


RESEARCH PAPER

WILEY

Global Ecology
and BiogeographyA Journal of
Macroecology

Gauging support for macroecological patterns in helminth parasites

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Funding information

The Macroecology of Infectious Disease Research Coordination Network (funded by NSF/NIH/USDA DEB 1316223) supported this work.

Abstract

Aim: To explore spatial patterns of helminth parasite diversity, and to investigate three main macroecological patterns – (a) latitude–diversity relationships, (b) positive scaling between parasite and host diversity, and (c) species–area relationships – using a largely underutilized global database of helminth parasite occurrence records.

Location: Global.

Methods: We examined the London Natural History Museum's collection of helminth parasite occurrence records, consisting of over 18,000 unique host species and 27,000 unique helminth parasite species distributed across over 350 distinct terrestrial and aquatic localities.

Results: We find support for latitudinal gradients in parasite diversity and a strong relationship between host and parasite diversity at the global scale. Helminth species diversity–area relationships were not detectable as a function of host body mass, but larger geographic areas supported higher parasite richness, potentially mediated through higher host richness.

Main conclusions: Our findings indicate that helminth parasites may obey some of the macroecological relationships found in free-living species, suggesting that parasites may offer further support for the generality of these patterns, while offering interesting counterexamples for others. We conclude with a discussion of future directions and potential challenges in the newly emerging macroecology of infectious disease.

KEYWORDS

disease ecology, host body size, latitudinal gradient, macroecology, parasite biogeography, species diversity, species–area relationship

1 | INTRODUCTION

Helminth parasites are a global human health threat, but despite impacts comparable to Human Immunodeficiency Virus (HIV) and influenza in terms of morbidity and mortality (Lustigman et al., 2012; Mathers, Ezzati, & Lopez, 2007), helminthiasis remain among the

'great neglected tropical diseases' (Hotez et al., 2008). Helminths disproportionately affect human populations in developing countries (Crompton, 1999), representing a substantial medical, educational, and economic burden (Hotez et al., 2008). Efforts are currently underway to better understand the global distribution and burdens of helminth parasites in humans (Brooker, Hotez, & Bundy,

2010; Pullan & Brooker, 2012; Pullan, Smith, Jasrasaria, & Brooker, 2014), with the goal of guiding research and control efforts (Brooker et al., 2010). In contrast, few attempts have been made to elucidate the global distribution of helminths of wildlife (Chowdhury & Aguirre, 2001; see Figure 2). However, given the estimated richness of parasites (Dobson, Lafferty, Kuris, Hechinger, & Jetz, 2008) – and helminth parasites in particular (Larsen, Miller, Rhodes, & Wiens, 2017) – understanding the spatial distribution of parasite diversity represents an obtrusive knowledge gap in parasite ecology.

The search for general ecological rules related to the spatial distribution of diversity has promoted the development of macroecological theory (Brown, 1995; Gaston & Blackburn, 2008). This body of theory is traditionally applied to free-living species across space and time, aiming to identify general patterns that span systems (e.g. aquatic versus terrestrial). Many of these patterns focus on the distribution of species diversity. Three such examples are (a) latitudinal diversity gradients, (b) consumer–resource diversity scaling, and (c) species–area relationships. Latitudinal diversity gradients – the observation that species diversity is higher at lower absolute latitudes – have been observed in both terrestrial (Hillebrand, 2004) and marine (Tittensor et al., 2010) systems. Consumer–resource diversity scaling suggests that more diverse resource communities are associated with more diverse consumer communities (Jetz, Kreft, Ceballos, & Mutke, 2009), suggesting that more diverse host communities should support more species-rich parasite communities (Johnson et al., 2016; Wood & Johnson, 2016). Lastly, species–area relationships relate the area of a given habitat to species richness, based on the idea that larger areas are more diverse and capable of supporting a greater number of species (Evans, Warren, & Gaston, 2005).

Parasite ecology has only recently begun to address the extent to which macroecological patterns apply to parasites (Hechinger, 2015; Kamiya, O'dwyer, Nakagawa, & Poulin, 2014a; Krasnov, Shenbrot, Khokhlova, & Allan Degen, 2004; Poulin, 2007). These efforts have been facilitated by increased parasite occurrence data availability (Carlson et al., 2017; Gibson, Bray, & Harris, 2005), and the pressing need to understand how host–parasite interactions will change across a shifting environmental landscape (Lafferty, 2009). Recent parasite macroecology studies – for example, Morand and Krasnov (2010), Stephens et al. (2016) and Guernier, Hochberg, and Guégan (2004) – have also revealed that parasites can provide interesting and unique tests of macroecological theory. This is, in part, because the spatial distribution of parasites is controlled by two different filters. First, the external environment can influence the geographic distribution of parasites. In the case of helminths, abiotic factors such as temperature (Ford, Nollen, & Romano, 1998; Nollen, Samizadeh-Yazd, & Snyder, 1979; Shostak & Samuel, 1984), salinity (Ford et al., 1998; Howe & Nollen, 1992), humidity (Pandey, Chaer, & Dakkak, 1993) and pH (Howe & Nollen, 1992) can affect the survival of parasite stages that persist outside the host. Second, the occurrence of helminth parasites is determined by the presence and abundance of suitable host species. Thus, helminth parasites are subject to environmental and host availability constraints that have resulted in a variety of helminth behavioural, physiological and morphological adaptations (Hayunga, 1991) likely placing controls on helminth species distributions. Notably, a greater understanding of how these two filters interact to shape parasite occurrences can promote the development of predictive models of helminth parasitism (Dallas, Park, & Drake, 2016), and facilitate studies of how shifting host

