Received: 27 July 2021 | Revised: 24 November 2021 | Accepted: 15 December 2021

DOI: 10.1111/geb.13452

Global Ecology and Biogeography | A Journal of Macroecology

WILEY

RESEARCH ARTICLE

Parasite species richness and host range are not spatially conserved

Tad A. Dallas[1,2] | Pedro Jordano[3]

[1]Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana, USA

[2]Department of Biological Sciences, University of South Carolina, Columbia, South Carolina, USA

[3]Integrative Ecology Group, Estación Biológica de Doñana (EBDCSIC), Sevilla, Spain

Correspondence
Tad A. Dallas, Department of Biological Sciences, Louisiana State University of South Carolina, Columbia, South Carolina USA 29205, University of South Carolina examining questions in population and community ecology.
Email: tad.a.dallas@gmail.com

Funding information
Project HPC-EUROPA3, Grant/Award Number: INFRAIA-2016-1-730897

Handling Editor: Shane Blowes

Abstract

Aim: Interactor richness in host–parasite networks, corresponding to either parasite species richness for host species or host range for parasite species, can be a function of taxonomic or trait constraints. Species appearing in multiple networks can have similar interactor richness in each network owing to these taxonomic and trait constraints, resulting in a spatially conserved mean interactor richness and lower variation in interaction richness relative to a null expectation. Here, we used a global database of host–helminth interactions to examine the variability in interactor richness across a spatially explicit collection of 299 host–helminth networks.

Location: Global.

Time period: 1800–2003.

Major taxa studied: Helminth parasite species and their host species.

Methods: We used randomization tests to examine spatial conservation of species interactions for both host and helminth species.

Results: We failed to detect a signal of interactor richness conservation for > 95% of host and helminth parasite species relative to a set of three null models, where both the mean number of interactions per species and the variation in the number of interactions per species did not differ from a random draw. Furthermore, we detected a significant taxonomic signal in divergence in parasite species richness from a null model for host species, indicating that slight departures from null expectations are related to host phylogenetic relationships.

Main conclusions: Overall, this indicates that interactor richness can vary widely for the same species and that host and helminth parasite species can play very different functional roles in interaction networks across spatial or environmental gradients.

KEYWORDS
ecological network, helminth, host range, parasite macroecology, parasite species richness, parasite specificity

1 | INTRODUCTION

Species associations, including both antagonistic and mutualistic associations, can change across spatial or environmental gradients (Pellissier et al., 2018), as determined, in part, by species geographical range overlap, environmental conditions, density dependence and the context of the local community (Hart & Marshall, 2013; Menge et al., 2004). For host–parasite associations, the presence of a set of suitable host species is requisite, but numerous other ecological filters can determine the total number of interactions of host and parasite species, such as density dependence in parasite encounter and transmission, and the effects of the environment on parasite survival. This variation in host community composition and environmentally influenced encounter and transmission processes

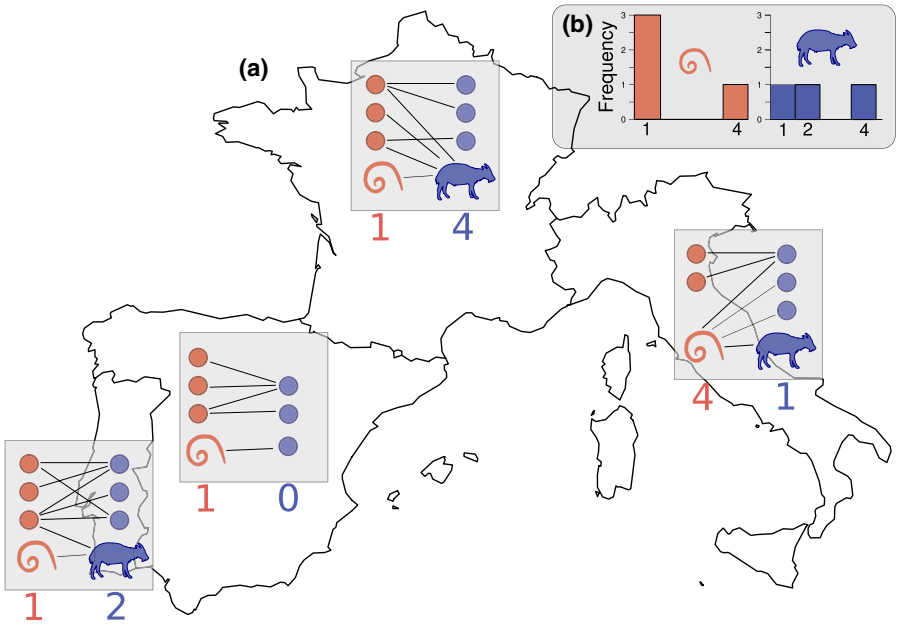

FIGURE 1 An example of spatial conservation of interactor richness in host (blue) and helminth parasite (red) species. The interactor richness of the focal species (organism silhouettes) is given below each network, representing the interactions of hosts and helminth parasites at the country level. The number of species in the networks changes, as does the presence of the focal species (i.e., the focal host species is not present in Spain). Understanding the drivers of this variation in interactor richness is fundamental in order to understand how biotic and abiotic variables shape host–parasite interactions across species ranges

leads to variation in parasite species richness for host species and variation in host range for parasite species (Poulin, 1997; Poulin & Morand, 2014). This would mean that the ecological processes influencing the frequency of interaction between host and parasite species can influence the resulting presence of an association itself (e.g., a host and parasite might be present in a location but not interact owing to host and parasite density falling below some transmission threshold). These processes could result in variation in the number of recorded associated species associations for a given host or parasite species along spatial or environmental gradients.

