

Research



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Food web structure selects for parasite host range

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Complex life cycle parasites, including helminths, use intermediate hosts for development and definitive hosts for reproduction, with interactions between the two host types governed by food web structure. I study how a parasite's intermediate host range is controlled by the diet breadth of definitive host species and the cost of parasite generalism, a putative fitness cost that assumes host range trades off against fitness derived from a host species. In spite of such costs, a benefit to generalism may occur when the definitive host exhibits a large diet breadth, enhancing transmission of generalist parasites via consumption of a broad array of infected intermediate hosts. I develop a simple theoretical model to demonstrate how different host range infection strategies are differentially selected for across a gradient of definitive host diet breadth according to the cost of generalism. I then use a parasitic helminth–host database in conjunction with a food web database to show that diet breadth of definitive hosts promotes generalist infection strategies at the intermediate host level, indicating relatively low costs of parasite generalism among helminths.

1. Introduction

Parasites demonstrate an amazing array of strategies to successfully complete their life cycle [1]. Some are host specialists, deriving high fitness from only a few host species, while others are more generalist, making use of a wider range of host species [2], but potentially deriving lower fitness from any one of them. Success of a generalist parasite strategy may therefore depend on low costs associated with infecting many different species. Complex life cycle parasites use at least two different host species to complete their life cycle, typically one for development (the intermediate host) and one for reproduction (the definitive host). A generalist parasite that can use one of many intermediate host species may be more likely to infect its definitive host if that host feeds broadly among several prey species. This suggests that food web structure may be an important selective force on parasites.

The case for integrating parasite species into food webs has been argued for decades [3]. Attention has typically focused on parasites as regulators of host populations with the potential to influence food web structure, dynamics and stability [4–12]. Research has also extended beyond host population sizes, demonstrating that parasites can affect food webs through trait-mediated effects on their hosts [13]. However, Lafferty *et al.* further recognized that parasites 'in turn, may be particularly sensitive to changes in food web topology themselves' [4] and later speculated 'It might be possible to ask how network structure affects things such as parasite persistence, host specialization and the potential for trophic transmission' [14]. Here, I argue that food web structure can differentially select for generalist parasites, and that recognizing this presents an opportunity to assess the cost of parasite generalism at a macroecological scale.

The logic behind this argument proceeds as follows. When a definitive host regularly preys on only a few species, this places a premium on parasites to infect those intermediate hosts that form part of the definitive host's diet.

This outweighs the intrinsic fitness a parasite derives from such intermediate hosts since there is no value to efficiently exploiting an intermediate host that never provides onward transmission to the definitive host. Consequently, a wide range of infection strategies may be viable, provided they include those few intermediate hosts that are preyed on by the definitive host, and that the reproductive number for the parasite exceeds one [15].

Conversely, when the definitive host has a relatively broad diet, the value to a parasite of infecting a moderately preferred intermediate host is diminished. Now, the fitness derived from intermediate hosts outweighs the identity of the infected species. This elevates the importance of the interaction between a parasite's host range and the cost of generalism. If the cost is high, parasite specialism should be favoured because infecting and developing in a relatively small subset of intermediate hosts, but with high probability, leads to a higher chance of infecting the definitive host. If the cost is low, parasite generalism should be favoured because a broad host range ensures higher chances of infecting the definitive host, since the fitness levels obtained by a generalist parasite will not be markedly lower than that of a specialist in this case.

These conjectures lead to a testable hypothesis. Observed levels of parasite specificity to intermediate hosts will be wide-ranging when definitive hosts have a relatively narrow diet and will tend to generalism as diet breadth increases, provided the cost of generalism is absent or low. However, if the cost of generalism is high then the parasite strategy will instead tend to specialism. To test this, I begin by building a simple model to illustrate these predictions more formally, confirming the cost-dependent relationship between definitive host diet breadth and parasite specificity. I then take a macroecological approach of integrating data across host and parasite species to test how specificity of parasitic helminths to intermediate hosts changes as a function of diet breadth of their definitive hosts.

