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Spatial variation in species' roles in host–helminth networks

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Species interactions may vary considerably across space as a result of spatial and environmental gradients. With respect to host–parasite interactions, this suggests that host and parasite species may play different functional roles across the different networks they occur in. Using a global occurrence database of helminth parasites, we examine the conservation of species' roles using data on host–helminth interactions from 299 geopolitical locations. Defining species' roles in a two-dimensional space which captures the tendency of species to be more densely linked within species subgroups than between subgroups, we quantified species' roles in two ways, which captured *if* and *which* species' roles are conserved by treating species' utilization of this two-dimensional space as continuous, while also classifying species into categorical roles. Both approaches failed to detect the conservation of species' roles for a single species out of over 38 000 host and helminth parasite species. Together, our findings suggest that species' roles in host–helminth networks may not be conserved, pointing to the potential role of spatial and environmental gradients, as well as the importance of the context of the local host and helminth parasite community.

This article is part of the theme issue 'Infectious disease macroecology: parasite diversity and dynamics across the globe'.

1. Introduction

The strength of interspecific interactions in a community may change along spatial, environmental or compositional gradients [1,2]. For instance, the abiotic stress gradient hypothesis suggests that interactions among competing plants tend to become more facilitative in more stressful environments [3]. This can be extended to sets of interacting species (e.g. plants and pollinators), where environmental gradients could influence pollinator preference and interaction specificity, thereby altering association strengths while maintaining the overall effect of the pollinator [4]. Shifts in interaction strength can have strong effects on overall network function [5], including the ability of the network to recover from a perturbation (i.e. resilience; [6]). Given that individual species can contribute strongly to the structure and stability of the overall network [5,7], understanding the variability in species contributions among distinct networks would help in understanding the conservation of species' roles in interaction networks [4,8].

A species' role in an interaction network—an attempt to quantify how each species participates in its community—can be defined in a number of ways, many of which are reviewed with respect to food webs in Cirtwill *et al.* [9]. For instance, centrality measures may capture aspects of species' importance to the network [10,11], as these measures attempt to assign an importance value to each node in the network based on the number of connections (degree centrality), shortest path distance which includes a given species (betweenness centrality), or the average path length to any other species in the network (closeness centrality). However, centrality is difficult to estimate on some networks—most notably when networks have few interactions relative to their overall size—and measures may not be comparable across networks.

Species importance may also be defined by measuring some property of the entire network, and examining the change in this measure as a result of removing each species from the network [8]. However, this approach is sensitive to the network measure examined, as well as the order of species removal. That is, removing a species could result in a large reduction of a certain network property, but this network-specific measure may not capture a species' role if the network measure fails to capture important characteristics of the network or if it is sensitive to the number of interacting species or number of interactions. Lastly, species' roles can be defined by identifying modules of interacting species within the network, and comparing the number of links to other species within the same module to species outside of the module [4,12–14]. Modules are distinct subsets of species (e.g. hosts and parasites) that interact more frequently among themselves than with other species in the network. This approach assigns species' roles relative to the interactions of other species in the network, thereby addressing concerns over the effects of the number of interacting species influencing species' role estimation.

Species' role estimation has previously been applied to plant–pollinator and play-seed disperser systems in order to identify the most important plant and pollinator species to network structure [4,12–15], and in host–parasite systems to examine species' roles in relation to species' life history and phylogeny [16,17]. Species' roles are quantified by considering the interactions between and within modules, where modules are identified as groups of species interacting more within their own module than between modules. Modularity in ecological networks is a common observation [4], and may be related to network stability [18]. While modular network structure is a commonly observed phenomenon, it is not necessary that networks be significantly modular to quantify species' roles.

Shifts in species' roles as a result of species invasions have been observed in plant–pollinator networks [14], suggesting that species' roles may be temporally dynamic, and subject to the influence of novel species. Demonstrating spatial variation in species' roles is the first step towards understanding how spatial and environmental gradients influence the composition and relative importance of species across networks. Apart from spatial or environmental structuring of species' roles, the estimation of species' roles allows the estimation of the consistency of species' roles for a given species. That is, how spatially variable are species' roles? Highly variable species' roles might suggest the effects of local climatic conditions or community composition [19]. Meanwhile, species that play a consistent role across space may provide a signal that the number of species interactions is constrained for each species, either through the effects of species' life history, or through evolutionary processes of specialization [20,21]. This consistency of species' roles has previously been observed in host–parasitoid [22] and plant–pollinator [23] systems, suggesting the possibility that species' traits and phylogenetic relationships fundamentally constrain the roles they play in ecological networks.

