positively associated with the number of ecoregions in which the parasite occurs but not associated with phylogenetic specialism or host richness (figure 2;

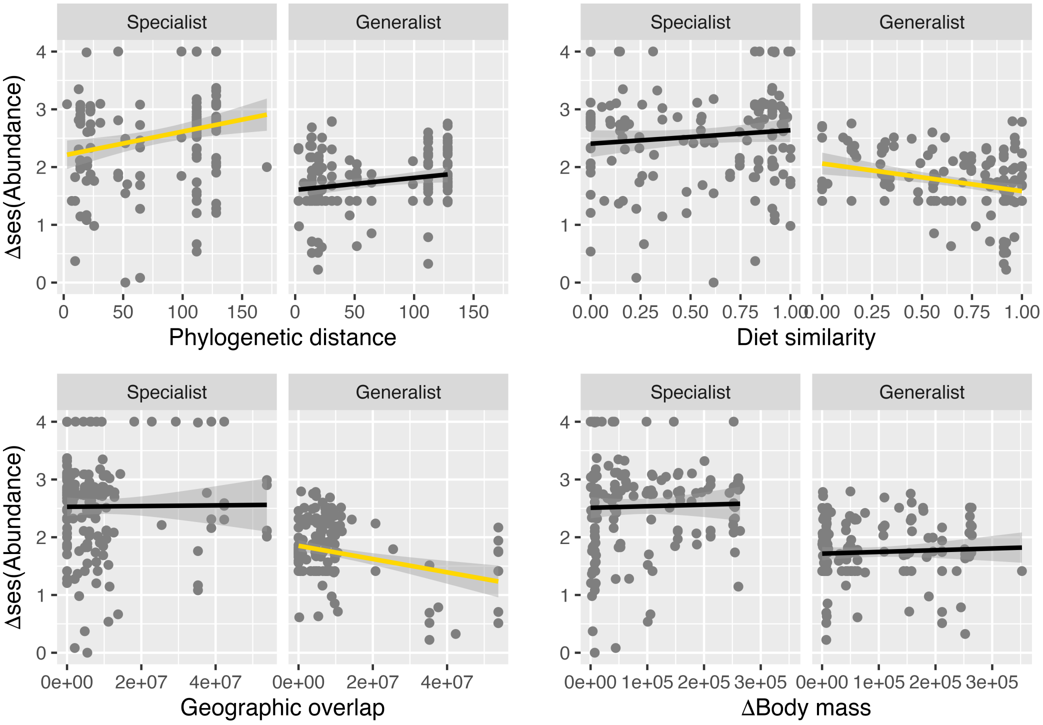

Figure 4. Differences in the standard effect sizes for parasite abundance between a parasite's principal host and other hosts. Specialist and generalist parasite groups were obtained using the lower (specialist) and higher (generalist) standard effect sizes for mean pairwise phylogenetic distance of hosts to form two balanced sets of comparisons. Linear regression relating each predictor variable to each parasite group's abundance values was performed, and statistically significant regressions (gold lines) were established by controlling for multiple comparisons across the eight models using the Holm method [48].

PGLM p-values: 0.004, 0.514, 0.768, respectively, with further details in electronic supplementary material, table S2). A corollary of this result is that parasites that infect few or many host species, or that infect related or unrelated host species, may attain comparable total abundances via different strategies.

(b) Abundance associated with a parasite's principal host

The single principal host for each parasite in terms of supporting high parasite abundance or its components tended to support higher relative and absolute abundance for specialist compared to generalist parasites (figure 3; electronic supplementary material, figure S3). Specialist parasites typically infect at least one host species that occurs at a higher population density than the hosts of phylogenetically generalist parasites (PGLM p-value < 0.01; figure 3; electronic supplementary material, figure S3, green line). They also achieve higher intensity infections (p-value ≤ 0.03; figure 3; electronic supplementary material, figure S3, purple line) and standard effect size for prevalence is higher for specialists (p-value < 0.01; figure 3; electronic supplementary material, figure S3, red line). While the components of parasite abundance are higher for the principal hosts of specialist parasites, they do not necessarily occur for the same host species per parasite (e.g. the principal host in terms of host population density may not be the same as the principal host in terms of intensity). Nevertheless, parasite abundance measured as the product of host population density, prevalence and intensity on a single-host species confirms that specialist parasites typically attain higher abundance on their principal host compared to generalist parasites on their principal host (p-value < 0.01; figure 3; electronic supplementary material, figure S3, gold line). Single-host parasite species exhibit large variation in intensity and abundance, compared to equivalent principal host measurements for multi-host parasites (electronic supplementary material, figure S1) such that some, but not all, single-host parasite species have higher metrics compared to their multi-host counterparts. Additionally, the median host population density for the single-host group is higher than the multi-host group, while their prevalence values are lower. However, raw prevalence measures are discernibly noisier than other metrics in this study (electronic supplementary material, figure S3, panel D).