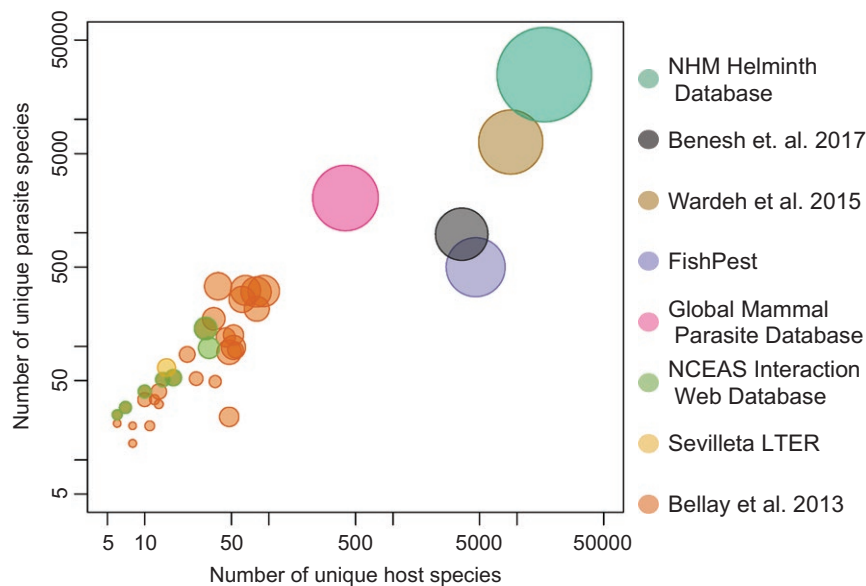


FIGURE 1 A comparison of data size of existing host–parasite databases demonstrates that the London Natural History Museum (LNHM) helminth occurrence database is the most species-rich and extensive collection of helminth parasite records – and, to our knowledge, all parasites – to date. Point size is proportionately to the log-transformed number of records in each database. Both the number of unique host species (x axis) and the number of unique parasite species (y axis) are on log-scale, allowing the visualization of smaller local or regional datasets that are commonly examined (e.g. National Center for Ecological Analysis and Synthesis (NCEAS) interaction web data)

distributions influence parasite distributions (Carlson et al., 2017). Moreover, examining parasites in this manner can address to what extent parasite macroecological patterns are simply emergent properties of host distributions as opposed to true relationships.

Here, we use an extensive database from the London Natural History Museum (Box 1) to provide some of the first tests of macroecological theory with helminth parasites at a global scale. First, we describe the global distribution of host and helminth parasite richness and address the role of variable sampling effort. Next, we gauge support for three central macroecological patterns: (a) latitudinal diversity gradients, (b) host and parasite richness relationships, and (c) parasite species–area relationships. For each of these relationships, we attempt to standardize parasite richness by the number of host species, with the aim of parsing out the influence of macroecological patterns in host species from those corresponding to helminth parasite diversity. We conclude with a discussion of the potential limitations and inherent challenges in testing macroecological theory with parasites.

Box 1: Helminth data from the London Natural History Museum

Parasitologists have accumulated large amounts of host–parasite association records for helminth parasites, which make the application of macroecological theory to parasites increasingly feasible. Along, with databases curating free-living species occurrence and biological trait data (e.g. <https://www.gbif.org/>, Jones et al., 2009), there are now unprecedented opportunities to address long-standing questions about the large-scale patterns of diversity and distribution of helminth parasites.

Several sources of animal host–parasite occurrence data have recently become freely available, including FishPEST (Strona & Lafferty, 2012) and the Global Mammal Parasite Database 2.0 (Stephens et al., 2017). Similar datasets also exist for humans (e.g. see <https://www.thiswormyworld.org/>), and compiled global occurrence datasets are rapidly becoming available (e.g. Carlson et al., 2017). In this study, we took advantage of an, as yet, underutilized source of host–helminth occurrence data curated by the London Natural History Museum (LNHM), and freely accessible to the public via a web-interface, a well-developed application programming interface, and an R package (helminthR; Dallas, 2016).

The LNHM parasite database is a collection of helminth occurrence data from published studies (Gibson et al., 2005), consisting of platyhelminths (trematodes and cestodes), acanthocephalans, and nematodes. The dataset contains over 18,000 unique host species and 27,000 unique helminth parasite species distributed across over 350 distinct terrestrial and aquatic localities. For comparison, the LNHM helminth database contains over 215,000 host–helminth occurrence records, which is over seven times the contents of the Global Mammal Parasite Database (Nunn & Altizer, 2005; Stephens et al., 2017; approximately 30,000 records) and more than double the US National Parasite Collection (Lichtenfels, Pilitt, & Hoberg 1992; approximately 90,000 digitized specimen records). In terms of both numbers of host and parasite species represented, the LNHM database is also the most species-rich, freely accessible, database currently being used by researchers to address large-scale questions about parasitism (Figure 1).