Interactions between host and parasite species represent an ideal system to test the conservation of species' roles, as parasite species may be quite specific to a subset of host species [24] or infect a wide range of host species [25,26], creating sizable variation in the number of potential associations. Furthermore, host and parasite species interact across large spatial extents, appearing either together or independently in multiple networks. Previous work with host

and helminth communities demonstrated that community composition decays quickly as a function of geographical distance, suggesting that species interactions likely change dramatically across their range [27]. However, while different networks can be composed of different numbers of species and interactions, it is possible that host and parasite species maintain their roles in different networks [19]. We examine this possibility using a global database of host–helminth interaction networks from the London Natural History Museum's host–parasite database [28]. Data on nearly 300 locations were used to create species' interaction networks and measure species' roles in each network. We measured species' roles using two different approaches, which allowed us to determine *if* species' roles are conserved, as well as *which* species' roles tended to be conserved. At the global scale we considered, we failed to detect the conservation of species' roles for any of the over 38 000 host and helminth parasite species. Furthermore, there was no consistency in species' role classification, either for a given species or when compared to the species' roles estimated for the global network of all host and helminth species. Together, our findings suggest that species' roles in host–helminth networks are not conserved, pointing to the role of spatial and environmental gradients, as well as the importance of the context of the local host and helminth parasite community.

2. Methods

(a) Host–helminth interaction data

Helminth parasite occurrence records on host species were obtained from the London Natural History Museum's host–parasite database [28], and accessed programmatically using the `helminthR` package [29]. These data currently represent one of the largest sources of host–parasite interaction data [28,30], despite being restricted to helminth parasites. Helminth parasites differ greatly in their transmission mode and life history, and diversity included Platyhelminthes (trematodes and cestodes), Acanthocephalans and Nematodes [28]. Host–helminth interactions are georeferenced to over 400 terrestrial and aquatic locations, largely determined by geopolitical boundaries (e.g. 'Spain'). Locations that were too vague or that other locations were nested within (e.g. 'Western Europe') were removed, resulting in a total of 299 unique locations. After data cleaning, host–helminth occurrence data for 14 933 host species and 23 601 helminth parasite species remained, resulting in 299 'local' networks at the scale of geopolitical boundaries (see electronic supplemental materials for more information). The combination of all realized host–helminth interactions were assembled into the 'global' network. We analysed changes in host–parasite species' compositions and their interactions across space.

