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Research

Compositional turnover in host and parasite communities does not change network structure

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Decreasing similarity between ecological communities with increasing geographic distance (i.e. *distance-decay*) is a common biogeographical observation in free-living communities, and a slightly less common observation for parasite communities. Ecological networks of interacting species may adhere to a similar pattern of decreasing interaction similarity with increasing geographic distance, especially if species interactions are maintained across space. We extend this further, examining if host–parasite networks – independent of host and parasite species identities – become more structurally dissimilar with increasing geographic distance. Utilizing a global database of helminth parasite occurrence records, we find evidence for *distance-decay* relationships in host and parasite communities at both regional and global scales, but fail to detect similar relationships in network structural similarity. Host and parasite community similarity were strongly related, and both decayed rapidly with increasing geographic distance, typically resulting in complete dissimilarity after approximately 2500 km. Our failure to detect a decay in network structural similarity suggests the possibility that different host and parasite species are filling the same functional roles in interaction networks, or that variation in network similarity may be better explained by other geographic variables or aspects of host and parasite ecology.

Keywords: β-diversity, species interaction network, host–parasite interactions, network dissimilarity

Introduction

Understanding how the composition of ecological communities varies spatially is a central goal of community ecology (Skellam 1952, Olesen et al. 2010, Vellend and Agrawal 2010). Many studies have found evidence for a relationship between geographic distance between sites and community similarity (Soininen et al. 2007); the so-called *distance-decay* relationship. This has suggested that community composition changes as a function of geographic or environmental distance, with increasing distance between sites resulting in more dissimilar communities (Morlon et al. 2008).

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Evidence in support of *distance-decay* relationships from a variety of natural systems (Yang et al. 2015, Miura et al. 2017) suggests that they may be incredibly general; applying not only to free-living species, but also to microbial (Green and Bohannan 2006), pollinator (Carstensen et al. 2014), and parasite communities (Poulin 2003, Oliva and Teresa González 2005).

Recent evidence suggests that *distance-decay* relationships may extend beyond ecological communities, as the similarity of species interaction networks may change predictably across geographic space (Poisot et al. 2012, Canard et al. 2014). Species interaction networks – specifically bipartite networks where two classes of nodes interact (e.g. plant–pollinator, host–parasite) – provide researchers a way to examine how interactions between species form detectable patterns (e.g. nestedness, modularity), identify species traits associated with specialism or generalism (Fenster et al. 2004), and provide insight into how individual species affect network stability (Proulx et al. 2005, Poisot et al. 2016). The comparison of species interaction networks in different locations permits the scaling of interactions at one locality to biogeographical and macroecological scales (Olesen et al. 2010, Hagen et al. 2012). While still in its infancy, tests of biogeographical hypotheses developed for communities are increasingly being applied to ecological networks. For instance, attributes of plant–pollinator networks may vary spatially (Burkle and Alarcón 2011, Traveset et al. 2015) and temporally (Olesen et al. 2008), and interactions between plant and pollinator species have been found to become more dissimilar with increasing geographic distance (Trøjelsgaard et al. 2015). Counter to this, other studies have found that network attributes are not strongly variable (Stouffer et al. 2012, Baker et al. 2015), even in the presence of high species turnover (Olesen et al. 2011). While the evidence is mixed, this at least suggests the possibility that species roles are conserved, and that interactions between parasitic species may follow similar relationships as free-living communities (Stephens et al. 2016). Lastly, it is possible that dissimilarity in network structure itself, without information on which species interact, follows spatial or temporal patterns (Schieber et al. 2017).

Host–parasite networks offer an interesting test of *distance-decay* relationships, as they networks differ markedly from other types of networks in their interaction patterns (Poisot et al. (2013)). Historically, host–parasite *distance-decay* relationships have largely been confined to examinations of relationships between host or parasite community turnover as a function of environmental or geographic distance (Oliva and Teresa González 2005, Thieltges et al. 2009, Warburton et al. 2016), or parasite community dissimilarity as a function of host traits or phylogenetic distance (Poulin 2010). Relating host and parasite dissimilarity to one another, Krasnov et al. (2012) was the first, to our knowledge, to link the similarity of host communities to the similarity of parasite communities among geographic locations (but see Pellissier et al. (2013) for a more recent example).