Typically, the number of parasite species infecting a given host species is referred to as the parasite species richness of that host, and the number of permissive host species that a given parasite can infect is referred to as the host range of that parasite (Gorter et al., 2015; Hellgren et al., 2009). Here, for clarity and generality, we use the term interactor richness for both of these and examine both simultaneously. A wealth of studies have examined parasite species richness patterns (for a review, see Kamiya et al., 2014) as a function of host geographical range size (Lindenfors et al., 2007), traits (Ezenwa et al., 2006; Lindenfors et al., 2007), demography (Arneberg, 2002) and phylogeny (Nunn et al., 2003; Poulin, 1995). Arguably, fewer studies have focused on host range (but see Dallas et al., 2017; Vesk et al., 2010), despite the importance of parasite host range as it relates to parasite exinction risk (Strona, 2015) and potential influence on co-extinction dynamics (Dallas & Cornelius, 2015; Farrell et al., 2015).

A null expectation is that interactor richness will remain relatively constant across space, as evolutionary and life-history traits influence the range of host species that a parasite can infect (Krasnov et al., 2004) or the number of parasite species that can infect a given host species (Poulin et al., 2013). This would suggest that interactor richness might be a conserved property of a given species (i.e., a specialist parasite is always a specialist parasite). However, this requires that each location where a parasite species is present also contains a set of potentially suitable host species, which might not be the case at large spatial scales (Dallas & Poisot, 2018). Spatial differences in host and parasite community composition might be countered by host and parasite species playing functionally similar roles in host–parasite interaction networks (Dallas & Jordano, 2021a; Dallas & Poisot, 2018); that is, host species might maintain their overall number of infective parasite species, whereas the identity of the parasite species might change among locations. This can be driven by the host immune response (Allen & Maizels, 2011; Anthony et al., 2007), the host life history (Johnson et al., 2012) or host species abundance (Canard et al., 2014). Likewise, parasite species might have a fairly narrow host range, whereas the identities of the suitable host species might change. For instance, this conservation of interactor richness has been observed previously in food webs (Baker et al., 2015). Given the broad spatial distributions of parasite species and the relatively common phenomenon of host switching (Araujo et al., 2015; Paterson & Gray, 1997), it is possible that interactor richness in host–parasite systems is also spatially conserved, meaning that we would tend to observe the same number of interacting species across all the networks in which a species is found.

Examinations of spatial and temporal patterns in ecological networks are a recent endeavour (Dormann et al., 2017; Pellissier et al., 2018; Tylianakis & Morris, 2017), with studies largely focusing on properties of entire networks instead of individual species. This has left spatial consistency of interactor richness (either host range or parasite species richness) a largely open question. To what extent is interactor richness conserved at global scales? We addressed this knowledge gap using a collection of 299 host–helminth interaction networks, consisting of 14,933 host species and 23,601 helminth species (Dallas, 2016; Gibson et al., 2005). For each host and helminth parasite species, we compared the observed mean and variation in estimated interactor richness and relative interactor richness across the geographical range of each species with several null models (Figure 1). This addressed two different questions. By examining

the mean interactor richness, we asked about interaction specificity and the average number of species associations relative to a null (i.e., is the mean number of interactions different for a given species?). By examining variability in interactor richness, we asked whether the variation in interactor richness observed across the geographical range of a species is different from a null expectation (i.e., is interactor richness spatially conserved?). We failed to detect a difference between empirical variation in interactor richness and our null expectations for a vast majority (> 95%) of host and helminth species, suggesting that the variation in interactor richness was not different from that expected by chance. Together, we found that the number of species that host and helminth parasite species interact with across their ranges is not a species-level trait, but is contingent upon the availability of suitable interaction partners and spatial or environmental gradients, which may contribute to the degree of generality (or specificity) in host–helminth associations.

2 | METHODS

2.1 | Host–helminth interaction data

Records of helminth parasite occurrences on host species were obtained from the parasite database of the London Natural History Museum (Gibson et al., 2005) and accessed programmatically using the HELMINTHR package (Dallas, 2016). These data currently represent one of the largest sources of host–parasite interaction data (Dallas et al., 2018; Gibson et al., 2005), despite being restricted to helminth parasites, including Platyhelminthes (trematodes, cestodes and monogeneans), Acanthocephalans and Nematodes (Gibson et al., 2005), constituting > 250,000 host–helminth association records. Although host–helminth associations exist in the data for captive hosts and experimental infections, we consider in the present analyses only those host–helminth associations that were observed in wild populations.

Host–helminth interactions in this data resource are georeferenced to > 400 terrestrial and aquatic locations, largely determined by geopolitical boundaries (e.g., "Spain"). These locations can be large in overall area and almost certainly vary in their sampling effort (e.g., there are not many host–helminth records from North Korea). Locations that were too vague or within which other locations were nested (e.g., "Western Europe") were removed, resulting in a total of 299 locations. Geographical locations related to coastal areas or other marine environments are liable to contain marine hosts and associated helminth parasites and might not be comparable to terrestrial host–helminth networks. We explored this by removing aquatic and marine locations (see Supporting Information Figures S1–S8), finding that our results were not strongly influenced by the inclusion of aquatic and marine locations. Hence, we have included aquatic and marine locations in our analyses. For more information on the host–helminth interaction data, see Carlson et al. (2020), Dallas (2016), Dallas et al. (2019), Dallas and Jordano (2021b) and Gibson et al. (2005).