As predicted, the modelling results confirm that when the definitive hosts of parasites exhibit a narrow diet breadth, both specialist and generalist strategies can be viable. Further, as definitive host diet breadth increases then either specialism or generalism can prevail, with the cost of generalism being the critical determinant. The empirical data also show that specificity is wide-ranging when definitive hosts have a narrow diet breadth, but parasites are more generalist when definitive host diet breadth increases. These data demonstrate how food web structure creates differential selection for specialist parasites and indicate that parasitic helminths may not pay a severe cost for generalist infection strategies at the intermediate host level.

2. Theory

I begin by defining a specialist parasite by $p_s = (1, 0)$ and a generalist parasite by $p_g = (1 - c, g(1 - c))$, where the first and second elements in each vector represent the probabilities of infecting intermediate host species I_1 and I_2 . The parameter g represents the degree of generalism (how much less fit the generalist parasite is in association with its non-preferred host) and parameter c represents the cost of generalism (note that $0 \leq g, c \leq 1$). We define the definitive host feeding strategy by $f_1 + f_2 = 1$, where f_j is the probability of

feeding on intermediate host I_j , and the summation to one represents the need for the definitive host to feed on an intermediate host. The probability of completing the life cycle is $w_s = f_1$ for the specialist parasite and $w_g = f_1(1 - c) + f_2g(1 - c)$ for the generalist parasite. The construction so far assumes that the specialist and generalist parasite have the same preferred intermediate host. The alternate scenario is modelled by using $p_s = (0, 1)$ and $w_s = f_2$.

The relative sizes of w_s and w_g may be used to infer which parasite strategy will be favoured by natural selection, and may easily be calculated as a function of infection strategy parameters (g, c) and definitive host diet (f_1). Because outcomes are conditional on whether the two parasite strategies have the same preferred intermediate host, we may average across the event space that includes both possibilities, resulting in a parameter space (g, c, f_1) where the outcome is that specialism prevails, generalism prevails or both strategies may prevail (figure 1).

This analysis demonstrates how parasite infection strategies at the intermediate host level interact with definitive host diet breadth. With large diet breadth, we expect specialism to be selected for if the cost of generalism is high. Otherwise, we expect generalism to be selected for. With low costs of generalism, generalist parasites will be selected for across a larger range of diet breadths if the parasite has a high degree of generalism, meaning it derives the same fitness from alternative intermediate hosts. At narrower diet breadths, both specialist and generalist infection strategies may prevail, determined by whether parasites exhibiting different strategies have the same preferred intermediate host or not.

3. Data

A recently published life cycle database for parasitic helminths reports recorded associations between helminth parasite species and their intermediate and definitive host species [16]. The full dataset contains 8510 host–parasite associations involving 973 parasite species from the acanthocephalan, cestode and nematode groups. It additionally classifies hosts as either intermediate or definitive, and records which host number the association represents. For example, a parasite species may obligately use three host species: a first intermediate host (i), a second intermediate host (ii), and a definitive host (iii). Because patterns of specificity at higher host levels may be influenced by lower levels, I restricted the analysis to parasite species that use a single intermediate host and a definitive host to complete their life cycle. The most common number of intermediate host species per parasite species was one, with one parasite species found to be associated with 30 different intermediate host species (figure 2a). This subset of data was manipulated to a binary host–parasite association matrix.