(b) Quantifying species' roles

Species' roles were defined relative to other species in the network by considering the connections of each species to other species in its own module and connections to species in other modules [4,31,32]. Modules were defined using the short random walks method [33], which attempts to detect densely connected groups of species within a larger network. Then, we defined species' roles based on previously established methodology [4,13,14,32], which estimates species' relative position in a phase space composed of within-module degree (connections within the module) and among-module connectivity (connections between modules). Within-module degree
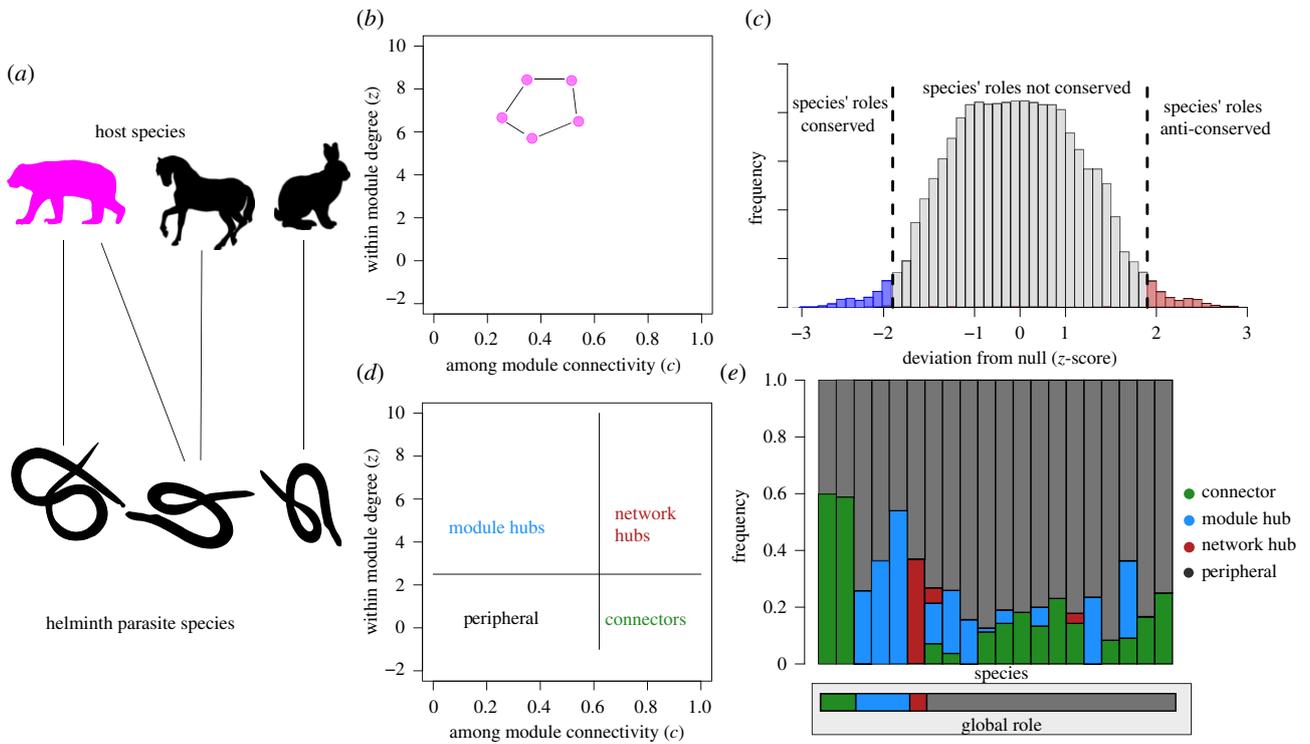
Figure 1. Given a host–helminth network (*a*), we quantified species' roles in the network in two ways. For a given species (e.g. the bear host highlighted in pink), we calculated the area in *cz* space (*b*) and compared this to a null model (*c*). Second, we used a classification approach (*d*) to determine if species consistently played a similar role across all the host–helminth networks where the given host or helminth parasite was found (*e*), comparing the role played in local networks to the species' role estimated from the global network. (Online version in colour.)

was standardized relative to other species in the network by computing a *z*-score for each species *i*

$$z_i = \frac{k_{is} - \bar{k}_s}{\sigma_{ks}},\tag{2.1}$$

where k_{is} is the number of connections of species *i* to other species within its module, and $\bar{k}_s$ and σ_{ks} are the average and standard deviation of the number of own-module connections of all other species in the given network.

Among-module connectivity—which is equivalent to the *participation coefficient P*—was defined as

$$c_i = 1 - \sum_{t=1}^{N_m} \left(\frac{k_{it}}{k_i}\right)^2,\tag{2.2}$$

where k_i is the total number of connections of species *i*, and k_{it} is the number of connections of species *i* to module *t*, which includes its own module. This measure is bounded between 0 and 1, where $c = 0$ corresponds to a species that is only connected to species within its own module.

This creates a continuous two-dimensional space consisting of *c* and *z* (figure 1), which can be used as continuous covariates, or to classify species into their roles [4,34,35]. Here, we perform both approaches, as they help to address two related questions.
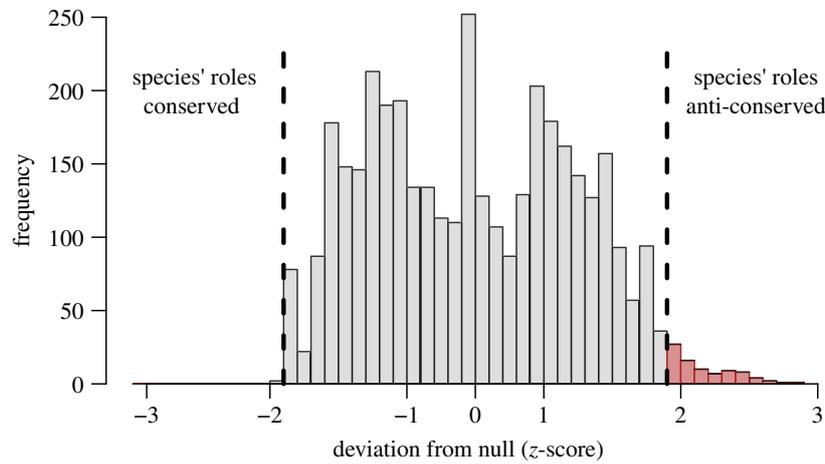
(c) Are species' roles conserved?