The consistency of interactions between a given host and parasite species across space is not guaranteed, as host–parasite associations may be geographically constrained. For instance, uninfected host species may colonize new habitat, at least temporarily escaping their natural enemies (i.e. enemy release hypothesis; Phillips et al. (2010)), resulting in the loss of host–parasite interactions in the newly colonized habitat. Spatial variation in host–parasite interactions can also be caused by different sensitivities of host and parasite species to environmental conditions (Olesen et al. 2010, Hagen et al. 2012, Kemp et al. 2017). This effect would be especially pronounced for ectoparasites, which are directly exposed to the external environment. Overall, this potential spatial variation in host and parasite community structure and host–parasite interactions may be quite important (Trøjelsgaard and Olesen 2016). Lastly, it is possible that spatial variability in obligate parasite interactions have a lower spatial variability, as the parasite community is constrained by the environment and also by the available host community, suggesting that *distance-decay* relationships for parasite communities may be less pronounced than relationships for host communities (Poisot et al. 2013).

There are four possible scenarios regarding the relationships between distance and both community and network similarity (Table 1). Evidence for *distance-decay* in host–parasite network structure could suggest that networks vary predictably across geographic distance (Baker et al. 2015), providing insight into parasite specialism, allowing prediction of host–parasite associations, and motivating further examinations into how abiotic and biotic factors influence host–parasite network structure. Meanwhile, if host–parasite

Table 1. Four potential combinations exist for observed *distance-decay* relationships in host and parasite communities and host–parasite network structure.

Community	Interaction	Interpretation
		Community composition and network structure do not vary across space.
✓		Community composition decays, but network structure remains constant. Interacting species are functionally redundant, as communities change composition while network structure does not.
	✓	Community composition does not predictably vary, but network structure does. Host-parasite network structure varies predictably across space, suggesting species interactions turnover predictably across space.
✓	✓	Both community composition and interactions vaiy across space. Community composition and network structure vaiy spatially, suggesting spatial distance controls both community composition and network structure.

network structure does not become dissimilar with spatial distance while communities turnover as a function of geographic distance, it would suggest that interacting species are functionally redundant, as network structure is insensitive to the identities of interacting species (Olesen et al. 2011).

We used an extensive global database of host–helminth interactions (Gibson et al. 2005) to investigate the effect of geographic distance on the decay of similarity in both community and network structure for host and parasite communities. Network dissimilarity was quantified using a recently developed measure (Schieber et al. 2017) which compares networks based on their node distance distributions and centrality values (discussed in more detail below). In doing so, we test the existence of *distance-decay* relationships in host and parasite relationships at the global scale, as well as the regional scale by focusing on *distance-decay* of host and parasite communities and networks among states in the United States of America. Lastly, we examined the relationship between network structural dissimilarity and compositional dissimilarity for both host and parasite communities, as more compositionally similar assemblages may also retain a similar set of interaction patterns. Together, we provided evidence for *distance-decay* relationships at both regional and global scales in both host and helminth parasite communities, but not in terms of network dissimilarity. This suggests that different host and parasite species are filling the same functional roles in interaction networks, or perhaps that variation in network similarity is explained by a currently unmeasured aspect of host–helminth interactions.

Methods

Helminth parasite occurrence data

Helminth parasite occurrence data were retrieved from the London Natural History Museum (LNHM) parasite database (Gibson et al. 2005) – the most speciose parasite occurrence database to date in terms of the number of unique host (over 18 000) and parasite (over 27 000) species – using the 'helminthR' *R* package (Dallas 2016). Helminth occurrence data are georeferenced largely at the geopolitical level (though some island groups and lakes are represented), and contain over 350 distinct terrestrial and aquatic localities. While host and parasite distributions likely do not respect artificial geopolitical boundaries, these regional networks provide discrete networks with which to study community and network dissimilarity. The LNHM data are a fantastic resource, but currently do not offer finer scale georeferencing; a future task requiring a herculean effort.

This set of locations was reduced to terrestrial locations which we could obtain latitude and longitude measures, those locations that were not nested within other locations, and those with enough unique sampled host and parasite species to compute dissimilarity measures, resulting in a total of 234 georeferenced locations (Fig. 1). Host–parasite networks varied greatly in the number of interacting host (between 2 to 1511) and parasite (between 2 to 2447) species. Networks also varied considerably in terms of connectance (0.002–0.667 fraction of realized links), and modularity of bipartite host–parasite networks (0–0.96), as well as unipartite projections (discussed below), for both host (0–0.88) and parasite (0–0.91) sharing networks.