Geopolitical locations vary in their area, habitat, topography and sampling effort. This is an inherent limitation, one which must be considered as how host–helminth associations change across the coarsely defined geographical range of host and parasite species. However, these data represent a herculean effort to compile, curate and distribute > 250,000 host–helminth associations distributed around the world (Gibson et al., 2005), creating opportunities to explore macroecological patterns in host–parasite associations (Dallas et al., 2018, 2019; Dallas & Becker, 2021; Dallas & Jordano, 2021b; Dallas & Poisot, 2018). Efforts are being made to aggregate and curate species interaction network data from individual studies at finer spatial scales (e.g., Poisot et al. (2016)), but even these collections suffer from some of the same geographical coverage biases present in the host–helminth association data used here (Poisot et al., 2021).

Host species in the data can be diverse, ranging from insects to mammals. This range in taxonomic breadth might make some comparisons of overall interactor richness more difficult to interpret. For instance, comparing the parasite species richness for a snail host species with a null distribution of parasite species richness of mammal, fish and insect species might be inappropriate. To explore the consistency of our overall findings, we subset the host species considered to be only mammalian host species. However, this did not change our results (see Supporting Information section "Considering only mammalian host species"). Hence, we report the overall findings here and discuss the influence of host taxonomic breadth further in the Supporting Information. Helminth parasite species are also incredibly diverse in their transmission modes and life histories. We explore differences in helminth parasite taxonomic groups further in the Supporting Information (see section "Examining differences among parasite groups"), finding no substantial differences among helminth parasite taxa (Figures S9 and S10).

2.2 | Quantification of interactor richness

Estimates of interactor richness for host and parasite species were examined for each host (n = 14,933) and helminth (n = 23,601) species occurring in ≥ 2 of the 299 sampled locations in the London Natural History Museum data. For each host–helminth network, we calculated the number of interaction partners for every host and helminth species (Figure 1). This measure is directly analagous to degree centrality, a commonly used node-level property in the study of ecological networks, which is simply the summed number of links between host and parasite species for each interactor in the network, corresponding to the number of parasite species infecting a given host species (parasite species richness) or the number of host species for a given parasite species (host range).

We also estimated interactor richness relative to the maximum observed values in the given network. This was performed by standardizing the estimates of interactor richness by the maximum observed value in each location-specific network and for each type of species (i.e., host or parasite), allowing the comparison of the relative values across space. The underlying idea is that variation exists

in the number of available host species or the number of parasite species present in each locality. By standardizing by the maximum observed value of interactor richness for hosts and parasites, we investigate the tendency of species to maintain the same number of interaction partners, scaled by some maximum value. Our results were strikingly similar regardless of standardization approach, and we report results for unstandardized interactor richness in the Supporting Information.

2.3 | Randomization approaches to determine conservation of interactor richness

Species are often found in more than a single location, resulting in multiple estimates of interactor richness for a given species. We used a set of randomization approaches to determine the conservation of interactor richness for each host and helminth parasite sampled. To do this, we compared the estimates of the mean and variation in interactor richness with a null distribution of values obtained through three randomization approaches. By comparing mean interactor richness, we examine the differences in interactor richness for a species relative to a null distribution (i.e., is the average number of species interactions for a given species significantly different from a null distribution?). Comparing the standard deviation in interactor richness with a null distribution then addresses the spatial conservation of species interactions (i.e., is the variation in interactor richness estimates for a given species different from we would expect from some null model?).

All three approaches selected a set of interactor richness estimates based on some criteria (described below) and calculated mean and standard deviation in the sample. The null model randomization approaches, in order of increasing stringency, were as follows:

1. The first approach maintained the number of interactor richness estimates and the species type (i.e., host or helminth parasite), but sampled interactor richness randomly across space. This approach tacitly assumes that there is no spatial variation in interactor richness.
2. The second null model did the same as the first, but now was constrained to maintain the number of locations from which a species was sampled (± 1). This begins to incorporate geographical variation by sampling the same number of unique networks as those in which the empirical species is found.
3. The final null model constrained the spatial sampling further by sampling only those locations in which the focal species was also found. This explicitly considers only those geographical locations where a species is found.

The underlying idea of these null models is that differences in spatial conservation of interactor richness in the empirical data could be different from a randomized null model that makes no assumption about species identity or spatial location. That is, if we see a departure in empirical interactor richness for a species relative to the null models described above, it would suggest that interactor richness is spatially conserved in comparison to the simple assumptions of the null models. By incorporating different assumptions into the null models, as described above, we attempt to tease apart which additions to null models are important to interactor richness conservation.

These null models each incorporate different assumptions about the conservation of interactor richness. For instance, the first null model samples host or parasite interactor richness from any location from around the globe, although the set of locations where the given host or parasite species is observed is likely to be much more geographically constrained or clustered. The failure to detect differences from this simple null model would suggest that the mean and/or variability for the observed species is not substantially different from a random pull from the set of global possibilities. In the most restrictive null model, we sample only the specific set of locations where the host or parasite species of interest was sampled, which starts to address issues of geographical variation in species richness or interaction specificity.