To address the question of whether species' roles are conserved, we can calculate the area encompassed by the minimum convex polygon in this two-dimensional *cz* space for each species. That is, species occur in multiple networks, which creates a number of points in *cz* space (figure 1). The area encompassed by this set of points for each species was compared to a null assumption, where points in *cz* space were selected randomly from the set of all species at all locations. This randomization does mean that species may be used more than once, as species occurring in multiple networks may be sampled multiple times. The number of

sampled points in the null model is equal to the number of points for a given species in this *cz* space, i.e. the number of local networks in which a given species, was found. This random sampling procedure was repeated 1000 times for each species, and species' *cz* area was compared to the null distribution using *z*-scores (equation (2.1)) comparing the empirical *cz* area to the mean and variance in *cz* area for the null model simulations. We infer the species' role to be conserved if the area of the minimum convex polygon of a species is lower than the null model expectation. That is, if a species' area in this *cz* space is smaller than what would be expected if species were made up of entirely randomly chosen species across any network, then we would say that the species' role is conserved. Some host and parasite species were recorded in a small number of locations, making area estimation feasible for a subset of 1770 host species and 2016 helminth parasite species.

(d) Which species' roles are conserved?

To address the question of which species' roles are conserved, we implemented a classification approach [4,34]. The area approach described above addresses the conservation of roles, in that a smaller area—or larger *z*-score difference between empirical and null area—suggests the tendency for the species to play a consistent role across networks. But what role is that species playing? Species' *cz* area may be small, but the species could be located anywhere within the *cz* space. To address species' location in the *cz* space, we classified species into four main types of roles in ecological networks: peripherals, network hubs, module hubs, and connectors (figure 1). Thresholds for classification were used for within-module degree (*z* threshold of 1.65), and among-module connectivity (*c* threshold of 0.75). Both thresholds were based on the distribution of the data, set as 95% percentile thresholds. The *c* threshold was selected based on the biased distribution of the data and the extensive classification of species' roles as peripheral, and corresponds to the 95th percentile (95% of values of *c* are less than or equal to 0.75).

Figure 2. We failed to detect any conservation of species' roles for any of the species' studied, when species' roles were defined in terms of the area of cz space occupied by a species. In a small number of extreme cases, we found that species occupied larger areas in cz space than expected under our randomization procedure, suggesting overdispersion in cz space and species with highly variable roles across local networks. (Online version in colour.)

Peripheral species are below both z and c thresholds. Connector species tend to have high among-module connectivity (c) but low within-module degree (z), serving to link modules while not strongly contributing to its own module. Module hubs are the opposite of connectors—having low among-module connectivity (c) but high within-module degree (z)—and serve to strengthen the coherence of the module they belong to. Lastly, network hubs have both high among-module connectivity (c) and high within-module degree (z), contributing to the coherence of their own module while also serving to connect different modules.

Using this approach, we classified species into one of these groups for every local network they occurred in. Furthermore, we combined all these local networks to form a global network of host–helminth interactions. We computed c and z values for every species in this global network, allowing the comparison of species' roles in local networks relative to the species' role in the global network. For instance, the fraction of times the species' role from the set of local networks matched the species' role in the global network could be used to start to understand the influence of scaling on species' roles, as estimated using this established methodology [4].

3. Results

We found a predominance of peripheral species and roles in these networks, as expected from the extremely low connectance of the networks and their marked disassortativity. Module hubs were also infrequent, suggesting a role of generalist taxa but with preserved specificity to certain groups of hosts or parasites. These module hubs can also be species with broad distributions and sizable host or parasite ranges that show turnover of interactions yet whose interactions are restricted to specific taxonomic subsets. Finally, super generalists appear to be either the network hubs—either generalized parasites or hosts with many infecting helminth parasites—or the connectors—also generalist species interacting with multiple partner types yet with reduced specificity compared to the network hubs.