Dissimilarity measures

Dissimilarity among host and parasite communities was estimated as Sørensen dissimilarity (i.e. Bray–Curtis dissimilarity on binary data; Koleff et al. (2003)), a common dissimilarity measure suitable for presence–absence data. The metric is calculated by relating the shared species present between two communities (X and Y) divided by the summed species richness of both sites, where the number of species in each community corresponds to the length of the vectors X and Y.

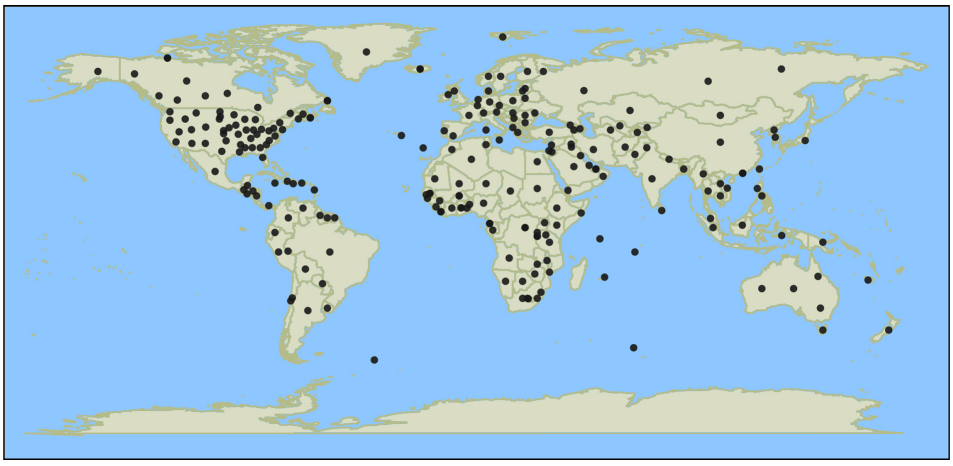

Figure 1. Localities included in the current analysis, based on data contained in the London Natural History Musuem's helminth database. Centroids of geopolitical locations are indicated with points.

$$X = X_1, X_2, \ldots X_n$$
$$Y = Y_1, Y_2, \ldots Y_m \quad (1)$$
$$S = \frac{2|X \cap Y|}{n+m}$$

To estimate dissimilarity in network structure, we first constructed host and parasite sharing networks (also called co-occurrence networks), which are unipartite projections of the bipartite networks consisting of host–parasite interactions (Fig. 2). These networks capture the relationships among one class (e.g. host species) by simplifying the identity of nodes of the other class (e.g. parasites). However, some information is maintained, as the edge weights of the graph correspond to the number of shared parasites for the unipartite projection of host species (i.e. the parasite sharing network) or the number of shared host species (i.e. host sharing network). Here, we lose information on the identity of second class of nodes, but we gain insight into host or parasite sharing relationships (Fig. 2). These unipartite projections have been used previously to examine host centrality and parasite sharing (Gómez et al. 2013, Pilosof et al. 2015). For each bipartite network of host–helminth interactions, we constructed two networks describing parasite sharing among host species (parasite sharing network), and host sharing among parasite species (host sharing network).

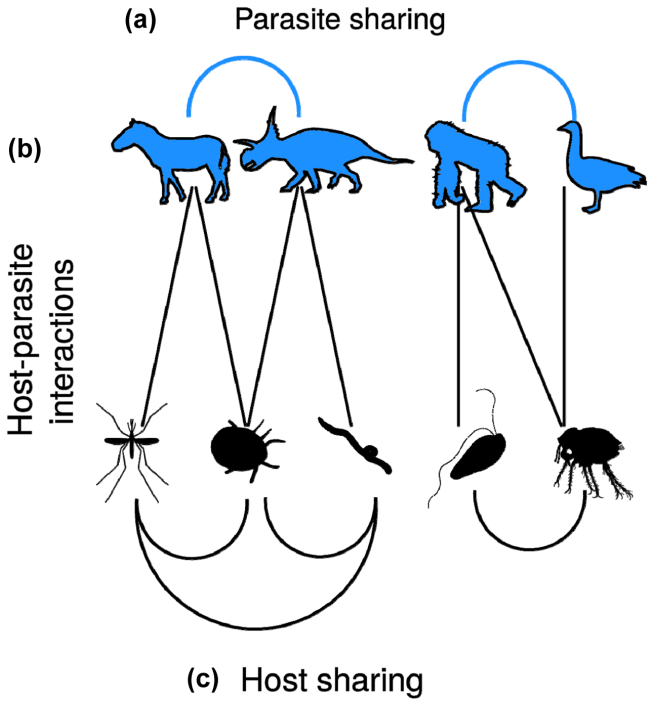

Figure 2. Host and parasite species interactions can be represented as a bipartite network (b) or be broken into their respective unipartite components, either a network of host species connected by instances of shared parasitism (parasite sharing network; (a)), or parasite species connected by shared host species (c). Host and parasite silhouettes were obtained from PhyloPic (<http://phylopic.org/>).