The relatedness of host species within this subset was established using the R Open Tree of Life package [17], which accepts Latin binomial species names and returns a phylogenetic tree based on a synthesis of phylogenetic and taxonomic data [18]. The tree (which matched $n = 928$ of the intermediate host species) does not contain branch lengths, and so relatedness between two species was measured as the number of nodes of the tree traversed between the two species via their most recent common ancestor, resulting in

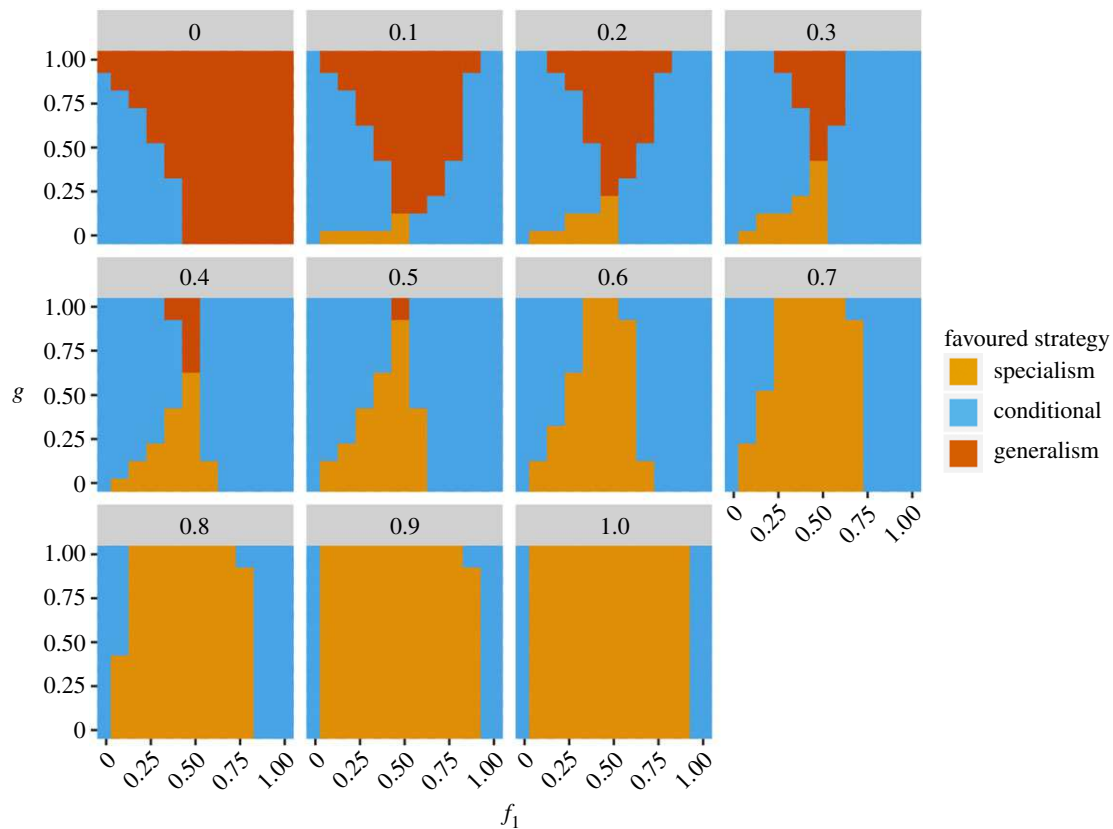


Figure 1. Parasite strategies with the larger fitness values (w_s , w_g) as a function of cost of generalism (c , panel titles), degree of generalism (g , y-axis) and diet breadth (f_1 , x-axis). Note that several zones represent parameter spaces where the fitness inequality is conditional, depending on whether the parasites have the same, or different, preferred intermediate hosts. Central values on the x-axis represent maximum diet breadth (equally likely to feed on intermediate hosts I_1 and I_2). (Online version in colour.)