(a) Are species' roles conserved?

Using the area estimation approach, we compared the area each species occupied in cz space to a random sample from any species and any location. Area estimation was only possible for species with a minimum of three unique points in this cz phase space ($n = 3786$). By comparing the area for each species to the null area from our randomization approach,

smaller areas than the null distribution would correspond to conserved species' roles, and larger areas than the null distribution would correspond to anti-conserved roles, where species' roles are actually *more* variable than a null expectation. Based on z-scores comparing empirical and null area values, we failed to detect a single instance of area being smaller than the null model (figure 2), a situation which would correspond to species' roles being conserved. While the majority of species did not significantly differ from the null model, some species occupied a larger area than expected (figure 2), suggesting that some species' roles are less conserved (anti-conserved) than expected at random (2% of species).

(b) Which species' roles are conserved?

By classifying species in categorical roles based on their positions in cz space, we can estimate the frequency of times species occupied different regions of cz space, and use this information to address if species' roles are conserved, and which species' roles are conserved. We find little evidence for the conservation of any of the four species' roles (figure 3). Species tended to play peripheral roles in the majority of networks they occurred in. Furthermore, species' roles in the global network were not reflected in the local networks (figure 3). For each species' role, we compared the global role to the fraction of time where the species served the same role in the local network as in the global network, finding species rarely served the role in local networks as they did in the global network. The exception to this is peripheral species (figure 4), which appeared to be quite conserved. However, due to the imbalance of species' roles, this is likely simply a function of the dominance of peripheral roles, and not an indicator of actual species' role conservation.