We estimated dissimilarity of these networks using a recently proposed measure of network dissimilarity (Schieber et al. 2017) that is both computationally efficient and captures differences in three core aspects of network structure (i.e. distance among nodes, connectivity of each node, and node centrality). This measure – the *D* statistic – does not use information on node identity, but provides a comparison of the structural similarity between two networks (Schieber et al. 2017). Both dissimilarity indices used (*D* statistic and Sørensen) are bounded between 0 and 1, where lower values correspond to more similar communities or networks, and larger values to more dissimilar communities or networks.

The *D* statistic is made up of 3 components; 1) dissimilarity in average node connectivity, 2) dissimilarity in a node dispersion metric (*NDD*), and 3) dissimilarity in node alpha centrality. Together, these components compose the most thorough network dissimilarity measure to date. Network node dispersion (*NDD*) quantifies the distributions of distances between nodes in a graph, and allows for comparison of two graphs based on the distance distributions of each graph.

$$NND(G) = \frac{\tau(P_1, \ldots, P_N)}{\log(d+1)} \quad (2)$$

where $\tau(P_1, \ldots, P_N)$ corresponds to the Jensen–Shannon divergence (a dissimilarity measure) for node distance distributions $P_1, \ldots, P_N$, where N is the number of nodes in the graph. Relying heavily on the *NND* of each graph (G_1 and G_2), the resulting calculation of the *D* statistic is

$$D(G_1, G_2) = \omega_1 \sqrt{\frac{\tau(\mu G_1, G_2)}{\log 2}} + \omega_2 \left| \sqrt{NND(G_1)} - \sqrt{NND(G_2)} \right| + \omega_3 \left(\sqrt{\frac{\tau(P_{aG_1}, P_{aG_2})}{\log 2}} + \sqrt{\frac{\tau(P_{aG_1^c}, P_{aG_2^c})}{\log 2}} \right) \quad (3)$$

where μ values correspond to mean distance distribution for each graph, the subscript *c* corresponds to the compliment of the graph, and *w* values correspond to user set weights which scale the relative importance of each of the three dissimilarity components to one another. Through experimentation, Schieber et al. (2017) recommend setting these weights as $w_1 = w_2 = 0.45$, and $w_3 = 0.1$, which emphasizes dissimilarity in node distance distributions between graphs. The *D* statistic has been found to outperform previously used measures of graph dissimilarity (i.e. Hamming distance and graph edit distance) after thorough testing on both simulated and empirical networks (Schieber et al. 2017).

For every combination of 234 georeferenced locations (Supplemental material Appendix 1), we computed

dissimilarity between host and parasite community composition, and dissimilarity in host and parasite sharing network structure. Spatial distance was quantified as the haversine distance between georeferenced locations.

The effect of spatial scale on *distance-decay* relationships

Distance-decay relationships are typically measured over relatively small spatial scales, as barriers to dispersal can create clear breakpoints in community (and potentially network) dissimilarity. To explore how spatial scale influenced the detectability of *distance-decay* relationships in network structure and community similarity, we focused a secondary analysis on host–parasite community and network dissimilarity between states within the United States of America.

At both regional and global scales, we performed procrustes rotational analyses, which attempts to minimize the sum-of-squared differences (m^2_{12}) between two matrices through rotation of one of the matrices. In our analyses, our two matrices consisted of 1) a distance matrix which captured pairwise geographic distances among localities, and 2) a pairwise dissimilarity matrix containing measures of either network structural or compositional similarity. To assess statistical significance, we performed 10 000 permutations of the Procrustes analysis, and compared sum-of-squared differences between rotated and observed matrices.

Data deposition

Data and analytical code are available available from Figshare Digital Repository: <https://doi.org/10.6084/m9.figshare.5174413> (Dallas and Poisot 2017).

