

Review and synthesis

Latitudinal gradients of parasite richness: a review and new insights from helminths of cricetid rodents

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The latitudinal diversity gradient (LDG), or the trend of higher species richness at lower latitudes, has been well documented in multiple groups of free-living organisms. Investigations of the LDG in parasitic organisms are comparatively scarce. Here, I investigated latitudinal patterns of parasite diversity by reviewing published studies and by conducting a novel investigation of the LDG of helminths (parasitic nematodes, trematodes and cestodes) of cricetid rodents (Rodentia: Cricetidae). Using host–parasite records from 175 parasite communities and 60 host species, I tested for the presence and direction of a latitudinal pattern of helminth richness. Additionally, I examined four abiotic factors (mean annual temperature, annual precipitation, annual temperature range and annual precipitation range) and two biotic variables (host body mass and host diet) as potential correlates of parasite richness. The analyses were performed with and without phylogenetic comparative methods, as necessary. In this system, helminths followed the traditional LDG, with increasing species richness with decreasing latitude. Nematode richness appeared to drive this pattern, as cestodes and trematodes exhibited a reverse LDG and no latitudinal pattern, respectively. Overall helminth richness and nematode richness were higher in areas with higher mean annual temperatures, annual precipitation and annual precipitation ranges and lower annual temperature ranges, characteristics that often typify lower latitudes. Cestode richness was higher in areas of lower mean annual temperatures, annual precipitation and annual precipitation ranges and higher annual temperature ranges, while trematode richness showed no relationship with climate variables when phylogenetic comparative methods were used. Host diet was significantly correlated with cestode and trematode species richness, while host body mass was significantly correlated with nematode species richness. Results of this study support a complex association between parasite richness and latitude, and indicate that researchers should carefully consider other factors when trying to understand diversity gradients in parasitic organisms.

Keywords: latitudinal diversity gradient, biodiversity, E4 award, helminth, host–parasite system, rodents

Introduction

Since Dobzhansky's 1950 'Evolution in the Tropics', dozens of papers and literature reviews have explored the latitudinal diversity gradient (LDG; the pattern of higher species diversity at lower latitudes) and the factors believed to cause this phenomenon (Hutchinson 1959, Fischer 1960, Pianka 1966, Rohde 1992, 1998, 1999, Chown and Gaston 2000, Gaston 2000, Hillebrand and Azovsky 2001, Lyons and Willig 2002, Mittelbach et al. 2007, Brown 2014). Over 30 hypotheses have been proposed to explain the LDG (Table 1; see Pianka 1966, Rohde 1992, Willig et al. 2003, Fine 2015 for reviews of these hypotheses), although exceptions have been found for almost every hypothesis. It is unlikely that any one factor alone drives a pattern across all taxa (Gaston 2000, Willig et al. 2003); rather, multiple factors acting on different spatial and temporal scales influence and sustain the latitudinal patterns across taxa, generated by varying speciation, extinction and migration rates.

Factors that affect multiple taxa simultaneously, such as geographic area, ecological and evolutionary time, solar energy, productivity and climate stability, have received support as influential drivers of the LDG (Pianka 1966, Ricklefs 1973, Brown and Gibson 1983, Rohde 1992, Chown and Gaston 2000, Willig et al. 2003, Condamine et al. 2012, Fine 2015, Valentine and Jablonski 2015, Jablonski et al. 2017). For example, primary productivity, as often measured by actual evapotranspiration and potential evapotranspiration, has been proposed to explain the LDG as it is often significantly correlated with species richness (Willig et al. 2003, Gillman et al. 2015). Solar energy has been proposed to influence latitudinal gradients (Currie 1991, Rohde 1992) through the increase of environmental temperatures, which in turn increases metabolic activities of animals (which shortens generation times which increases speciation rates) and oxygenic photosynthesis (which increases productivity; Valentine and Jablonski 2015; see also temperature correlations with the evolutionary speed hypothesis, Table 1, Rohde

Table 1. Factors hypothesized to cause and/or maintain latitudinal diversity gradients, with original citations provided (when available). These factors are adapted from Pianka (1966), Rohde (1992) and Willig et al. (2003).