4. Discussion

The ecological roles of the host and parasite species' roles analysed here relate to the specificity of the interactions between host and parasite species across a large set of globally distributed local networks. Using a set of approaches to understand the conservation of species' roles in host–helminth networks, we failed to detect any indication that species served similar roles across their ranges. Species'
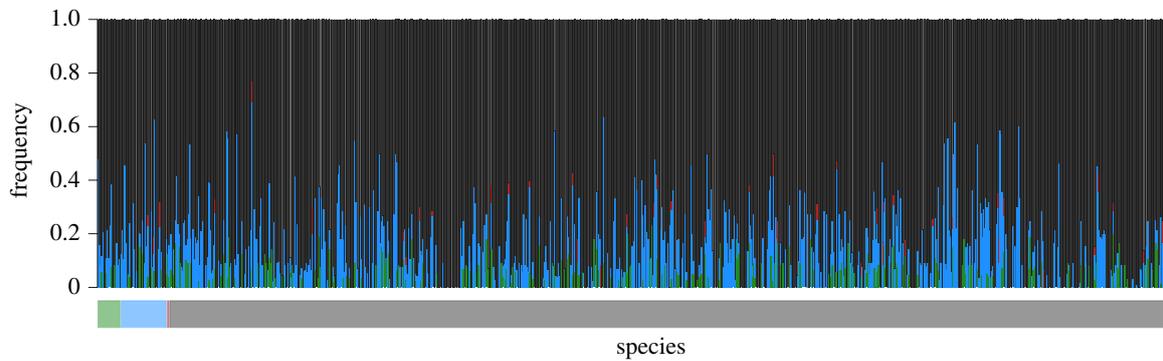
Figure 3. Species' roles identified in the global network (lower bar, where colours correspond to roles in the global network) differed from species' roles identified in the set of local networks. Each vertical bar is a species, where colour indicates the fraction of times the species was observed to be a connector (green), module hub (blue), network hub (red) or peripheral (black) species. Only species found in 10 or more locations were plotted here for clarity. (Online version in colour.)
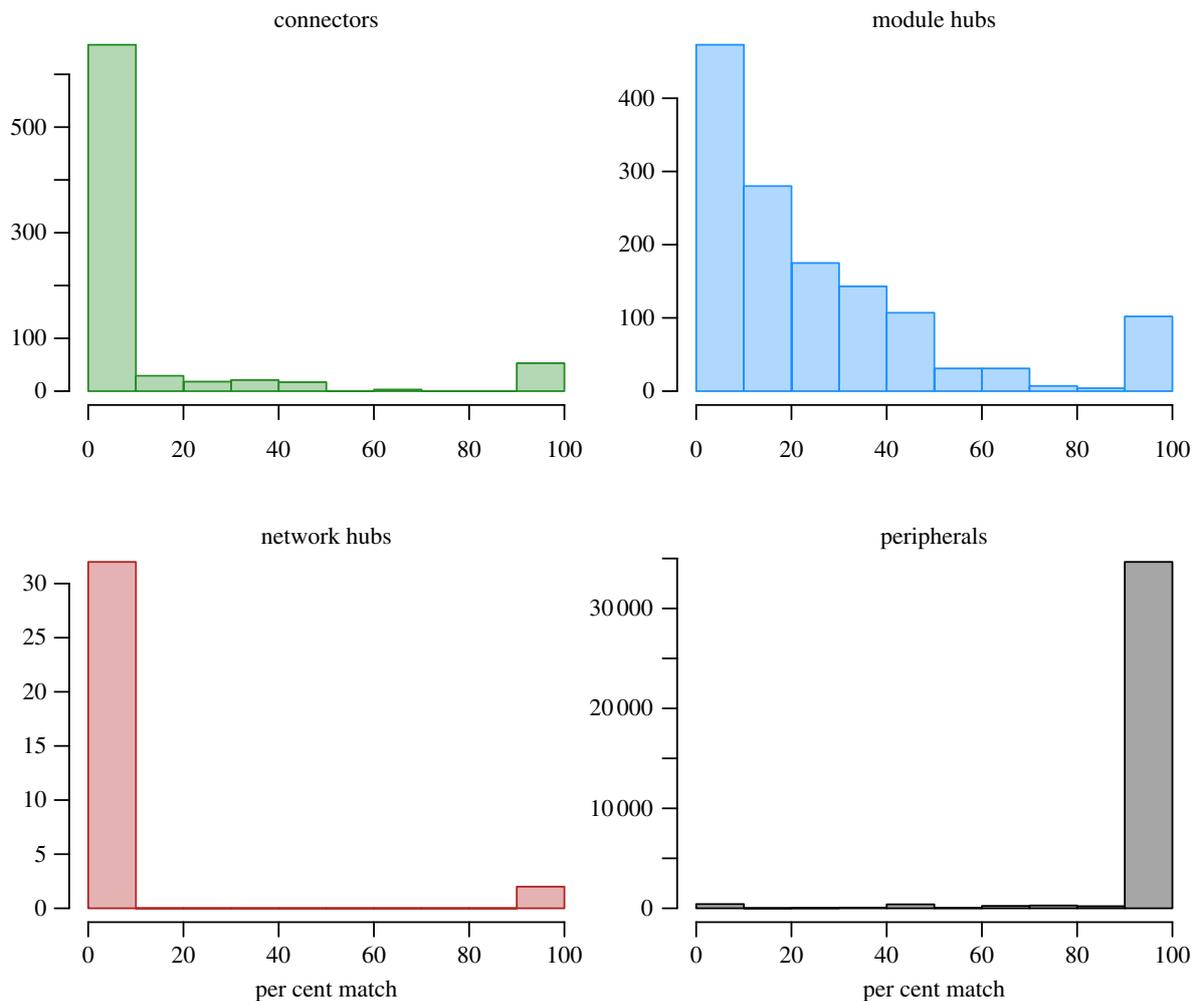
Figure 4. For each species' role (the four panels), the percentage of locations that each species' local role matched the role determined from the global network. Peripheral species were the most common, leading to an inflated agreement between local and global species' roles. Meanwhile, the other roles show large variation in agreement, where some species had consistent roles in the local networks compared to the global network (those near 100% match) while others showed little agreement between species' role classification at local relative to global scales (those near 0% match). (Online version in colour.)

roles were generally identified to be peripheral in both *local* networks and overall in the *global* host–helminth network, though some instances of super generalist hub species existed, as well as the existence of connector species, which tended to bridge subgroups. These species, in particular, may be important as shifting biodiversity may (de)couple potential transmission of parasite or host sharing due to the inclusion or exclusion of these connector species. Together,

our findings suggest that species' roles in host–helminth networks may not be conserved, pointing to the role of spatial and environmental gradients, as well as the importance of the context of the local host and helminth parasite community.