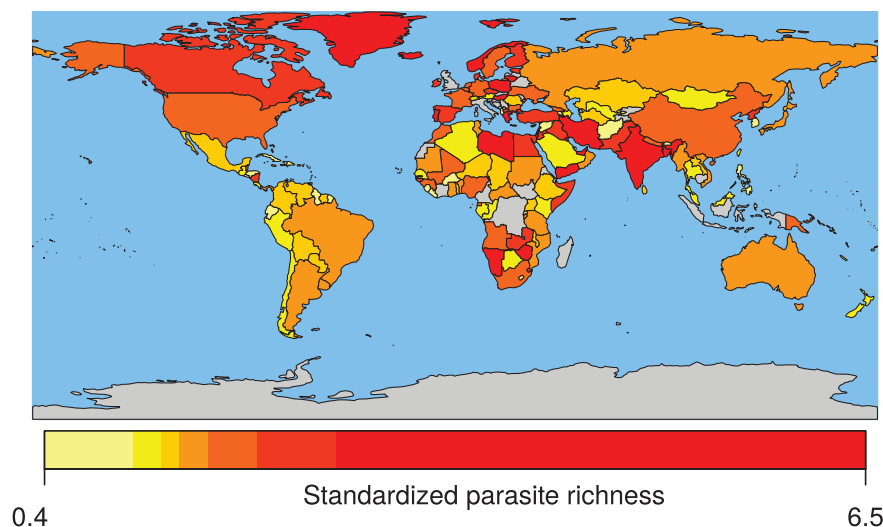


FIGURE 2 The global distribution of the standardized parasite richness (i.e. log-transformed mean number of parasite species per host species) according to the London Natural History Museum's extensive helminth parasite occurrence database

2 | HELMINTH MACROECOLOGICAL PATTERNS

2.1 | Spatial distribution of helminth parasite diversity

Global parasite richness estimates vary widely (Dobson et al., 2008; Larsen et al., 2017), and only recently have efforts been made to understand the spatial distribution of parasite richness on a global scale (Han, Kramer, & Drake, 2016; Stephens et al., 2016). The size of the LNHM data allows for the creation of global helminth parasite richness maps at the country level. Understanding species global distributions is a pressing need given land use change and an accelerating rate of species extinctions (Carlson et al., 2017; Cizauskas et al., 2017; Pimm et al., 2014). Further, understanding hotspots of parasite richness and diversity is a first step toward understanding spatial variation in transmission risk and parasite spillover (Poulin, Guilhaumon, Randhawa, Luque, & Mouillot, 2011; Poulin, Krasnov, Mouillot, & Thieltges, 2011).

Based on helminth occurrence records from the published literature contained in the LNHM helminth database, we find that helminth richness is heterogeneously distributed globally. As geographic localities with more host species would be expected to also have higher parasite richness (see Scaling between host and helminth parasite richness), we considered the global distribution of parasite richness standardized by host species richness (i.e. the mean number of parasite species per host species). Using this approach, we observed several helminth parasite richness hotspots for example, in western Europe, India, and southern Africa (Figure 2). However, variation in research effort among countries and publication biases favouring host-helminth occurrences published in journals written in English may result in incomplete estimates of total parasite diversity. To visualize this effect, we quantified sampling effort as the mean number of citations in support of each unique host and helminth species pair (Supporting Information Figure S1), and examined the relationship between sampling effort and standardized parasite species richness.

Sampling effort was unrelated to standardized parasite species richness at the country scale ($\rho = .078$, $p = .13$). Thus, while sampling biases undoubtedly exist in large-scale databases based on published literature and museum specimens, the lack of detected bias suggests that our standardized measure of helminth diversity managed to capture relative patterns of species richness fairly well. It is also possible that our measure of bias failed to capture the underlying sampling bias adequately, thus we examined the issue of spatial biases further in the Supporting Information.

In the rest of the paper, we focus on testing three macroecological patterns: (a) latitudinal diversity gradients, (b) scaling between host and parasite diversity, and (c) parasite species-area relationships.

2.1.1 | Latitudinal patterns of parasite richness

The latitudinal diversity gradient (LDG) is one of the most striking and pervasive biogeographic patterns, where diversity increases toward

the tropics for many free-living taxonomic groups (Hillebrand, 2004; Tittensor et al., 2010). A similar pattern has been predicted for parasites (Poulin & Leung, 2011); however, previous investigations have yielded mixed results for parasites infecting wild primates (Nunn, Altizer, Sechrest, & Cunningham, 2005) and humans (Guernier et al., 2004; Murray et al., 2015).