Results

Distance-decay relationships in host and parasite communities

Both host (global: $m^2_{12}=0.86$, $r_p=0.38$, $p < 0.001$; regional: $m^2_{12}=0.77$, $r_p=0.48$, $p < 0.001$, Fig. 3a) and parasite (global: $m^2_{12}=0.87$, $r_p=0.36$, $p < 0.001$; regional: $m^2_{12}=0.78$, $r_p=0.47$, $p < 0.0001$, Fig. 3b) communities grew increasingly dissimilar with increasing geographic distance. This relationship saturated after approximately 2500 km, where the majority of geographic locality combinations further than this distance from one another had nearly completely dissimilar host and parasite communities on average. At large geographic distances, dispersal barriers may strongly enforce *distance-decay* relationships, suggesting that *distance-decay* relationships should be examined both at global and regional scales. However, we found similar results when focusing on host–parasite networks in the United States of America, calculating dissimilarity in host and parasite communities at the state-level (Fig. 4).

Distance-decay relationships in network structure

While *distance-decay* in similarity of host and parasite communities was clearly observed at both global (Fig. 3) and regional (Fig. 4) scales, we found marginal evidence of a decay in network similarity with increasing geographic distance at either global (Supplementary material Appendix 1 Fig. S1) or regional (Fig. 5) scale. That is, while correlations from our Procrustes rotation analyses were significant, these correlation values tended to be small for host sharing networks (global: $m^2_{12}=0.94$, $r_p=0.25$, $p < 0.001$; Fig. 5; regional: $m^2_{12}=0.92$, $r_p=0.29$, $p=0.16$, Supplementary material Appendix 1 Fig. S1) and parasite sharing networks (global: $m^2_{12}=0.93$, $r_p=0.26$, $p < 0.001$, Fig. 5;

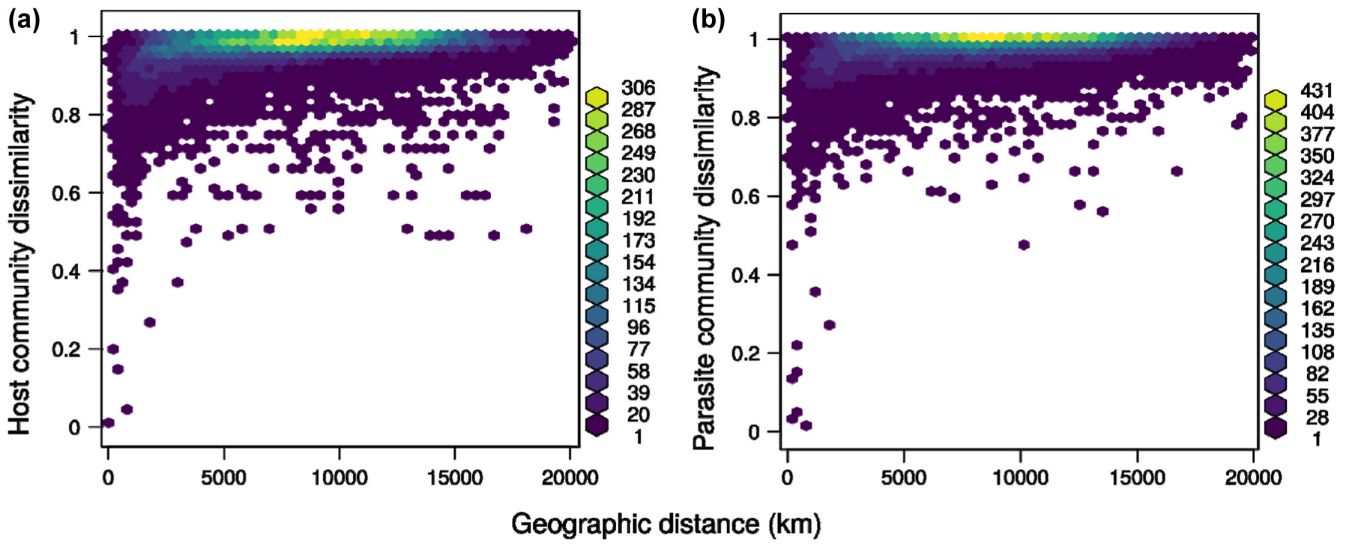

Figure 3. Host (a) and parasite (b) community dissimilarity as a function of geographic distance between locations. Community dissimilarity follows similar patterns for host and parasite communities, as community pairs become completely dissimilar as geographic distance surpasses around 2500 km. Color of hexagonal bins indicates data concentration (yellow colors correspond to highest concentration of data points).