Factor/hypothesis	References
Environmental harshness*	Thiery 1982, Brown and Gibson 1983
Environmental stability°	Klopfer 1959, Klopfer and MacArthur 1961
Environmental predictability°	Slobodkin and Sanders 1969, Janzen 1970
Productivity°	Pianka 1966, MacArthur 1969
Abiotic rarefaction°	Dobzhansky 1950, Connell 1978
Physical heterogeneity°	Pianka 1966, Huston 1979
Latitudinal decrease in angle of the sun above the horizon°	Terborgh 1985
Geographic area°/Mid domain effect	Connor and McCoy 1979, Currie 1991
	Colwell and Hurtt 1994, Colwell and Lees 2000
Aridity°	Begon et al. 1986
Seasonality°	Begon et al. 1986
Number of habitats°	Pianka 1966
Evolutionary time	Pianka 1966, Pianka 1988
Ecological time	Fischer 1960, Pianka 1966
Habitat patchiness*	McCoy and Connor 1980
Temperature dependence of chemical reactions	Alekseev 1982
Energy	Hutchinson 1959, Currie 1991
Abiotic-biotic	Kaufman 1995, 1998
Competition*	Dobzhansky 1950, Pianka 1966
Biotic spatial heterogeneity*	Huston 1979, Thiollay 1990
Increased evolutionary speed in the tropics/Evolutionary rates	Rensch 1959, Stehli et al. 1969
	Brown and Gibson 1983, Brown 1988
Epidemics*	
Mutualism*	Brown and Gibson 1983
Population size*	Boucot 1975, Rohde 1978
Niche width*	Ben-Eliahu and Safriel 1982, Brown and Gibson 1983
Epiphyte load*	Strong 1977
Host diversity*	Rohde 1989
Predation*	Paine 1966, Pianka 1966
Population growth rate*	Huston 1979
Rapoport's rule°	Rapoport 1982, Pianka 1989
Energetic-equivalents	Allen et al. 2002
Scale hierarchy	Whittaker et al. 2001

*Based on available data, Rohde (1992) determined these factors to be circular, where the factors assume/require that higher diversity is already present in some taxa.
°Rohde (1992) determined these factors to be insufficiently supported by the available data.

1992, Willig et al. 2003, Fine 2015). Climatic stability promotes high diversity through decreased range sizes, increased specializations and decreased extinction rates (Fine 2015). The current tropical peak in diversity has not been consistent through time, further supporting the role of climate in driving diversity patterns: over the past few hundred million years, a tropical peak in diversity has been associated with cold climatic periods, while a temperate diversity peak or no latitudinal pattern is often seen during warmer periods (Mannion et al. 2014), with overall richness higher during warmer periods (Mayhew et al. 2012). The modern LDG is believed to have developed only within the past 4 million years during the Pliocene–Pleistocene epochs (Yasuhara et al. 2012a, Marcot et al. 2016).

The LDG is generally accepted as one of the dominant biodiversity patterns on the earth. Its presence has been corroborated across multiple taxa (Hillebrand 2004), including mammals (Kaufman 1995, Kaufman and Willig 1998, Buckley et al. 2010, Rolland et al. 2014, 2015), fish (Hobson 1994, Macpherson and Duarte 1994, Hanly et al. 2017), insects (Condamine et al. 2012, Fattorini and Baselga 2012, Heino et al. 2015), aquatic invertebrates (France 1992, Yasuhara et al. 2012a, b), bacteria (Pommier et al. 2007, Fuhrman et al. 2008, Andam et al. 2016) and plants (Dobzhansky 1950, Janzen 1970, Heino and Toivonen 2008, Xu et al. 2015), among others. However, there are exceptions to the LDG, generally demonstrated when investigating latitudinal diversity patterns at smaller geographic or lower taxonomic scales. Boreal forest plant communities (Marshall and Baltzer 2015), ectomycorrhizal fungi (Sánchez-Ramírez et al. 2015), Chilean mollusks (Kiel and Nielsen 2010), New World Lamprolaelini snakes (Pyron and Burbrink 2009), galling insects (Price et al. 1998), parasitoid wasps (Janzen 1981, Skillen et al. 2000), aquatic mosses (Heino and Toivonen 2008), pelagic seabirds (Chown et al. 1998), pinnipeds (Procheş 2001), lagomorphs (Rolland et al. 2014) and many parasitic taxa (Poulin 1995, Poulin and Leung 2011, Kamiya et al. 2014), among others, are not believed to follow the traditional LDG based on current evidence. These taxa either demonstrate a positive relationship with latitude, with species richness increasing towards the temperate or polar regions (a reverse LDG), no pattern at all, or a mixed gradient depending on specific taxa and taxonomic and geographic scale.