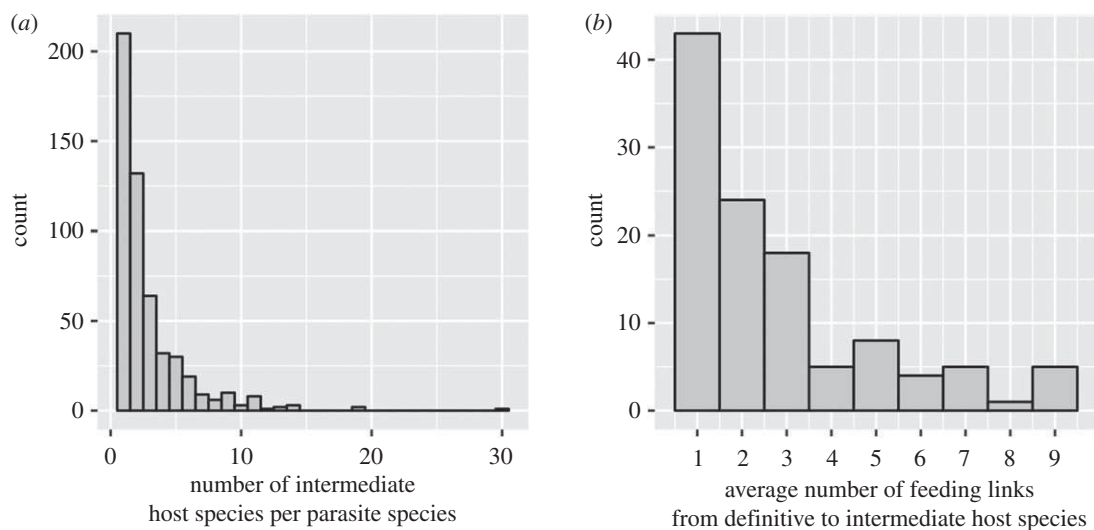


Figure 2. Quantitative summary of association data. (a) Number of intermediate host species per parasite species; (b) average number of feeding links from definitive to intermediate host species. Feeding links per definitive host species were averaged across study sites in which they occurred and in the case of non-integer averages, they are displayed as rounded-up integer values.

a distance matrix similar to methods previously proposed [19]. The distance matrix was used in conjunction with the host–parasite association matrix to calculate standard effect sizes for the mean pairwise distances between hosts of a given parasite, using the Picante package in R [20]. This calculation was performed using a null model in which the host–parasite association matrix was randomized 1000 times with the independent swap algorithm [21], which maintains occurrence frequencies of host and parasite species.

The result of this operation is a score for each parasite species, with negative scores indicating relative specialism (hosts more related than expected by chance) and positive scores indicating relative generalism (hosts less related than expected by chance). However, this analysis was not focused on statistical significance of specialism, which is known to be easily satisfied across a wide range of parasitic taxa [2], but rather on how the standard effect size for phylogenetic specificity is explained by definitive host diet breadth.