For helminth parasites contained within the LNHM database, we observed latitudinal diversity gradients, in which helminth species richness peaked around 30–40°N, with smaller secondary and tertiary peaks in the tropics (Figure 3a). The atypical temperate zone peak may reflect the existence of a sampling bias toward developed countries in the northern temperate regions. This is evident in the similar peak of number of countries and host species with records. Uneven sampling across regions has been a major obstacle to investigating parasite biogeographic patterns and potential drivers (Poulin, 2014; Poulin & Morand, 2000; Stephens et al., 2016). For example, the larger number of parasite species per host species near the Arctic region (primary peak in Figure 3c) than that in the tropics (secondary peak) is similar to previous findings of helminth species richness in freshwater fish (Poulin, 1997). However, until the effect of potential sampling bias toward charismatic Arctic animals like the polar bears and Arctic foxes can be removed, it is difficult to interpret this pattern as an implication of any biological mechanism (Poulin, 1997). As a simple way to account for sampling effort in our dataset, we divided the number of parasite species by the number of countries, as data on number of overall records was unavailable and the number of sampled countries is likely proportional to sampling processes. This correction revealed a pattern more similar to the classic LDG, showing a primary diversity peak between 20 and 0°N and a secondary peak between 0 and 20°S (Figure 3d). This pattern suggests that the LDG might indeed apply to parasitic helminths. Developing algorithms capable of accounting for sampling biases (e.g. Guernier et al., 2004) is crucial for further validation, but our analysis with simple sampling bias correction suggests that an LDG may potentially be a globally dominant pattern for helminth parasites, and thus invite further investigation of the underlying mechanisms.

The distribution pattern of species diversity is shaped by the spatial configuration of diversification and range dynamics (Jablonski et al., 2013; Mittelbach et al., 2007; Roy & Goldberg, 2007; Stevens, 1989). Because the distribution of parasite species is largely dependent on the distribution of their host species, it seems reasonable to expect parasites to have similar LDGs as their hosts (Poulin, 2014). However, many parasites can disperse across ranges of more than one host species (Cumming, 1999), while others might not persist throughout the entire ranges of their host species (Hopper et al., 2014; Phillips et al., 2010). Thus, the resulting mismatches between host and parasite range dynamics at large scales (reviewed in Hillebrand (2004)) suggest that correlations between parasite and host diversities found in some cases (e.g. Figure 3a and Murray et al., 2015) might be governed by fundamental ecological principles. For example, fundamental biogeographic properties, such as climatic conditions and regional history (Marzal et al., 2011; Murray et al., 2015), might be equally (or more) important