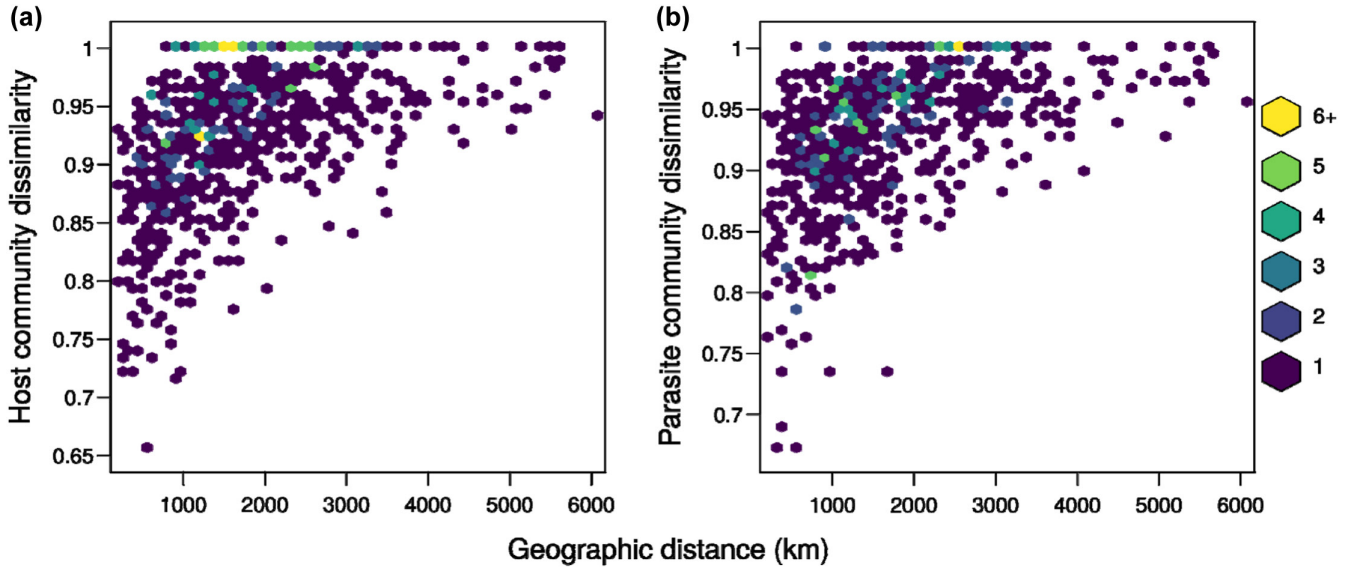

Figure 4. Host (a) and parasite (b) community dissimilarity as a function of geographic distance between states in the United States of America. Community dissimilarity follows similar patterns for host and parasite communities, similar to the global *distance-decay* relationship. Color of hexagonal bins indicates data concentration (yellow colors correspond to highest concentration of data points).

regional: $m^2_{12}=0.94$, $r_p=0.25$, p=0.32, Supplementary material Appendix 1 Fig. S1). The weak *distance-decay* relationship observed in network structural dissimilarity and strong *distance-decay* relationship for host and parasite community composition may suggest that host and parasite species are functionally redundant. That is, host and parasite community composition changed markedly with geographic distance, but networks were similarly structured regardless of distance and host and parasite species identity.

Lastly, we found that host and parasite community dissimilarity values were strongly related (global: $m^2_{12}=0.18$, $r=0.91$, $p<0.0001$, Fig. 6), suggesting that more dissimilar host communities tended to also have more dissimilar parasite communities. This is likely common among spatially separated host and parasite communities, as parasite species are obligate to their respective host communities and parasite species tend to infect spatially and phylogenetically similar host species (Poulin 2010). A related observation of similarity in network dissimilarity between host and parasite networks is a result of the same underlying data being used to create both host and helminth networks (Fig. 4).