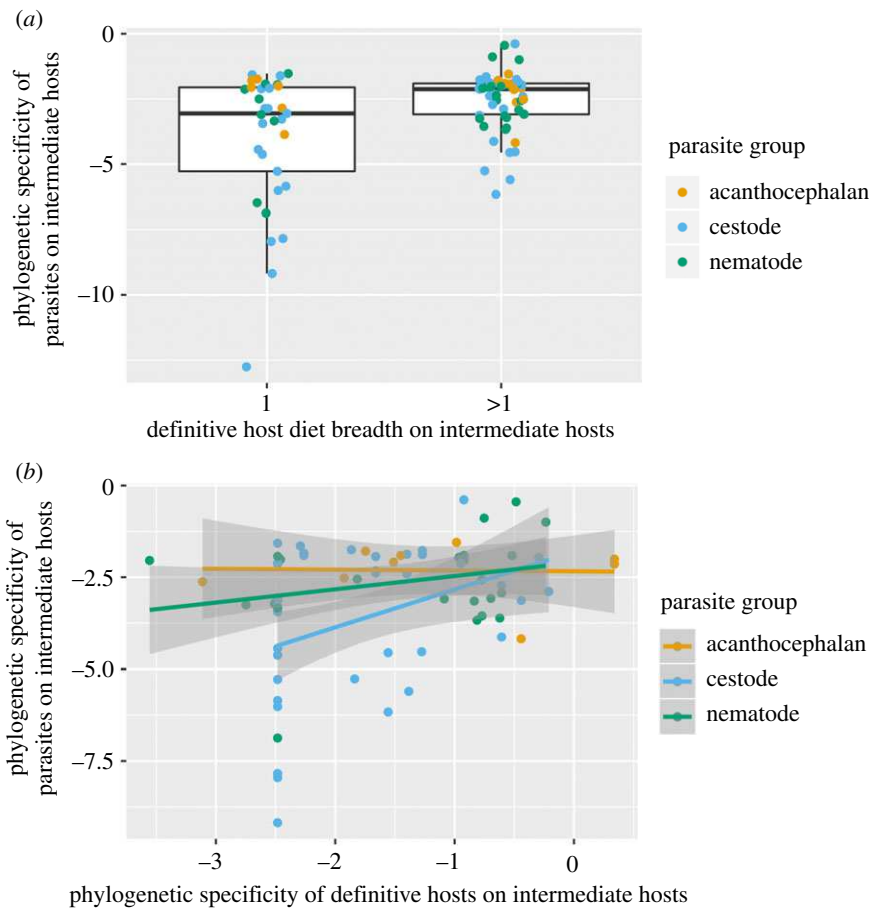


Figure 3. Definitive host diet selects for parasite specificity on intermediate hosts. (a) Boxplot of standard effect sizes for parasite phylogenetic specificity at the intermediate host level, grouped by diet breadth of definitive host species and coloured by parasite group. More negative specificity scores represent more specialist parasites. (b) For multi-prey definitive hosts, the same measure of parasite specificity as a function of definitive host (predator) phylogenetic specificity by parasite group. (Online version in colour.)

Single-host parasites at the intermediate level were removed at this stage, as the host relatedness metric requires at least two intermediate host species. For parasite species from which a phylogenetic specificity metric was obtained, their definitive and intermediate hosts were queried in a large food web database [22] resulting in matches for 90 parasite species ($n = 15$ acanthocephalans, $n = 43$ cestodes, $n = 32$ nematodes). The data were grouped by study site ($n = 14$) so that feeding links per definitive host were only counted where prey species co-occurred. Diet breadth for each definitive host species was calculated as the number of feeding links with intermediate host species averaged across the study sites in which they occurred. This analysis resulted in 113 definitive host species, 53 intermediate host species and 608 feeding links. Definitive host species covered five distinct classes: Actinopteri ($n = 64$), Aves ($n = 38$), Mammalia ($n = 5$), Chondrichytes ($n = 4$) and Reptilia ($n = 2$). Averaged across study sites, the diet breadth of definitive host species was right-skewed ranging from 1 to 9 intermediate host species, with a single feeding link being the most common pattern (figure 2b). To relate the metric to parasite species, it was then averaged across all the definitive hosts of each parasite. This resulted in the formation of two groups reasonably balanced in size: those parasites whose definitive hosts had one feeding link on average ($n = 43$), and those where the average was greater than 1 ($n = 70$).

Parasite specificity at the intermediate host level was found to be strongly dependent on the diet breadth of

definitive hosts (figure 3a; Wilcoxon rank-sum test: p -value = 0.014). The parasites of definitive hosts with a narrow diet exhibited a large range of parasite specificity values at the intermediate host level, with average values representing relatively strong phylogenetic specificity (median standard effect size specificity score = -3.06). Conversely, parasites of definitive hosts with a broader diet were more phylogenetically generalist at the intermediate host level, though still more specialist than expected under a random null model (median standard effect size specificity score = -2.13). Parasite group (acanthocephalan, cestode or nematode) was not predictive of specificity scores (Kruskal–Wallis rank-sum test: p -value = 0.12).