Parasites, in particular, are an interesting possible exception to the LDG. Parasitism is a life history strategy, not a taxonomic classification, so these possible exceptions to the classic LDG pattern span multiple phyla and encompass multiple life history traits and life cycle types. Parasites are dependent on their hosts, with host traits significantly influencing parasite diversity and abundance, and might be expected to follow a similar LDG pattern as their hosts (Poulin 2014). Despite this expectation, different parasitic taxa across multiple host taxa show varying LDG patterns (see below). In general, however, investigations of the LDG in parasitic organisms are lacking (Bordes et al. 2010)

compared to investigations in free-living organisms. With around 40% of known biodiversity estimates representing parasitic species and an estimated 75 000–300 000+ species of helminths (parasitic nematodes, trematodes, cestodes and acanthocephalans) alone (Dobson et al. 2008), the need to document the biodiversity of parasitic organisms is certainly no less than that of free-living species. However, much of the current diversity of parasitic organisms is unknown (Poulin and Morand 2000), limiting ecological and biogeographical investigations. Given the changes in projected distributional range and species abundance (Altizer et al. 2013), extinctions (Cizauskas et al. 2017), secondary extinctions and coextinctions (Colwell et al. 2012a) predicted with global climate and anthropogenic changes, the need to document parasite diversity is pressing and critical to increasing our knowledge of the biodiversity, biogeographical patterns and ecology of parasitic organisms before this biodiversity is lost. More parasite surveys of unsampled host species and localities as well as investigations of biogeographical and ecological patterns are needed to fill in these gaps in knowledge.

A review of past studies on the latitudinal diversity patterns of parasites

While exceptions to the LDG in free-living organisms are generally found at lower taxonomic scales or at smaller geographic scales, mixed latitudinal gradients of parasite diversity have been found across different scales. For example, Poulin and Leung (2011) and Kamiya et al. (2014) searched for global latitudinal patterns of parasite diversity across large, diverse groups of host and parasite taxa. Poulin and Leung (2011) compiled a dataset from 950 published surveys of helminth communities in 650 species of vertebrate hosts and found no consistent, significant relationship between latitude and species richness. Conducting a meta-analysis of 62 published studies, Kamiya et al. (2014) analyzed parasites of animals, plants and fungi and failed to find significant relationships between latitude and parasite species richness. After Kamiya et al. (2014) reduced the scale to include just animals and their metazoan parasites, they found a significant positive relationship with parasite species richness increasing with increasing latitude, contrary to the classic LDG pattern.

Poulin (1995), Rohde and Heap (1998), Choudhury and Dick (2000), Poulin (2001), Krasnov et al. (2004), Nunn et al. (2005), Lindenfors et al. (2007) and Guilhaumon et al. (2012) similarly used large-scale datasets, but each looked for latitudinal diversity patterns at lower host taxonomic scales. Examining latitudinal patterns of parasitic taxa at these lower host taxonomic scales may provide more insight into the true patterns of diversity and help elucidate drivers and mechanisms of the parasite LDG. The immediate habitat of a parasite is usually the body of its host; thus, parasites are likely influenced both by the internal environment of the host as well as the external environment, experienced through the body of the host and during free-living stages (if

present). Furthermore, parasites are often host specific (where one parasite species is only found on or within only one host species, genus, or family, although there are many exceptions) and parasite taxa infecting related hosts may be exposed to more similar abiotic and biotic conditions. By examining parasites at lower host taxonomic levels, it may be possible to reveal and better understand ecological and biogeographical patterns of species diversity.