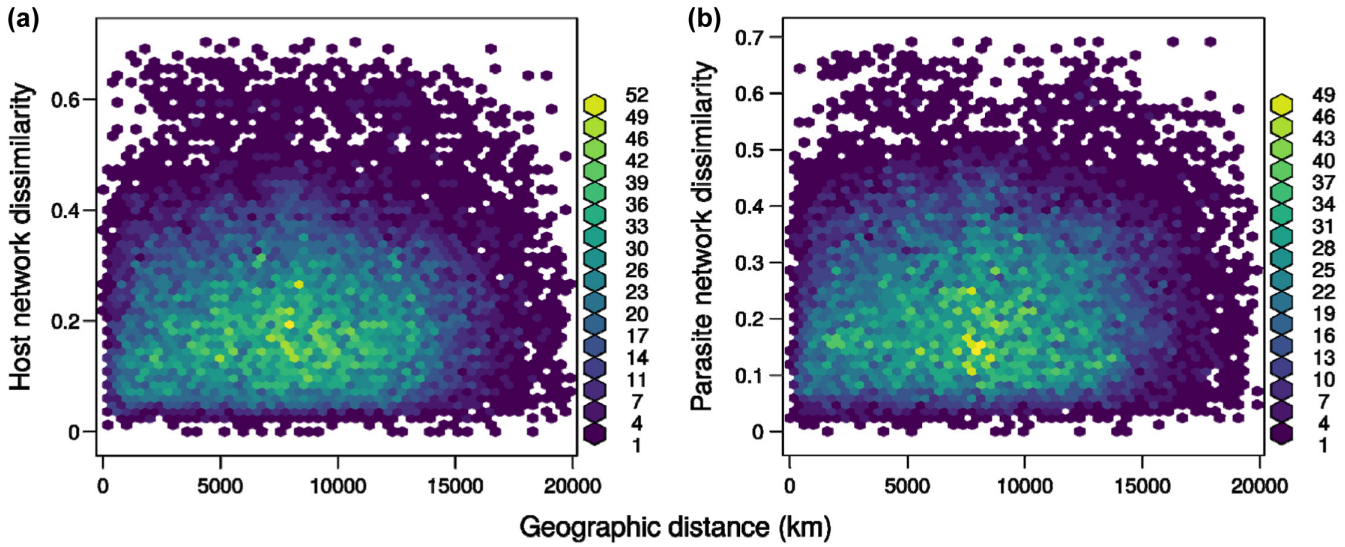

Figure 5. Host (a) and parasite (b) network dissimilarity as a function of geographic distance between locations. There is no clear relationship between network dissimilarity and geographic distance. Color of hexagonal bins indicates data concentration (yellow colors correspond to highest concentration of data points).

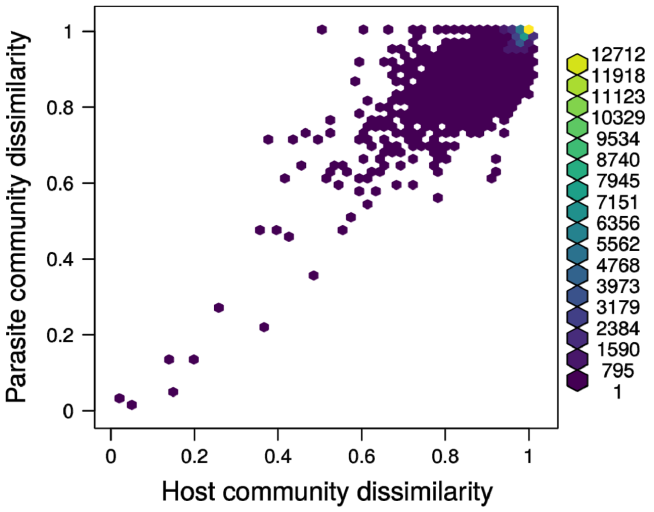

Figure 6. The relationship between host and parasite dissimilarity values, indicating a strong link between the compositional dissimilarity between host and parasite communities. Color of hexagonal bins indicates data concentration (yellow colors correspond to highest concentration of data points).

Discussion

The negative relationship between community similarity and geographic distance is a common observation in communities of free-living (Soininen et al. 2007) and – to a lesser extent – parasitic (Thieltges et al. 2009) organisms. Here, we examined whether compositional shifts in host and parasite communities at a global scale also correspond to changes in host–parasite interaction patterns. Our findings suggest that host and helminth parasite communities become dissimilar non-linearly with increasing geographic distance at both regional and global scales, but that network structure does not similarly decay with geographic distance. This suggests that host and parasite interaction patterns are maintained across geographic space, even when host and parasite community composition change considerably. That is, under the assumption that species interaction patterns relate to structural stability (Thébault and Fontaine 2010, Rohr et al. 2014), species are serving functionally redundant roles despite compositional shifts. Finally, we found that host and helminth community dissimilarities were clearly related to one another, suggesting more dissimilar host communities also tended to have more dissimilar parasite communities. Together, we provide evidence for a clear *distance-decay* relationship in host community composition and associated helminth parasite communities, but not for entire host–parasite networks, suggesting host and parasite species may serve functionally redundant roles in host–parasite networks.