In addition to measuring definitive host diet breadth by counting intermediate host prey species, a phylogenetic measure of diet was also obtained. For parasite species that associated with at least one definitive host species known to consume at least two intermediate host species, a phylogenetic specificity ‘predator’ score for those parasites was obtained as the average definitive host phylogenetic specificity score on intermediate hosts. This metric was obtained in exactly the same way as parasite phylogenetic specificity. Linear regression of parasite specificity on predator specificity showed the same positive relationship, with and without including parasite group as an additional predictor (figure 3b; p -value = 0.0043 without parasite group, p -value = 0.014 with parasite group). Although there appear to be differences in the strength of this relationship among parasite

groups, with cestodes then nematodes exhibiting the strongest relationships (figure 3*b*), there is insufficient power to detect a significant difference among parasite groups, potentially due to the necessary exclusion of parasite species whose definitive hosts do not consume at least two intermediate host species.

Given that the causal mechanism investigated is the definitive host diet effect on parasite specificity on intermediate hosts, the association between specificity at the two host levels (intermediate and definitive) was determined to assess support for alternative hypotheses that could be driven by parasite specificity on definitive hosts. The phylogenetic measure of specificity for parasite species was established in definitive host species using the same method detailed above. For parasite species infecting at least two definitive and two intermediate host species ($n = 76$), their specificity scores at the two host levels were not correlated (Pearson's product-moment correlation test: $\rho = 0.14$, p -value = 0.23), suggesting that patterns reported are not driven by infection strategies on definitive host species.

Using a phylogenetic measure of specificity partly ameliorates the perennial problem of sampling bias. Given a true host richness and a true phylogenetic specificity, richness drops by one unit for every unsampled host species, whereas the specificity metric is averaged across all host species pairs, rendering it more robust to sampling issues. However, there was still a negative relationship between the number of citations for each parasite and its specificity (Kruskal–Wallis rank-sum test: p -value = 0.025), meaning that well-studied parasites are more phylogenetically specialist. However, the grouping of parasites by diet breadth of their definitive hosts was not influenced by citation count (χ^2 test: p -value = 0.071). The tendency for parasites that infect large diet breadth definitive hosts to be less specialist at the intermediate host level compared with their counterparts supports the idea that parasitic helminths do not pay a large cost of generalism.

4. Discussion

Understanding parasite host range is a longstanding goal in evolutionary ecology [1], and here I demonstrate an important role for food web structure to influence the host range of complex life cycle parasites. This neglected selective force may help to explain the observed host range of many parasitic helminth species, in combination with other factors including geography, host traits and parasite community structure [23,24]. Importantly, parasites are more than simply perturbators of the food webs of their hosts and are themselves potentially experiencing strong selection pressure from the food webs they inhabit. The observed tendency for specialist parasite life-history strategies to associate with definitive hosts that exhibit a narrow diet breadth and generalist strategies to associate with broad diet breadths suggests that parasitic helminths may not pay a severe fitness cost at the intermediate host level. The absence of such costs naturally raises the question: why are not all parasites generalist? A component of that answer lies in the biotic context (i.e. food web) in which the parasite exists.

The two-level food webs that characterize the transmission of many complex life cycle parasites from intermediate to definitive hosts may well be echoed in

vector-borne disease systems where parasites undergo an obligate cycle between arthropod species, such as mosquitoes, and vertebrate hosts. Vector species vary in feeding preference and evenness on vertebrate species [25]. Consequently, observed vertebrate host ranges of vector-borne parasites may be influenced by the hematophagous food web. Avian malaria, for example, can be transmitted between many arthropod and vertebrate species, and the parasite strains vary in vertebrate host specificity, with the more generalist parasite species at no obvious fitness disadvantage [26]. The maintenance of variation in parasite specificity could potentially be explained by patterns of blood feeding of the vectors transmitting malaria parasites.