This procedure was repeated 500 times, resulting in a null distribution of 500 estimates of interactor richness mean and standard deviation, to which the empirical interactor richness estimates for a given species could be compared. By example, following the first null model described above, we would draw interactor richness values randomly based on the overall number of interactor richness estimates existing for a given species (i.e., the number of geopolitical locations where the species was found). The mean and standard deviation of this single random draw would be computed, and this process would be repeated 500 times, creating null distributions of both mean and standard deviation in interator richness. This assesses whether species tended to have more similar (mean) and consistent (standard deviation) interactor richness estimates than expected relative to the set of three null models. We compared the null distributions with the empirical estimates of interactor richness using *z*-scores, which standardize the difference between empirical and null means by the standard deviation of the null distribution ($\bar{x} - x / \sigma$), capturing the number of standard deviations away from the mean that the empirical estimate is from the null distribution. This allows the calculation of the probability of observing a given empirical interactor richness by chance given the null distribution. Species with larger mean or variation in empirical interactor richness than expected would have a negative *z*-score. If species interactor richness is conserved, we would expect *z*-scores for variation to be more positive, which would correspond to the observed deviance in interactor richness estimates for a species being less than that predicted by the null model.

2.4 | Taxonomic signal in interactor richness conservation

The degree to which species deviate from null expectations might be related to species phylogenetic relationships. For host species, this would mean that the extent to which interactor richness is

conserved is phylogenetically constrained, such that more closely related host species tend to be more similar in their degree of interactor richness conservation. This conservation of interactor richness would mean that the number of parasite species infecting a given host species is more constant than expected compared with a null expectation across the host species geographical range. We estimated the taxonomic signal in deviation between observed parasite species richness and the null expectation as a function of host taxonomic relationships obtained through the *taxize R* package (Chamberlain & Szöcs, 2013) and an Abouheif test based on Moran's *I* from the *adephylo* (Jombart & Dray, 2010) R package.

R code and data to reproduce all analyses and figures are available on figshare at https://doi.org/10.6084/m9.figshare.9977420.v1.

3 | RESULTS

We failed to detect significant conservation of mean interactor richness relative to our set of null models for a majority of host species (14,300, 14,070 and 13,875 species for null models 1, 2 and 3, respectively, out of 14,933 total species; Figure 2) or helminth parasite species (22,618, 22,237 and 21,825 species for null models 1, 2 and 3, respectively, out of 23,601 species; Figure 2). Conservation of mean interactor richness was present for no species in null models 1 and 3, but existed for a small number of host (n = 23) and helminth parasite (n = 38) species under null model 2. This suggests that the mean number of host species infected by a helminth parasite or the mean number of parasite species with which a host species is infected is not significantly different from a null distribution. Our findings were consistent whether we measured standardized interactor richness (Figure 2) or unstandardized interactor richness (see Supporting Information).

We also failed to detect significant differences from the null models in terms of spatial variation in interactor richness for a majority of host species (6,799, 6,684 and 6,530 species for null models 1, 2 and 3, respectively, out of 7,005 total species; Figure 3) or helminth parasite species (11,045, 10,952 and 10,533 for null models 1, 2 and 3, respectively, out of 11,439 species; Figure 3). The total number of species for which the standard deviation of interactor richness could be estimated was lower owing to some species occurring only once. A single host species, which was a freshwater snail (*Lymnaea truncatula*), was found to have significantly lower variation in interactor richness for null model 1. However, null model 2 uncovered the presence of species interactor richness conservation for a small number of host species (n = 23) and helminth parasite species (n = 31). Our findings were consistent whether we measured variation in standardized interactor richness (Figure 3) or unstandardized interactor richness (see Supporting Information).

Divergence from null expectations (measured using z-scores) for both mean and variation in interactor richness were unrelated to parasite taxa and very weakly related to the number of locations where the interactor species was found (see Supporting Information). For host species, we detected a phylogenetic signal in the z-scores of mean parasite species richness (Table 1), suggesting that host taxa differed in their average parasite species richness. However, we failed to detect a signal in the z-scores of variability in parasite species richness (Table 1), providing evidence that taxonomic relationships among host species cannot explain the degree of variation in interactor richness across spatial gradients.

4 | DISCUSSION

We failed to detect a difference for the majority of species in terms of both the mean and variation in interactor richness relative to a

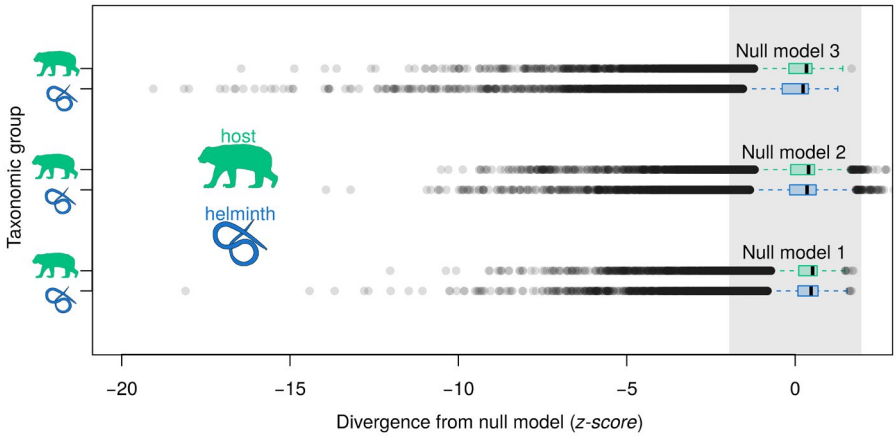

FIGURE 2 Boxplots of the difference between empirical mean interactor richness relative to a null model that randomly selects species of the same type (i.e., host or helminth). Divergence from the null is measured as the z-score comparing the empirical value with the null distribution, whereby more positive values are indicative of a smaller mean or deviation in the empirical data relative to the null distribution, and more negative values are indicative of the opposite. The grey shaded area indicates the 95% confidence threshold ($z = \pm 1.96$; $\alpha = 0.05$). Shaded boxes for the null models indicate 25th and 75th percentiles; black vertical lines indicate the median z-score; black points are outliers