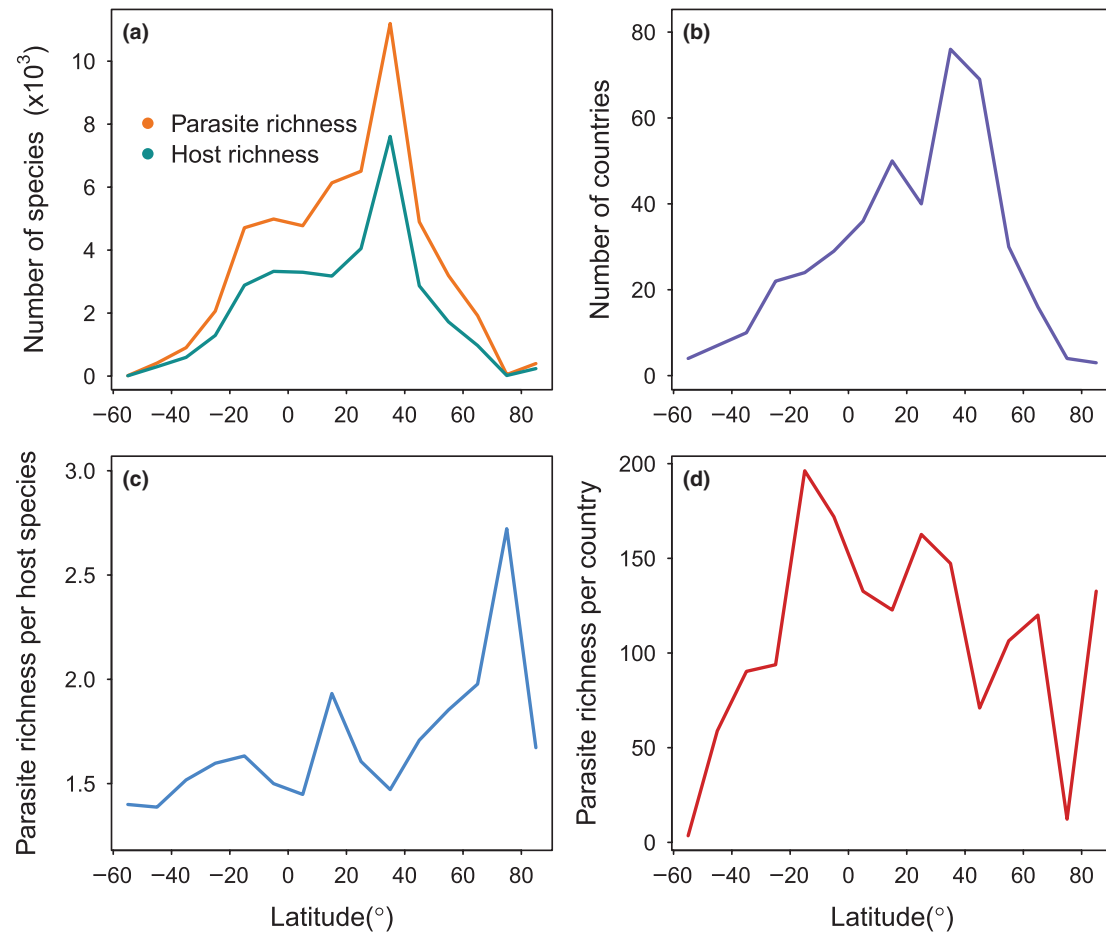


FIGURE 3 The latitudinal patterns of parasite diversity, relative to host diversity and the number of countries in each 10 latitudinal bin. Host and parasite diversity (a) and the number of countries included in each latitudinal bin (b) peaked around 40 latitude. However, when parasite diversity was standardized by the number of host species (c) or the number of countries (d) in each latitudinal bin, different patterns emerged, with parasite diversity per country suggestive of the classic latitudinal diversity relationship, but parasite diversity per host species tending to increase at higher latitudes, suggestive of low species richness of host and parasite species confounding the ability to detect any macroecological relationship

as host distribution in determining parasite distributions, and both biogeographic and host factors are considered key constraints operating on a parasite's niche. Similar to free-living organisms, how different parasites respond to the variation (and future change) in different niche constraints depends on the biological traits of the parasites, including dispersal (transmission) strategy and life history (Mazé-Guilmo, Blanchet, McCoy, & Loot, 2016; Poulin, Krasnov, et al., 2011). Understanding the relative role that parasite versus host and environmental traits play in shaping the distribution of parasites will shed light on the mechanisms giving rise to the patterns of diversity we describe here.

2.1.2 | Scaling between host and helminth parasite richness

The relationship between habitat heterogeneity and species diversity is a commonly observed macroecological pattern (Tews et al., 2004). Given that the host represents the habitat for helminth parasites, we

would expect host species richness to be positively associated with helminth species richness, mirroring the species diversity–habitat diversity association in many free-living systems (MacArthur, 1958). However, the slope of the relationship between host and parasite species richness may differ as a function of spatial area or spatial grain size (Wood & Johnson, 2016), mediated through incomplete sampling, or nonlinear relationships between increasing spatial area and habitat heterogeneity.

We detected a strong positive relationship between country-level host and parasite species richness ($\rho = .96$, $t = 63.259$, d.f. = 344, $p < .0001$; Figure 4). There was no detectable effect of country area on the slope of the relationship between host and parasite diversity (Figure 4). Further, this relationship was not strongly influenced by sampling effort, which we estimated as the total number of citations per country divided by the number of host species in that country (Figure 4). Our findings are qualitatively similar when using independent estimates of animal species diversity at the global scale, which we further explore in the Supporting Information. Similar host and

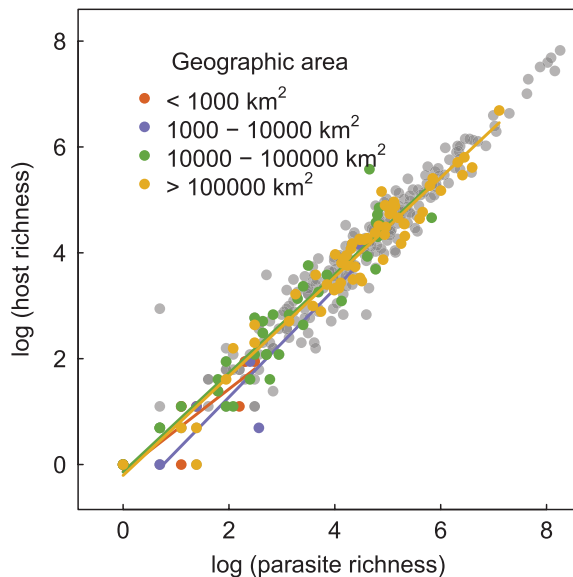


FIGURE 4 The number of host species was strongly related to the number of parasite species. Each georeferenced country is plotted as a point, and point colour corresponds to the land area of the given country. Points in grey represent localities for which data on geographic area were unavailable. Coloured lines are best fit linear models to each data subset

parasite diversity relationships have been observed in bird–trematode (Hechinger & Lafferty, 2005) and small mammal–flea systems (Krasnov et al., 2004). To our knowledge, this is the first examination of the relationship between host and parasite species richness at the global scale.

The observed relationship between host and helminth parasite species richness is consistent with recent studies linking ecosystem health and parasite richness (Hudson, Dobson, & Lafferty, 2006; Lafferty, 2008), where intact host diversity may sustain parasite diversity. Indeed, a recent meta-analysis has suggested that this is a general pattern across parasite taxa (Kamiya, Odwyer, Nakagawa, & Poulin, 2014b) despite inherent complications related to spatial processes (Krasnov et al., 2004; Wood & Johnson, 2016). The close relationship between host and parasite species richness – after controlling for the effects of country area – suggests that the loss of host diversity could result in the loss of parasite diversity. Given ongoing debate about the generality of links between host diversity and infectious disease risk (Huang, Langevelde, Estrada-Peña, Suzan, & Boer, 2016; Keesing, Holt, & Ostfeld, 2006), further research on the causal mechanisms underlying this relationship, as well as the identification of outliers (e.g. parasite diversity is higher than expected given host diversity), is warranted. Understanding how changes in host and parasite species diversity influence disease risk has clear public health implications: as such, understanding the mechanisms by which parasite diversity is constrained by existing host communities is a fundamental gap in our understanding of diversity.