(c) Differences in abundance patterns across host sets for specialist and generalist parasites

Phylogenetic specificity of parasites is negatively related to evenness in relative parasite abundance across host species (electronic supplementary material, figure S4, with further details in electronic supplementary material). Essentially, phylogenetic specialist parasites attain a more consistent abundance across their host set compared to generalists, which are characterized by higher variability in abundance across their host set, including larger differences in parasite abundance between principal and auxiliary hosts.

Specialist and generalist parasite groups show different relationships of parasite abundance variation with host phylogenetic distance and ecological similarity (figure 4, where gold lines indicate statistically significant relationships). Compared to parasite abundance in a parasite's principal host, specialist parasites achieve similar abundances on hosts that are closely related to the principal host (phylogenetic distance subplot, p-value = 0.020). In comparison, generalist parasites achieve similar abundances to their principal host on hosts that have similar diet to, or relatively large spatial overlap with, the principal host species (p-values = 0.002 and 0.001, respectively). For both parasite groups, there was no correlation between similarity in host body mass and similarity in parasite abundance.

4. Discussion

The abundance of parasites is generated by the availability of hosts and the intensity and prevalence of infections across different hosts. These axes of abundance are each determined by a variety of factors ranging from evolutionary constraints, opportunities for infection, and trade-offs in performance across hosts. Parasites that generalize by infecting multiple, unrelated host species are anticipated to pay costs associated with contending with host resources that vary in terms of within-host navigability [49], spatial niche availability [50], tissue resources and immune defenses [51]. Using a database of parasite abundances for helminths of mammals, we find that across parasite species, higher total abundance is not necessarily driven by any one component; some parasites preferentially infect abundant host species, some attain high prevalence, while others generate high-intensity infections. We also show that while high total abundance across all host species is associated with a large geographic range, there is no evidence it is driven by the number of host species a parasite infects or their relatedness to each other. Rather, the phylogenetic specificity of parasites is more informative of their abundance in association with their principal hosts.

The total estimated abundance of parasitic helminth species infecting terrestrial mammals is partly explained by their evolutionary history, as revealed by phylogenetic signal. Testing for, and finding, such signals in ecological traits of parasites is rare and could indicate trait evolution in underlying processes, especially fecundity and longevity [52]. Previous research of ectoparasites has demonstrated that mean parasite intensity, a key component of abundance, shows a strong phylogenetic signal, indicating the potential for parasite abundance to be similar between related parasite species [53].

Phylogenetic specificity is a strong predictor of all components of parasite abundance in the principal host species because it directly reflects the biological constraints on a parasite's ability to expand its host range. The high abundance and fitness of specialists in their principal host species shown in our data strongly suggest that adaptation favours the colonization of host species that represent reliable resources, captured via host population density and sheds light on previous studies that show positive relationships between parasite species richness and host population density [15,54], since high host density is probably a valuable resource that many parasite species may benefit from and adapt to. Both the higher infection success of specialist parasites, captured by prevalence, and their higher within-host abundance, captured by intensity, indicate costs of generalism. Logically, these costs are associated with encountering multiple, distinct sets of host defenses [16,17] and may compromise both colonization of, and persistence within, hosts as generalist parasites contend with various ecological, physiological and immunological defenses that differ between phylogenetically distinct host species [17]. A correlation between prevalence and intensity was observed for many, but not all, parasites. This indicates that some parasite species may be able to overcome host defenses, for example, against parasite colonization, but then fare relatively poorly once inside a host. However, the broadly positive correlation, which has also been observed in fish–parasite interactions [16], suggests that specialization avoids several costs associated with generalist parasite establishment in hosts.