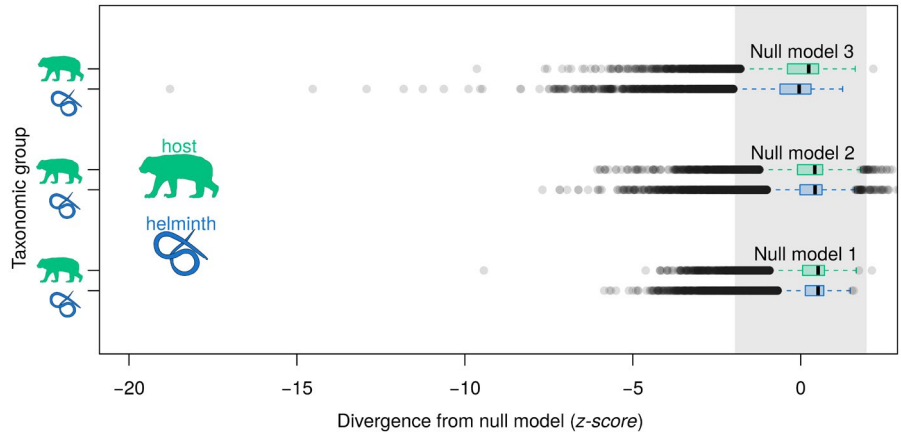

FIGURE 3 Difference between empirical variation (*SD*) in interactor richness relative to a null model that randomly selects species of the same type (i.e., host or helminth). Divergence from the null is measured as the *z*-score comparing the empirical value with the null distribution, whereby more positive values are indicative of a smaller mean or deviation in the empirical data relative to the null distribution, and more negative values are indicative of the opposite. The grey shaded area indicates the 95% confidence threshold ($z = \pm 1.96$; $\alpha = 0.05$). Shaded boxes for the null models indicate 25th and 75th percentiles; black vertical lines indicate the median *z*-score; black points are outliers

Variable	Relative	χ	$\bar{\chi}_s$	*p*-value
Mean interactor richness	Yes	0.0458	2.02	**.039**
	No	0.0421	1.87	**.047**
SD in interactor richness	Yes	−0.0102	−0.23	.574
	No	0.0426	1.83	.051

TABLE 1 The existence of a phylogenetic signal in *z*-scores of mean and variation in interactor richness compared with a null model based on values of the empirical test statistic (χ) and mean values from randomization tests ($\bar{\chi}_s$)

Note: Deviation in mean interactor richness from a null model had a significant phylogenetic signal ($\alpha = 0.05$) considering relative interactor richness (interactor richness divided by the maximum for each spatial location) and non-standardized values (indicated by the "Relative" column). There was no observable phylogenetic signal in interactor richness variation divergence from a null expectation.

set of three null models. For helminth parasites, this indicates that the number of host species they can infect is not a conserved value at the species level. That is, helminth parasite species do not infect the same number of host species across the their spatial distribution, and the burden of helminth parasitism differs on any given host species across its spatial distribution. This variation for a given helminth parasite host range across different spatial locations could indicate that differential availability or usage of host species, dispersal limitation or environmental controls on parasite transmission might determine parasite specificity or generality in any given location. For host species, this might indicate that the number of helminth parasite species infecting a given host is not conserved. That is, variables promoting increased parasite richness at the host species scale, such as body size and geographical range size (Kamiya et al., 2014), might capture species-level parasite richness (the number of parasite species that might infect a given host species) but fail to capture local-scale parasite species richness. These results were insensitive to the use of relative interactor richness or unstandardized interactor richness (for analyses of unstandardized richness, see Supporting Information). However, we did observe a host phylogenetic signal in divergence from the null for mean parasite species richness, providing support to previous findings that host phylogeny is important in estimating parasite species richness. However, we observed no differences in the variation in parasite species richness and no differences between parasite groups in mean or variation in host range. Together, our findings suggest that interactor richness is not conserved and that each host and helminth parasite can serve a different role in different locations, which is important to consider to when attempting to predict the impact of an invasive host or parasite species on the existing interaction network.

Although the number of species interactions for hosts (parasite species richness) and helminths (host range) might not be a trait of the species, this does not mean that these properties are not associated with species traits or phylogenies (Guégan & Kennedy, 1996; Kamiya et al., 2014; Krasnov et al., 2004). Based on previous studies, it is clear that interactor richness for both host (Lindenfors et al., 2007; Nunn et al., 2003) and parasite (Dallas, Huang, et al., 2017; Dallas, Park & Drake, 2017; Pulgarín-R et al., 2018) species can be predictable quantities and are a function of species life history (Kamiya et al., 2014). Furthermore, multiple studies have found that interactor richness can have a phylogenetic signal, in that the number of parasite species infecting a set of host species is related to the

phylogenetic distance between host species (Nunn et al., 2003; Poulin et al., 2013; Presley et al., 2015). Our failure to detect the conservation of mean interactor richness could come from the null sampling process and the skewed nature of the data. Species were often found in only a small number of geographical locations, such that estimates of the mean might have been coarse. Furthermore, even for widespread species there was a pronounced right skew to the number of interactions made by a species, whereby estimates of interactor richness were small for a majority of geographical locations for a given species, but rather large in a small number of geographical locations. There are a number of explanations for this, including the possibility that the spatial variation in the availability of suitable species with which to interact might drive spatial variation in interactor richness (Harris & Dunn, 2010; Kennedy & Guégan, 1994), making it necessary to consider each host–helminth network separately. This would suggest that studies considering the full network, ignoring the spatial distribution of host and parasite communities, might fail to capture the important variables constraining interactor richness more locally. That is, predictive models trained on local host–parasite networks might find different variables to be important in estimating interactor richness. The consistency of the relative importance of explanatory variables in estimating interactor richness remains an open question.