2.1.3 | Parasite species–area relationships

Larger geographic areas are expected to sustain a higher number of species both due to random accumulation of species with finite ranges, and over broader scales the accumulation of different habitats (and associated species with specialized ecological niches). In conventional macroecology, the Arrhenius species–area relationship (SAR) is a canonical scaling pattern that suggests richness should usually scale (in log-log space) relative to area to the one-quarter power. However, that relationship has recently been shown to be scale-dependent and tends toward zero at continental scales (Harte, Smith, & Storch, 2009), which can be further affected in complex ways by fragmentation, geometry, and evolutionary history. Moreover, while species–area relationships are typically measured by a regression of the number of free-living species in an increasing geographic area, even this definition leaves substantial methodological flexibility. For example, the *island* SAR refers to comparing different non-overlapping areas like islands or countries, whereas the *nested* or *continental* SAR refers to the accumulation of species richness over increasing nested scales (Harte et al., 2009).

Whether or not parasites follow consistent species–area relationships, similar to those of free-living species, is presently a largely unaddressed question, with a handful of exceptions (Gregory, 1990; Guilhaumon, Krasnov, Poulin, Shenbrot, & Mouillot, 2012; Krasnov et al., 2004; Price & Clancy, 1983). Species–area relationships in parasites would occur if parasite species richness was related to geographic area, either through the relationship with host richness in combination with host SARs, or as a function of habitat heterogeneity promoting parasite diversity (Johnson et al., 2016). However, the concept of the species–area relationship is frequently ‘adapted’ for the parasitic life cycle, formulated as the scaling between parasite richness and host species geographic range, or parasite richness and host body size (both on a per-host basis). Any of these given relationships, rather confusingly, may be referred to as the species–area relationship. For clarity, we distinguish between these by referring to them as the island species–area relationship and the body size species–area relationship, respectively (discussed below).

The nested species area is a universal property of finite space (in that the term itself makes no description of the shape of the curve), but no canonical slope has been suggested for this parasite species–area relationship. What limited work has been done suggests a range of slopes comparable to those for free-living species (between 0.1 and 0.3; Price & Clancy, 1983)s. On the other hand, some argue that these same species–area relationships may often fail to emerge when formulated using host range size (Strona & Fattorini, 2014). More common is the observation that host body size, a proxy for ‘area’, scales with parasite species richness (the body size species area relationship, or BS-SAR; e.g. Guégan & Hugué, 1994). Based on island biogeography theory, host species may be considered patches of available habitat, and hosts with more habitable area (and a greater number of complex structures on which parasites can specialize, internally or externally) should harbour a greater number of parasite species. Previous studies have investigated these patterns

independently for helminth parasites across subsets of habitat types and host species.

Comparisons of host range versus parasite richness generally support the SAR pattern (Gregory, 1990; Price & Clancy, 1983), as do tests of the relationship between host body size and helminth species richness (Ezenwa, Price, Altizer, Vitone, & Cook, 2006; Kamiya et al., 2014a; Nunn, Altizer, Jones, & Sechrest, 2003). Perhaps the strongest evidence for a parasite SAR comes from a recent meta-analysis which suggests that host body size, geographic range size, and population density are typically positively related to parasite richness (Kamiya et al., 2014a). On the other hand, the studies examined in the meta-analysis were at substantially smaller spatial scales, and we based on fewer host-parasite association records relative to this work. Given the scale dependence of most biodiversity drivers, the patterns that generally hold true in studies at regional or taxonomically limited scales may fail to emerge at the continental or global scale. Thus, our analyses expand on previous work by exploring relationships between helminth parasite richness and (a) country area and (b) host adult body mass at a global scale. Whichever types of species–area relationships are observed could provide evidence that parasite diversity patterns are sufficiently strong to counter effects such as that of parasite specialization, inconsistencies in host and parasite range overlap, and other reasons discussed in further detail in Strona and Fattorini (2014) and in Krasnov et al. (2004).

First, we examined the island species–area relationship by relating host and parasite species richness to land area for each sampled country ($n = 121$). Both parasite and host diversity scale linearly on a log-log scale with country area (Figure 5), with essentially equivalent scales (parasites: $z = 0.449$, adjusted $R^2 = .366$; hosts: $z = 0.436$, adjusted $R^2 = .357$). The same qualitative pattern is produced for standardized richness, that is, species counts divided by citation counts (parasites: $z = 0.371$, adjusted $R^2 = .351$; hosts: $z = 0.358$, adjusted $R^2 = .303$). Based on this finding, we found little evidence to suggest parasite richness scales differently than host richness. In fact, when parasite richness is standardized by host richness, we failed to detect an effect of country area on standardized parasite richness ($z = 0.001$, adjusted $R^2 < .001$). This pattern could be explained by at least two macroecological null hypotheses: either parasite richness is simply an emergent property of host richness that scales with country area, or parasite and host diversity scale independently with area at the same rate. Given that host and parasite richness scale more strongly with each other than they do with geographic area (see Figure 4), the former appears more likely.