Single-host parasite species are not defined in terms of phylogenetic specificity, which is measured as average pairwise phylogenetic distance between host species. Neither is it possible to calculate their within-host group measures of components of parasite abundance (i.e. the extent to which metrics for principal hosts are above average compared to auxiliary hosts). While many single-host parasite species appear to infect hosts of relatively high population density, achieving high-intensity infections and abundance, others do not show this pattern. This may be due to sampling; until a second host species is identified for a parasite, either by more intensive surveillance or by natural host range expansion, we are never sure what its specificity could be. Second, an important strength of our approach lies in characterizing the *relative performance* of parasites on principal host species compared to auxiliary hosts. In contrast, single-host parasites are restricted to *absolute performance* metrics (raw host population density, prevalence and intensity), which may vary across parasite species idiosyncratically, due to evolutionary history and ecological circumstance.

For multi-host parasites, across their range of hosts, other differences emerge as a result of specificity. First, compared to generalists, specialist parasites have a more even distribution of abundances across host species. Generalist parasites appear to pay a cost in that while infecting a broader number or diversity of host species, their auxiliary hosts sustain relatively small parasite population sizes compared to their principal hosts. Generalist parasite abundance in association with principal hosts shows weaker evidence for adaptation as metrics such as prevalence and intensity are not dramatically different from parasite group means (averaged over both principal and auxiliary hosts). Furthermore, our data suggest that the decline in parasite abundance across host species operates along different latent gradients depending on specificity; specialist parasite abundance declines from the principal host along a host phylogenetic distance gradient, whereas generalist abundance declines along ecological gradients that reflect opportunity for infection, namely geographic overlap with, and diet similarity to, principal hosts. Such opportunistic infections frequently appear to support only small parasite populations, reflected in low evenness of parasite abundance in principal and auxiliary hosts. Previous related research has noted contrasting results in abundance of parasitic fleas of small mammals versus metazoan parasites of fish [55,56]. Flea abundance on auxiliary host species tends to drop sharply with taxonomic distance from the principal host [55], whereas taxonomic distance was less informative in the study of fish parasites, which attained similar abundance to principal hosts in all but the most taxonomically distant host species [56]. Interestingly, there is some evidence that parasitic fleas of small rodents are more generalist than metazoan fish parasites, evidenced by the relatively low sample size of auxiliary hosts that are closely related to principal hosts among fleas.

This may indicate that the importance of phylogenetic versus ecological gradients in predicting parasite population sizes of specialist versus generalist parasites extends beyond the helminth parasites of mammals in our study.

Within major parasitic groups, including helminths, but also viruses, bacteria, arthropods and protozoa, there is considerable variation in phylogenetic specificity of parasite species [8], indicating that both specialist and generalist life histories are viable. Having identified several costs to generalism among parasitic helminths, it is important to also consider both cryptic advantages and mechanisms that maintain generalism in spite of costs. Generalist parasites are less dependent on any one of their host species and so may be buffered against local extinction when host populations become locally extinct or are reduced to low abundance [57,58]. However, generalist parasites can still be negatively impacted by reduced interspecific transmission, habitat fragmentation and host range expansion to novel communities [59,60]. Even if cryptic advantages to generalism are slight, such life-history strategies may occur through necessity. Some parasite species may have evolved generalist infection strategies due to being inferior competitors with other parasites [61]. Indeed, for ectoparasites of birds, there is macroevolutionary evidence that competition has been associated with multiple transitions from specialist to generalist strategies [62]. Lastly, some auxiliary host species may simply be a by-product of transmission mode, including the use of intermediate hosts, that creates exposures to multiple species [63].