Given the variability in parasite specialization and host permissiveness to infection by parasite species, it was expected that some subset of host and helminth parasites would serve a

consistent role across *local* networks. For instance, it is thought that generalist parasites should consistently parasitize many host species across different networks, which should produce a relatively small occupied area in *cz* space than expected under the null model. Our failure to detect significant conservation of species' roles for hosts and helminth parasites suggests the paramount importance of the local network relative to constraints on the number of host–parasite interactions. That is, predicting parasite species' richness for host species cannot be achieved solely with global estimates of host permissiveness to infection. Information on the composition of the local community will inform the relative parasite burden of host species found in the local network, or the host range of parasite species. Furthermore, the spatial variation in species' roles may be spatially or environmentally structured, suggesting the possibility that variability in species' roles may follow biogeographical gradients. Taken together, our findings suggest that species' roles in host–parasite networks may not be conserved across large distances, as species composition and network structure is generally not [27]. Globally defined species' roles are unlikely to match species' roles in local networks, creating the need to understand both how species-level properties influence global roles, but also how spatial, environmental, or compositional gradients may structure variation in locally defined species' roles.

The disconnect between species' roles at local and global scales is important when attempting to infer species' roles in local networks from either the global network or from nearby local networks [36]. Local networks are always a subset of global interactions, creating a distinction between the species' local role given the community at that site versus the global role assuming that the full diversity of interaction partners are present. These can be used to answer different questions, as local-scale networks can be used to address spatial variation in species interactions and community composition [37,38], while global-scale networks address the species' traits that *allow* host–parasite interactions to occur, regardless of spatial constraints [11,36,39]. This has further implications for the estimation of parasite specificity given limited sampling area, as specificity measured in a part of the parasite species' range may not be indicative of specificity in a different area. This variation in specificity could relate to functional variation in available resources (e.g. host species with a certain trait), or to spatial or environmental gradients which influence the encounter and transmission of helminth parasites. Understanding the underlying causes of this spatial variation in specificity may therefore provide insight into the flexibility of species' specificity (e.g. parasite species can infect multiple species, but prefer to infect a small subset under certain conditions).

We defined species' roles based on previous studies which attempted to visualize species in a two-dimensional space consisting of the interactions of a species within and outside its given module [4,34]. However, this assumes that species can be clearly grouped into modules to begin with, as the resulting statistics are based on group membership [4]. The identification of network modules is a longstanding question in graph theory, and numerous methods have been developed to estimate group membership [40,41]. Though the community detection approach we used is well-accepted [33], examining the sensitivity of community detection method on the resulting species' roles is an interesting future step, perhaps using some other community detection algorithms available [42], as different algorithms may come to very different conclusions [43]. Additionally, species' roles may be quantified in several ways, and defining species' roles incorporating data on species abundance, fitness effects of different parasites, and frequency of interaction may provide different insights into the conservation of species' roles. By taking a network approach, we wished to examine the topological properties of each species, and to estimate if this topological role was conserved across local networks. Another approach could consider the overall number of interactions for each host and helminth species, and determine if the number of interactions per species is fairly constant across species' range.

Understanding the spatial variation in host–parasite interactions, and species' roles in ecological networks, is an intriguing research frontier. There is an apparent utility in applying network approaches to questions of spatial host–helminth interactions, as tools from network theory allow for the identification, classification and quantification of the patterns of interactions for a given species or group of species [2,44]. By comparing empirical network structure to expectations from crafted null models which include relevant processes, it is possible to examine divergence of a species or group from a null expectation [45]. For example, exploring the relationship between autocorrelation in interaction similarity across networks lies and autocorrelation in species' assemblage similarity given geographical distance [27]. These, and similar approaches from network theory, allow for the estimation of species and network level properties along spatial and environmental gradients [1,2,46], with the potential of quantifying a clear spatial or environmental pattern in species' roles in ecological networks [47], or in the overall structure of the network itself [44]. In the context of host–parasite networks, this could lead to insight into spatial or environmental controls on host utilization, with implications to host switching, parasite fitness and spillover potential.

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