Second, we tested for a host body size–parasite species relationship, examining if the number of helminth parasite species infecting a host species depended on the body mass of the host species. Larger hosts are larger habitat patches for parasites (Kuris, Blaustein, & Alio, 1980); this larger habitat may lessen the effects of competition (Telfer et al., 2010), or enhance encounter rates between host and parasite species. Because host body mass estimates were obtained from Pantheria (Jones et al., 2009), this analysis was confined to mammals, which comprised a subset of

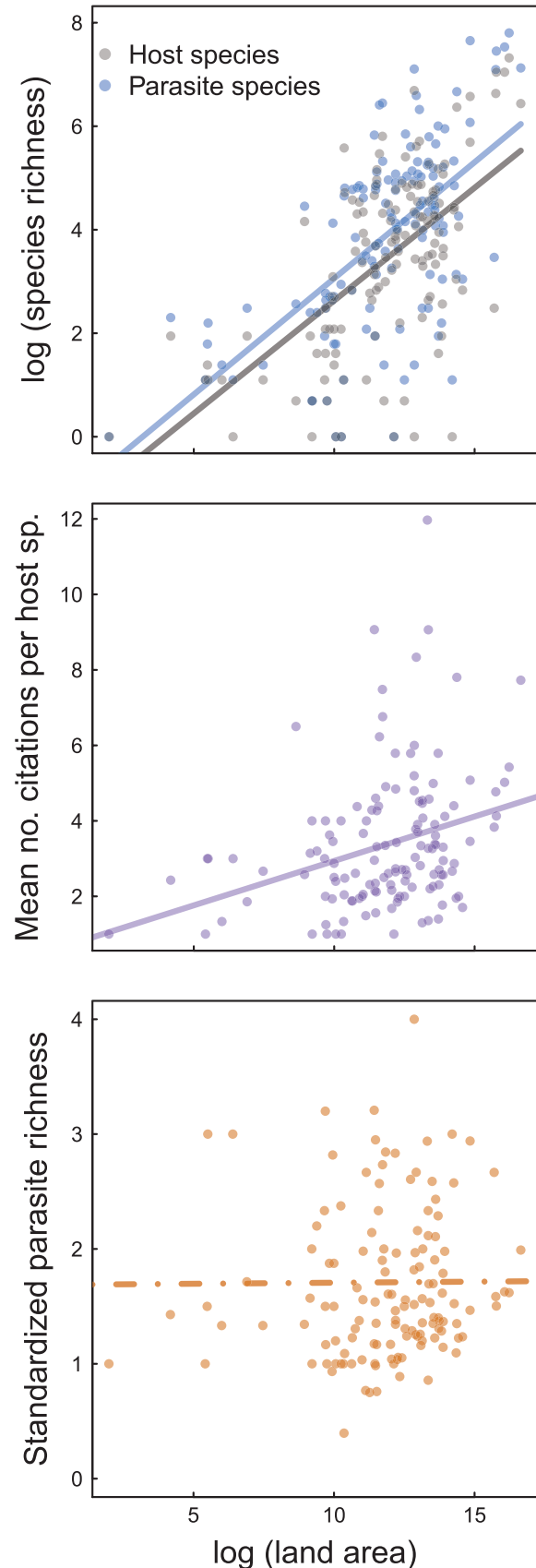


FIGURE 5 The geographic area of a country (km^2) was positively related to host and parasite diversity, but not to a standardized measure of parasite diversity. This suggests that geographic area–parasite richness relationships may arise as a consequence of positive geographic area–host richness relationships

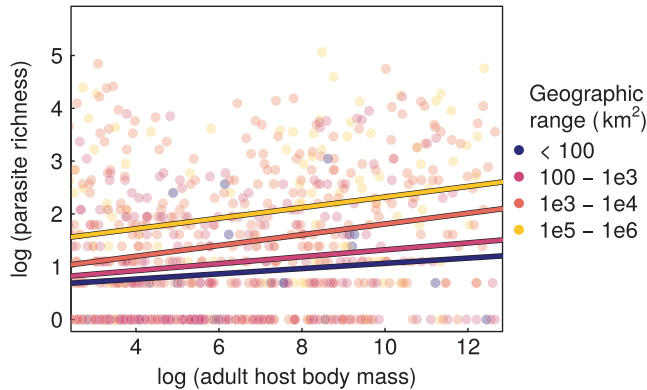


FIGURE 6 We failed to detect an effect of adult host body mass on parasite diversity, even when attempting to control for host geographic range size. Body mass is used here as a surrogate for habitat available for parasite colonization. We separated hosts based on geographic range size as geographic range and body size are often conflated. Parasites may compete for space on or within host species, and larger host species should hypothetically be able to harbour more parasites due to their size

1,105 host species in the LMNH dataset. We failed to detect a strong influence of host body mass on helminth parasite richness, even when controlling for host geographic range size (Figure 6). We examine the relationship more thoroughly in the Supporting Information, finding a weak positive relationship between host body mass and parasite species richness, but the fit model was only marginally better than an intercept-only model, and explanatory power was minimal (Supporting Information Tables S1 and S2). Previous meta-analyses have found strong evidence in the literature for the BS-SAR, even controlling for other confounding factors (Kamiya et al., 2014a). Host body size is still likely an important constraint or covariate of parasite diversity at ecosystem scales, or within host and parasite clades; but the weak global BS-SAR suggests that body size may not be a universal covariate of helminth diversification, compared to raw host diversity. We however caution that parasite specificity, the distribution of available host individuals of a given body size, and body size variation within individual host species may confound the search for a global parasite diversity host body size relationship, as may additional factors like group social behaviour or sexual selection.