Distance-decay relationships are a common observation in both free-living (Soininen et al. 2007, Korhonen et al. 2010) and parasitic (Poulin 2003, Warburton et al. 2016) communities. There are numerous reasons why we would expect helminth parasite communities to become dissimilar with increasing geographic distance. Helminth species have environmental tolerances that restrict their spatial distributions, have limited dispersal ability except when inside of a host individual, and often specialize on a subset of available host species (Cooper et al. 2012). Together, this suggests that helminth parasite communities may just reflect variation in host communities. That is, *distance-decay* relationships in helminth communities are simply a result of *distance-decay* relationships in host communities. This is suggested by the nearly one-to-one relationship between host and helminth community dissimilarity (Fig. 6). Further tests of the generality of this relationship are needed, including examinations of parasite community dissimilarity in systems where no *distance-decay* in host community similarity is observed.

Interestingly, even some nearby (< 500 km apart) geographic locations had markedly different host and parasite composition. There are at least two potential reasons for this. First, some islands had high community dissimilarity, including Sumatra and Sabah, which could represent different geologic history or dispersal limitation. Second, some countries may simply be poorly sampled due to variation in sampling effort or as a result of geopolitical reasons. For instance, North Korea and South Korea have very dissimilar host (0.97) and parasite (0.94) communities, but this is potentially a result of political reasons and our current limited understanding of host and parasite communities in North Korea. While sampling biases may explain some of the high compositional dissimilarity values, we provide strong evidence that host and parasite communities become increasingly compositionally dissimilar with increasing geographic distance for well-sampled areas (states within the United States of America), suggesting that our findings are not simply a function of inherent sampling biases.

The idea that interaction patterns in host–parasite networks may be determined based on host and parasite abundance – as predicted by neutral theory – has some supporting evidence (Canard et al. 2014). Here, we provide further support of this idea, as we demonstrate that interactor identity does not influence variation in network dissimilarity, suggesting the possibility host species are functionally interchangeable. However, this does not necessarily mean that host–parasite interactions are neutral, but simply that host and parasite communities have functionally similar members. That is, host and parasite abundance are not the only drivers of interactions, but different host species with similar parasite species richness and roles in the host–parasite network could also lead to the patterns we observed. We have demonstrated previously that the host community of helminth parasites is predictable based on sets of host traits (Dallas et al. 2017a) – and that host–parasite interactions may be predictable more generally (Dallas et al. 2017b) – providing support to the idea that interaction patterns may be determined by host traits.

Previous work has suggested that interaction networks tend to be conserved over spatial extent, but that this apparent similarity belies highly variable individual interactions (Carstensen et al. 2014, Kemp et al. 2017). While the data

used for our analyses may be too coarse to examine species-level interaction patterns, our findings provide further evidence for the spatial conservation of interaction network structure, suggesting that even at large spatial scales, and in host–parasite networks, network structure does not change predictably over geographic distance. Understanding which variables are related to network dissimilarity is an obvious next step and pressing research need, as variables that drive dissimilarity between networks may also change through time. This would suggest that network structure – which has previously been related to network stability (Thébault and Fontaine 2010, Feng and Takemoto 2014, Gravel et al. 2016) – may predictably change with time as environmental conditions change. The incorporation of environmental distance is a possible next step, though variation in country size and the resulting difficulty quantifying mean environmental conditions without finer scale georeferencing presents a challenge in examining environmental *distance-decay* relationships using the LNHM database.

Understanding the drivers of variation in mutualistic (e.g. plant–pollinator) and antagonistic (e.g. host–parasite) networks is a current challenge in ecology (Olesen et al. 2010, Hagen et al. 2012), and has resulted in several interdisciplinary collaborations bridging the fields of ecology, biogeography, and graph theory together. Further, recent efforts have suggested that a large scale views from biogeography and macroecology may provide insight into generalities of patterns of interactions between host and parasite species (Stephens et al. 2016). Our study contributes to this growing body of literature by suggesting that helminth parasite species and their respective host species may be functionally redundant in their interactions, despite clear evidence for *distance-decay* patterns in host and parasite community similarity at both regional and global scales.

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Supplementary material (Appendix ECOG-03514 at < www.ecography.org/appendix/ecog-03514 >). Appendix 1.