Despite the fact that the London Natural History Museum host–helminth interaction database is one of the most extensive host–parasite data sources currently available (Dallas et al., 2018), the majority of the data are based on published literature and museum records, which are likely to contain sampling, detection and identification biases. Lastly, the host–helminth interactions are georeferenced to political boundaries, which few host or parasite species respect. However, the majority of these biases are present in all large-scale data. We attempted to address many biases through data cleaning by removal of nested or ambiguous locations and through additional analyses examining the effect of the removal of aquatic and marine locations (see Supporting Information). All the data and analytical code used in the analysis are openly available (https://doi.org/10.6084/m9.figshare.9977420.v1), promoting further analyses and continued refinement of this extensive data source.

The availability of large-scale data on species interactions has promoted the development and testing of macroecological theory for trophic interactions (Gravel et al., 2011). For instance, spatial and environmental gradients leading to specialization on a smaller subset of resources has been observed in insect diets (Forister et al., 2015). The application of similar approaches using large-scale data of host–parasite interactions could advance the exploration of environmental and spatial gradients in parasite specialization (Poulin et al., 2011; Wells & Clark, 2019). This has clear implications to host–parasite network structure and to identifying areas where hosts and parasites are more likely to go extinct in a changing climate (Brooks & Hoberg, 2007; Carlson et al., 2017). A continued incorporation of analytical approaches (Connor et al., 2017; Dormann et al., 2017), a consideration of the multiple nested spatial scales at which host and parasite species interact (Penczykowski et al., 2016) and further development of macroecological theory related to host–parasite interactions (Dallas et al., 2018; Stephens et al., 2016) will contribute greatly to our understanding of host–parasite interactions across space.

ACKNOWLEDGMENTS

The work has been performed under the Project HPC-EUROPA3 (INFRAIA-2016-1-730897), with the support of the European Commisssion Research Innovation Action under the H2020 Programme; in particular, the authors gratefully acknowledge the support of the Barcelona Supercomputing Centre.

CONFLICTS OF INTEREST

The authors have no conflicts of interest to declare.

AUTHOR CONTRIBUTIONS

Both authors conceptualized the project. T.A.D. performed the analysis. Both authors contributed to manuscript writing.

DATA AVAILABILITY STATEMENT

Data and R code are available on Figshare at: https://doi.org/10.6084/m9.figshare.9977420.v1.

ORCID

Tad A. Dallas https://orcid.org/0000-0003-3328-9958
Pedro Jordano https://orcid.org/0000-0003-2142-9116

REFERENCES

Allen, J. E., & Maizels, R. M. (2011). Diversity and dialogue in immunity to helminths. *Nature Reviews Immunology*, *11*(6), 375–388.

Anthony, R. M., Rutitzky, L. I., Urban, J. F. Jr, Stadecker, M. J., & Gause, W. C. (2007). Protective immune mechanisms in helminth infection. *Nature Reviews Immunology*, *7*(12), 975–987.

Araujo, S. B., Braga, M. P., Brooks, D. R., Agosta, S. J., Hoberg, E. P., von Hartenthal, F. W., & Boeger, W. A. (2015). Understanding host-switching by ecological fitting. *PLoS One*, *10*(10), e0139225.

Arneberg, P. (2002). Host population density and body mass as determinants of species richness in parasite communities: Comparative analyses of directly transmitted nematodes of mammals. *Ecography*, *25*(1), 88–94.

Baker, N. J., Kaartinen, R., Roslin, T., & Stouffer, D. B. (2015). Species roles in food webs show fidelity across a highly variable oak forest. *Ecography*, *38*(2), 130–139.

Brooks, D. R., & Hoberg, E. P. (2007). How will global climate change affect parasite–host assemblages? *Trends in Parasitology*, *23*(12), 571–574. https://doi.org/10.1016/j.pt.2007.08.016

Canard, E., Mouquet, N., Mouillot, D., Stanko, M., Miklisova, D., & Gravel, D. (2014). Empirical evaluation of neutral interactions in host-parasite networks. *The American Naturalist*, *183*(4), 468–479.

Carlson, C. J., Burgio, K. R., Dougherty, E. R., Phillips, A. J., Bueno, V. M., Clements, C. F., Castaldo, G., Dallas, T. A., Cizauskas, C. A., Cumming, G. S., & Doña, J. (2017). Parasite biodiversity faces extinction and redistribution in a changing climate. *Science Advances*, *3*(9), e1602422.

Carlson, C. J., Dallas, T. A., Alexander, L. W., Phelan, A. L., & Phillips, A. J. (2020). What would it take to describe the global diversity of parasites? *Proceedings of the Royal Society B: Biological Sciences*, *287*(1939), 20201841. https://doi.org/10.1098/rspb.2020.1841

Chamberlain, S., & Szöcs, E. (2013). taxize: Taxonomic search and retrieval in R. *F1000Research*, *2*, 191.