Poulin (1995) used published parasite surveys on 203 bird, mammal and fish genera to investigate the LDG of both gastrointestinal parasites and ectoparasites within these three host groups and found no significant relationships between species richness and latitude in any of the host groups. Rohde and Heap (1998) found a negative relationship between latitude and ectoparasite richness in 108 species of teleost fish, following the classic LDG, but no significant relationship between latitude and gastrointestinal helminth species richness in 55 species of teleost fish. Choudhury and Dick (2000) and Poulin (2001), using the same dataset of the helminth fauna of 165 tropical and Nearctic freshwater fish species, both found a positive relationship between helminth species richness and latitude, in contrast to the classic LDG. Krasnov et al. (2004) found a positive relationship between latitude and flea species richness in rodents. In non-human primates, Nunn et al. (2005) found no significant relationship between parasite species richness and latitude when all parasite types were combined, and only protozoan species richness was significantly and negatively correlated with latitude when analyzed separately. Parasites of carnivores were found to follow an inverse LDG, with a positive relationship between parasite species richness and latitude (Lindenfors et al. 2007). Further, when parasite species were broken down into groups of helminths, protozoa, bacteria and viruses, only helminth species richness was positively and significantly correlated with latitude (Lindenfors et al. 2007). Guilhaumon et al. (2012) found no relationship between latitude and flea species richness of mammals from six continents. On smaller geographic scales, tick species richness is higher closer to the equator across eastern Africa (Cumming 2000). Merino et al. (2008) failed to find a significant relationship between latitude and richness of three genera of haematozoa (blood parasites) in 26 species of forest birds in Chile. Using small mammals from Brazil, Linardi and Krasnov (2013) found that flea species richness was not significantly related to latitude and mite species richness was significantly and positively correlated with latitude, with mite richness increasing with distance from the equator.

Schemske et al. (2009) and Poulin (2014) suggested that investigations of the LDG of parasites within a single, widely-distributed host species may provide stronger tests of latitudinal patterns than studies combining host taxa, given that the taxonomic composition of host and parasite communities change between temperate and tropical areas and might therefore be incomparable (Poulin 2014). However, few studies have explored the LDG within a host species, and even fewer have used a globally-distributed species, as

recommended by Poulin (2014). The few studies that have been performed at these taxonomic levels have found different trends. Calvete et al. (2003) found an inverse relationship between species diversity and latitude in their investigation of helminth communities of a partridge species in Spain, with higher diversity at lower latitudes (although the study area covered approximately six degrees in latitude). In another geographically restricted study, Blaylock et al. (1998) found a significant and positive relationship between parasite species richness and latitude in one species of halibut at high latitudes (approximately 40–60 degrees north) along the western coasts of Canada and Alaska, with richness increasing with latitude. Thieltges et al. (2009) and Torchin et al. (2015) each sampled two snail host species for parasitic trematodes. Torchin et al. (2015) examined trematodes along the east and west coasts of the southern United States to Panama and found that species richness increased with increasing latitude. Thieltges et al. (2009) found trematode species richness was not significantly correlated with latitude in European seas. Illera et al. (2015) failed to find a significant relationship between latitude and richness of three genera of haematozoa and coccidians in spectacled warblers in Macaronesia. I am aware of a single LDG study using a global dataset of parasites from a single host species: in humans, Guernier et al. (2004) found that viruses, helminths, protozoans and arthropods followed the classic LDG, with species richness increasing with decreasing latitude, while bacteria and fungi exhibited no significant relationship.