Classical macroparasite models demonstrate a clear, positive relationship between the fitness of a parasite and its fecundity and longevity, traits that also promote large population sizes [64]. In using parasite abundance to make inferences about fitness and adaptation, it is important to recognize that the abundance/fitness equivalence is complicated by factors that are unmeasured in our data but should be investigated in the future. These include the survival of free-living stages, which vary across parasite species, environmental gradients and due to anthropogenic effects [65,66]. Furthermore, the strength of intraspecific density dependence may vary across parasite species [67]. Also, because the fate of parasites is tied to their hosts, the level of virulence can modify the fitness of a parasite species, and a parasite may co-occur in a host with other parasite species that could either promote or inhibit its population size through both susceptibility and parasite clearance mechanisms [68,69]. While these factors contribute to observed estimates of parasite abundance, we acknowledge that they are not measured explicitly in our study. In addition to these parasite effects, levels of host resistance and tolerance are generally not known for the host-parasite combinations studied. The potential for evolved resistance means that parasite adaptation may not always lead to increased parasite abundance [18]. Similarly, variation in host tolerance across species may lead to different levels of parasite intensity in hosts, and mortality tolerance may increase prevalence through increased infectious periods, whereas fecundity tolerance may do the opposite [70].

Large databases like the GMPD are always subject to some bias in coverage, towards, for example, some geopolitical regions, certain mammal taxa and parasites of human health concern [71], and in some cases, data had to be omitted if, for example, both prevalence and intensity were not measured. However, the study of over one hundred parasite species from over 40 host species has provided an unparalleled opportunity to examine how the abundance of parasite species varies with degree of generalism. Our results highlight important costs and benefits associated with a host range comprising principal and auxiliary hosts and pave the way to a deep, mechanistic understanding of parasite generalism. We focused on interactions between parasites and their definitive hosts, for which we have high-quality data from the GMPD [34]. Previous work estimating a related component of parasite abundance, namely the proportion of parasites surviving their infection of a host, suggested that integration of complex lifecycle parasite data, i.e. multiple parasite species and both intermediate and definitive host types [72], presents weak evidence of phylogenetic signal, due to both variability among parasite species, but also variation in survivorship of a given parasite species across host types [73]. Consequently, for parasites in our study that use both intermediate and definitive hosts, their high abundance via definitive hosts may be enhanced or compromised depending on their fitness in association with intermediate host species, with host food web structure providing a promising way to consider costs of generalism in the broader context of transmission opportunities [74].

Costs of parasite generalism are often invoked to explain the diversity of parasite host ranges and associated traits [75–79], but are rarely measured, except in amenable laboratory systems [80–82]. Quantifying costs of generalism helps us understand constraints on a parasite's host range [83]. Importantly, equivocal evidence for the importance of average phylogenetic distance to humans as a predictor of zoonoses [84,85] suggests that fitness-weighted approaches, where transmission risk includes parasite fitness in the source hosts, could improve risk assessment for emerging infectious diseases. Similarly, estimation of a parasite's host range would inform the risk factors (phylogenetic, spatial overlap, diet similarity) for novel parasite jumps to new species of public health and conservation concern [86]. The findings also suggest a generalism-based predictability to evenness in parasite abundance across a host set which could be leveraged to identify parasites with uneven abundances to efficiently support parasite populations, in cases of undesirable parasite extinction effects on ecosystem processes [87,88], or depress parasite populations in targeted control efforts [19].

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Code for 'Costs of parasite generalism revealed by abundance patterns across mammalian hosts' is available on Dryad [89].

Supplementary material is available online [90].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. A.W.P.: conceptualization, data curation, formal analysis, funding acquisition, methodology, project administration, software, visualization, writing—original draft, writing—review and editing; C.E.C.: conceptualization, formal analysis, methodology, software, visualization, writing—original draft, writing—review and editing; T.A.D.: conceptualization, methodology, writing—original draft, writing—review and editing; M.J.F.: conceptualization, formal analysis, methodology, writing—original draft, writing—review and editing; S.H.: conceptualization, formal analysis, methodology, writing—original draft, writing—review and editing; A.B.P.: conceptualization, writing—original draft, writing—review and editing; R.M.V.: formal analysis, methodology, software, visualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

Funding. This material is based upon work supported by the National Science Foundation under grant no. NSF DEB 1754255 and by the Macroecology of Infectious Disease Research Coordination Network (grant no. NSF DEB 1316223). S.H. was supported by the German Research Foundation (DFG, HU 2748/1-1).

Acknowledgements. We are grateful to Ignacio Morales-Castilla, Jonathan Davies, Ania Majewska and Anna Willoughby for useful discussions about this work.

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