Macroecology provides vital access to questions about generalist parasites, but it is important to acknowledge limitations and sources of bias. The underlying data are observed host–parasite associations. Parasite generalism is not independent of virulence, the pathogen-induced harm caused to the host [27]. In turn, virulence may create a sampling bias where we are more likely to observe infection events if they cause harm to the host. Consequently, the observed host range of a given parasite may be incomplete, with missing data representing a non-random set of host–parasite interactions. Indeed, it has been estimated that 20–40% of the host range of many parasite species is currently unknown [28], with statistical imputation of likely associations representing a promising way forward [29]. While phylogenetic measures of specialism are more robust to missing host–parasite associations generated by sampling bias compared to host richness, some bias probably still exists. The data studied suggest that increased sampling effort is more likely to uncover host–parasite associations involving hosts that are closely related to hosts of a given parasite, rather than more distantly related. This could revise specificity scores downwards (towards extreme specialism) and may do so more in parasites currently scored as relatively generalist, which were represented in both definitive host diet groups.

The macroecological approach combines data representing many host and parasite taxa, and consequently, it is not possible to isolate how the specificity of a particular parasite species varies across food webs of different structure. Combining taxonomically distinct species in one analysis may unintentionally mask important features of individual species that contribute to patterns. It is highly likely that other factors not considered here will additionally influence host–parasite associations. Host allometry has been shown to influence the evolution of parasite specificity [30], and directly influences components of parasite transmission including host longevity, host group size and susceptibility [31]. However, the fact that diet breadth alone can explain an appreciable amount of variation in parasite specificity is notable, though we must acknowledge that host species are not equivalent in the quality of resources they offer to parasites, and this may vary over time as host densities are often dynamic. Among the parasite species, there may additionally be variation in plasticity, which could alleviate costs of antagonistic pleiotropy in some generalist parasite species [27,32].

The underlying food web database is appreciably large, assembled from 290 distinct food webs [22]. Potential sources of bias include the exclusion of certain food webs, though this was typically done from the aspect of quality control, removing food webs that were poorly resolved, incomplete or

lacking in trait data. The theoretical model was developed for illustrative purposes, and is deliberately pared down for analytical tractability, and also due to lack of sufficient detail to justify a more complex model. More realistic models would ultimately help navigate how the many nuances of host–parasite and predator–prey interactions impact selection for parasite infection strategies. These include feedbacks between ecological and evolutionary processes, such as parasite-mediated reductions in host population sizes, which can reduce parasite fitness [33]. Additionally, variation in host susceptibility could be included, provided sufficient data, and is likely a trait with strong phylogenetic signal [34]. Species-level differences may be extended to host competency, considering the different abilities of host species to transmit, as well as acquire, a generalist parasite [35], though this would require significant empirical research. Lastly, more detailed food webs may ultimately permit analyses that include weighted links that reflect the dietary preference of definitive host species, rather than the number of links.

While multi-host parasites can negatively impact human and animal populations [36], our understanding of how generalist parasite strategies are maintained, and restricted by costs, is incomplete. Several experimental studies have developed exquisite knowledge on the costs of generalism, which include the potential for parasites to jump between only

closely related species because the benefit of parasite adaptations are similar in related host species [37], the loss of fitness in the original host species as a consequence of adaptation to a new species [38], maladaptive virulence [39] and avoiding poor-quality hosts to ameliorate costs [40]. For complex life cycle parasites, recognizing that the theoretical relationship between definitive host diet breadth and parasite specificity depends on the cost of generalism creates the opportunity to indirectly assess this cost in a group of parasitic taxa. While parasitic helminths probably pay unobserved costs in order to have a broad host range, the magnitude of such costs may not be severe, and the large spectrum of specialist–generalist infection strategies we observe is at least partly maintained by the food web structure of their intermediate and definitive host species.

Data accessibility. All data used in this study are available from published sources. The host–parasite data are from Benesh *et al.* [16], and the food web data are available from Brose *et al.* [22]. Code to reproduce the analyses and figures is provided on Figshare at <https://doi.org/10.6084/m9.figshare.c.4525694.v2> [41].

Competing interests. I declare I have no competing interests.

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