Connor, N., Barberán, A., & Clauset, A. (2017). Using null models to infer microbial co-occurrence networks. *PLoS One*, *12*(5), e0176751.

Dallas, T. (2016). helminthR: An R interface to the London Natural History Museum's host–parasite database. *Ecography*, *39*(4), 391–393.

Dallas, T. A., Aguirre, A. A., Budischak, S., Carlson, C., Ezenwa, V., Han, B., Huang, S., & Stephens, P. R. (2018). Gauging support for macroecological patterns in helminth parasites. *Global Ecology and Biogeography*, *27*(12), 1437–1447.

Dallas, T. A., & Becker, D. J. (2021). Taxonomic resolution affects host–parasite association model performance. *Parasitology*, *148*(5), 584–590.

Dallas, T., & Cornelius, E. (2015). Co-extinction in a host-parasite network: Identifying key hosts for network stability. *Scientific Reports*, *5*, 13185.

Dallas, T., Gehman, A.-L. M., Aguirre, A. A., Budischak, S. A., Drake, J. M., Farrell, M. J., Ghai, R., Huang, S., & Morales-Castilla, I. (2019). Contrasting latitudinal gradients of body size in helminth parasites and their hosts. *Global Ecology and Biogeography*, *28*(6), 804–813.

Dallas, T., Huang, S., Nunn, C., Park, A. W., & Drake, J. M. (2017). Estimating parasite host range. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1861), 20171250.

Dallas, T. A., & Jordano, P. (2021a). Spatial variation in species' roles in host–helminth networks. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1837), 20200361. https://doi.org/10.1098/rstb.2020.0361

Dallas, T. A., & Jordano, P. (2021b). Species–area and network–area relationships in host–helminth interactions. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1947), 20203143.

Dallas, T., Park, A. W., & Drake, J. M. (2017). Predictability of helminth parasite host range using information on geography, host traits and parasite community structure. *Parasitology*, *144*(2), 200–205. https://doi.org/10.1017/S0031182016001608

Dallas, T., & Poisot, T. (2018). Compositional turnover in host and parasite communities does not change network structure. *Ecography*, *41*(9), 1534–1542.

Dormann, C. F., Fründ, J., & Schaefer, H. M. (2017). Identifying causes of patterns in ecological networks: Opportunities and limitations. *Annual Review of Ecology, Evolution, and Systematics*, *48*, 559–584.

Ezenwa, V. O., Price, S. A., Altizer, S., Vitone, N. D., & Cook, K. C. (2006). Host traits and parasite species richness in even and odd-toed hoofed mammals, artiodactyla and perissodactyla. *Oikos*, *115*(3), 526–536.

Farrell, M. J., Stephens, P. R., Berrang-Ford, L., Gittleman, J. L., & Davies, T. J. (2015). The path to host extinction can lead to loss of generalist parasites. *Journal of Animal Ecology*, *84*(4), 978–984.

Forister, M. L., Novotny, V., Panorska, A. K., Baje, L., Basset, Y., Butterill, P. T., Cizek, L., Coley, P. D., Dem, F., Diniz, I. R., Drozd, P., Fox, M., Glassmire, A. E., Hazen, R., Hrcek, J., Jahner, J. P., Kaman, O., Kozubowski, T. J., Kursar, T. A., … Dyer, L. A. (2015). The global distribution of diet breadth in insect herbivores. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(2), 442–447.

Gibson, D., Bray, R., & Harris, E. (2005). *Host-parasite database of the Natural History Museum*. www.nhm.ac.uk/researchcuration/scientificresources/taxonomy-systematics/host-parasites/database/index.jsp

Gorter, F. A., Hall, A. R., Buckling, A., & Scanlan, P. D. (2015). Parasite host range and the evolution of host resistance. *Journal of Evolutionary Biology*, *28*(5), 1119–1130.

Gravel, D., Massol, F., Canard, E., Mouillot, D., & Mouquet, N. (2011). Trophic theory of island biogeography. *Ecology Letters*, *14*(10), 1010–1016.

Guégan, J.-F., & Kennedy, C. R. (1996). Parasite richness/sampling effort/host range: The fancy three-piece jigsaw puzzle. *Parasitology Today*, *12*(9), 367–369.

Harris, N. C., & Dunn, R. R. (2010). Using host associations to predict spatial patterns in the species richness of the parasites of North American carnivores. *Ecology Letters*, *13*(11), 1411–1418.

Hart, S. P., & Marshall, D. J. (2013). Environmental stress, facilitation, competition, and coexistence. *Ecology*, *94*(12), 2719–2731.

Hellgren, O., Pérez-Tris, J., & Bensch, S. (2009). A jack-of-all-trades and still a master of some: Prevalence and host range in avian malaria and related blood parasites. *Ecology*, *90*(10), 2840–2849.

Johnson, P. T., Rohr, J. R., Hoverman, J. T., Kellermanns, E., Bowerman, J., & Lunde, K. B. (2012). Living fast and dying of infection: Host life history drives interspecific variation in infection and disease risk. *Ecology Letters*, *15*(3), 235–242.

Jombart, T., & Dray, S. (2010). adephylo: Exploratory analyses for the phylogenetic comparative method. *Bioinformatics*, *26*, 1907–1909.

Kamiya, T., O'Dwyer, K., Nakagawa, S., & Poulin, R. (2014). What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biological Reviews*, *89*(1), 123–134.