3 | IMPLICATIONS OF HELMINTH MACROECOLOGICAL PATTERNS

We used the most extensive database on host–helminth interactions compiled to date to test three of the most common macroecological patterns observed in free-living species: (a) latitudinal diversity gradients, (b) scaling between host and parasite richness, and (c) species–area relationships. This three-pronged analysis allowed us to evaluate how two key constraints on parasite diversity and distributions – the environment and host biology – help shape the global distribution of helminth parasites. Overall, our results suggest

that helminth distributions are tightly linked to both environmental and host factors, and encourage future macroecological hypothesis testing on parasitic species. Specifically, we found support for the latitudinal diversity gradients for helminth parasites as well as strong positive scaling between host and parasite species richness across regional host–parasite assemblages. However, after standardizing parasite richness by observed host richness, we failed to detect significant species–area relationships in helminth parasites either as a function of region area or host body size, suggesting that some macroecological patterns observed for parasites may simply be emergent properties of the host community. Distinguishing between host-driven and parasite-driven macroecological patterns is an important consideration for future research.

By standardizing parasite diversity by host species richness in our species–area analyses, we address a fundamental aspect of testing macroecological theory with parasites; parasite diversity is constrained by the available host community. That is, parasite species richness may follow macroecological hypotheses simply because free-living host communities support macroecological hypotheses. This is especially clear when we considered the scaling between host and parasite species richness. While this represents a challenge, it also presents an opportunity to distinguish situations when parasites support macroecological hypotheses after controlling for the confounding effect of host species distributions. For instance, in our examination of latitude diversity gradients, we standardized parasite richness by the number of host species, providing evidence for an effect of latitude on parasite richness after considering the existing host community. Due to logistical constraints and a desire to utilize the full dataset, we included aquatic localities. However, data cleaning and curation efforts are underway to promote the use of these data to parse out the effects of inland water bodies on spatial diversity patterns. Studies on parasite macroecology should be sensitive to the potential effects that host distributions can have, and whether observed patterns are true support for macroecological hypotheses or simply artefacts of host diversity patterns.

Gauging support for macroecological hypotheses using these standardized measures of parasite species richness allows for comparison to patterns in free-living species. Similar work for microbial species has suggested that scaling patterns developed for macroscopic free-living species are supported for microbial species richness and evenness (Locey & Lennon, 2016), as well as for microbial diversity–abundance relationships (Shoemaker, Locey, & Lennon, 2017). Investigations of scaling relationships from macroecology may provide further evidence, or interesting counterexamples, of these established scaling relationships. Apart from the basic knowledge gained by using parasites to gauge support for macroecological phenomena, understanding the spatial distribution of parasites may allow forecasting of parasite distributional changes as a result of a shifting climate or shifting geographic distributions of host species (Carlson et al., 2017). This raises an important question: how will shifting species distributions influence the predictive power of current macroecological rules? Given that parasite species are dependent on free-living species diversity, will the resulting changes to

host species distributions enforce macroecological rules? Addressing these questions will facilitate further understanding of global parasite diversity patterns, helping to identify hotspots of parasite diversity (Han et al., 2016; Harris & Dunn, 2010), and potentially even promoting the conservation and management of parasitic species.

ACKNOWLEDGMENTS

We thank P. Peres-Neto, R. Poulin and an anonymous referee for constructive comments. The Macroecology of Infectious Disease Research Coordination Network (funded by NSF/NIH/USDA DEB 1316223) facilitated the discussions that led to this project and supported the work. SH thanks the Alexander von Humboldt Foundation for funding through a postdoctoral fellowship. CJC was supported by the National Socio-Environmental Synthesis Center (SESYNC) under funding received from the National Science Foundation DBI-1639145.

AUTHOR CONTRIBUTIONS

TAD, SH and CC contributed to data analysis and visualization. All authors contributed to the development of the ideas explored in the paper, manuscript writing and editing, and approved the final manuscript.

DATA ACCESSIBILITY

We thank the London Natural History Museum, and specifically D. A. Baylis, the original curator, and the current curation team (D. Gibson, R. Bray and E. Harris). All data are accessible at www.nhm.ac.uk/host-parasite-database or through R using *helminthR* (Dallas, 2016). Code to reproduce all analyses and figures is provided at <https://doi.org/10.6084/m9.figshare.6221987>.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Dallas TA, Aguirre AA, Budischak S, et al. Gauging support for macroecological patterns in helminth parasites. *Global Ecol Biogeogr*. 2018;00:1–11. <https://doi.org/10.1111/geb.12819>