Kennedy, C., & Guégan, J.-F. (1994). Regional versus local helminth parasite richness in British freshwater fish: Saturated or unsaturated parasite communities? *Parasitology*, *109*(2), 175–185. https://doi.org/10.1017/S0031182000076289

Krasnov, B. R., Mouillot, D., Shenbrot, G. I., Khokhlova, I. S., & Poulin, R. (2004). Geographical variation in host specificity of fleas (Siphonaptera) parasitic on small mammals: The influence of phylogeny and local environmental conditions. *Ecography*, *27*(6), 787–797.

Lindenfors, P., Nunn, C. L., Jones, K. E., Cunningham, A. A., Sechrest, W., & Gittleman, J. L. (2007). Parasite species richness in carnivores: Effects of host body mass, latitude, geographical range and population density. *Global Ecology and Biogeography*, *16*(4), 496–509.

Menge, B. A., Blanchette, C., Raimondi, P., Freidenburg, T., Gaines, S., Lubchenco, J., Lohse, D., Hudson, G., Foley, M., & Pamplin, J. (2004). Species interaction strength: Testing model predictions along an upwelling gradient. *Ecological Monographs*, *74*(4), 663–684.

Nunn, C. L., Altizer, S., Jones, K. E., & Sechrest, W. (2003). Comparative tests of parasite species richness in primates. *The American Naturalist*, *162*(5), 597–614.

Paterson, A. M., & Gray, R. D. (1997). Host-parasite co-speciation, host switching, and missing the boat. In D. H. Clayton (Ed.), *Host-parasite evolution: General principles and avian models* (pp. 236–250). Oxford University Press.

Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., Maglianesi, M. A., Melián, C. J., Pitteloud, C., Roslin, T., & Rohr, R. (2018). Comparing species interaction networks along environmental gradients. *Biological Reviews*, *93*(2), 785–800.

Penczykowski, R. M., Laine, A.-L., & Koskella, B. (2016). Understanding the ecology and evolution of host–parasite interactions across scales. *Evolutionary Applications*, *9*(1), 37–52.

Poisot, T., Baiser, B., Dunne, J. A., Kéfi, S., Massol, F., Mouquet, N., Romanuk, T. N., Stouffer, D. B., Wood, S. A., & Gravel, D. (2016). Mangal–making ecological network analysis simple. *Ecography*, *39*(4), 384–390.

Poisot, T., Bergeron, G., Cazelles, K., Dallas, T., Gravel, D., MacDonald, A., Mercier, B., Violet, C., Vissault, S., & Chapman, D. (2021). Global knowledge gaps in species interaction networks data. *Journal of Biogeography*, *48*(7), 1552–1563. https://doi.org/10.1111/jbi.14127

Poulin, R. (1995). Phylogeny, ecology, and the richness of parasite communities in vertebrates. *Ecological Monographs*, *65*(3), 283–302.

Poulin, R. (1997). Species richness of parasite assemblages: Evolution and patterns. *Annual Review of Ecology and Systematics*, *28*(1), 341–358.

Poulin, R., Krasnov, B. R., & Mouillot, D. (2011). Host specificity in phylogenetic and geographic space. *Trends in Parasitology*, *27*(8), 355–361.

Poulin, R., Krasnov, B. R., Pilosof, S., & Thieltges, D. W. (2013). Phylogeny determines the role of helminth parasites in intertidal food

webs. *Journal of Animal Ecology*, *82*(6), 1265–1275. https://doi.org/10.1111/1365-2656.12101

Poulin, R., & Morand, S. (2014). *Parasite biodiversity*. Smithsonian Institution.

Presley, S. J., Dallas, T., Klingbeil, B. T., & Willig, M. R. (2015). Phylogenetic signals in host–parasite associations for Neotropical bats and Nearctic desert rodents. *Biological Journal of the Linnean Society*, *116*(2), 312–327.

Pulgarín-R, P. C., Gómez, J. P., Robinson, S., Ricklefs, R. E., & Cadena, C. D. (2018). Host species, and not environment, predicts variation in blood parasite prevalence, distribution, and diversity along a humidity gradient in northern South America. *Ecology and Evolution*, *8*(8), 3800–3814.

Stephens, P. R., Altizer, S., Smith, K. F., Aguirre, A. A., Brown, J. H., Budischak, S. A., Byers, J. E., Dallas, T. A., Davies, T. J., Drake, J. M., & Ezenwa, V. O. (2016). The macroecology of infectious diseases: A new perspective on global-scale drivers of pathogen distributions and impacts. *Ecology Letters*, *19*(9), 1159–1171.

Strona, G. (2015). Past, present and future of host–parasite co-extinctions. *International Journal for Parasitology: Parasites and Wildlife*, *4*(3), 431–441.

Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental gradients. *Annual Review of Ecology: Evolution, and Systematics*, *48*(1), 25–48.

Vesk, P. A., McCarthy, M. A., & Moir, M. L. (2010). How many hosts? Modelling host breadth from field samples. *Methods in Ecology and Evolution*, *1*(3), 292–299.

Wells, K., & Clark, N. J. (2019). Host specificity in variable environments. *Trends in Parasitology*, *35*(6), 452–465.

BIOSKETCHES

Tad A. Dallas is an assistant professor at Louisiana State University examining questions in population and community ecology.

Pedro Jordano is a research professor at la Estación Biolñgica de Doñana.

This work was completed during a 3-month stay in Sevilla, during which time Tad was lucky enough to interact with amazing scientists and enjoy some Cruzcampo.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Dallas, T. A., & Jordano P. (2022). Parasite species richness and host range are not spatially conserved. *Global Ecology and Biogeography*, 31, 663–671. https://doi.org/10.1111/geb.13452