Conflicting latitudinal patterns of diversity are seen across host and parasite taxa and geography suggesting that, for parasitic organisms at least, broad generalizations of latitudinal patterns of diversity may not be possible even when investigated within a single host species. However, with the narrow latitudinal ranges covered by many of these studies, including a general lack of richness data from both tropical and polar latitudes, and with the various taxonomic scales under study, the mixed latitudinal gradients of many of these host–parasite systems should be interpreted and extrapolated with caution. As the LDG is a global biogeographic phenomenon in many free-living organisms, and proposed drivers such as climate likely operate on a global scale, investigations at large geographic scales should continue (Schemske et al. 2009, Bordes et al. 2010), particularly at lower host taxonomic levels (e.g. within a species; Schemske et al. 2009, Poulin 2014). Unfortunately, these types of investigations are limited by a lack of available parasitological data, with many widely-distributed and speciose host groups lacking records of their parasite fauna across their distributions.

Rodents, in particular, are an understudied host group. Distributed worldwide, rodents are often involved in zoonotic disease cycles and are expected to become the most prevalent mammals in environments with increasing anthropogenic changes (Bordes et al. 2015), yet investigations of the biogeographical patterns of much of their parasite fauna are lacking (but see Krasnov et al. 2004, Linardi and Krasnov 2013). While rodent surveys have been incorporated in

previous large-scale investigations of the LDG of parasites (Poulin 1995 and Poulin and Leung 2011), these investigations were often biased towards charismatic megafauna when using surveys of mammals, a problem plaguing LDG studies of free-living organisms as well (Kaufman 1995). One dataset in particular included more parasite studies on Carnivora than Rodentia (Poulin and Leung 2011); considering rodents comprise 39.3% of all mammal species (2552 species out of 6495 species) and carnivores only 4.7% (305 species; Burgin et al. 2018), this skewed representation may cause latitudinal patterns in rodent parasites to be overlooked. Further investigations of latitudinal patterns of rodent parasite fauna are warranted, and would add to the knowledge of the prevalence of the LDG within different host–parasite systems.

The search for new insights into the parasite LDG

Material and methods

To further explore latitudinal patterns in parasite diversity, I conducted a novel investigation to elucidate the presence and direction of a latitudinal gradient in the species richness of parasitic helminths of rodents, using a global dataset at the taxonomic scale of host family. The second largest family in the order Rodentia, Cricetidae, was chosen as the host taxon of interest as it has a wide geographic range (Fig. 1), a large number of species (792 species according to the most recent literature; Burgin et al. 2018), and represents one of the lowest taxonomic groups suitable for investigations of the LDG of helminths using available data. In addition to investigating general latitudinal patterns of helminths (to align with

many previous LDG studies), I also explored this pattern at a lower parasite taxonomic level, separately analyzing latitudinal gradients of parasitic nematode (phylum Nematoda), cestode (phylum Platyhelminthes, class Cestoda), and trematode (phylum Platyhelminthes, class Trematoda) richness. I also examined the relationships of various abiotic and biotic factors (chosen based on previous studies investigating correlates of parasite diversity) with patterns of helminth richness: annual precipitation, mean annual temperature, annual precipitation range, annual temperature range, longitude, host body size and host diet.

Climate factors can influence parasite development and transmission (Altizer et al. 2006), abundance (Froeschke et al. 2010), and richness (Guernier et al. 2004). Few of the previous LDG studies investigated the potential of climatic factors to influence their observed latitudinal patterns (but see Rohde and Heap 1998, Calvete et al. 2003, Guernier et al. 2004, Linardi and Krasnov 2013). Given that climatic factors have been implicated in shaping global diversity patterns of free-living organisms, exploring their influence in parasitic taxa may provide insights into the mechanisms shaping the observed biogeographic patterns; climate factors may shape the distribution of parasite diversity even if those taxa do not follow the traditional LDG. For the biotic factors, larger host body sizes may support higher parasite diversity by providing more habitable niches within the host (Morand and Poulin 1998). Host diet was included to test the hypothesis that diet type affects parasite diversity, likely through exposure to infective stages. Using previously published parasitological surveys of cricetid rodents, generalized linear models and phylogenetic comparative methods were used to analyze helminth richness data with latitude and with the abiotic and biotic factors listed above to investigate latitudinal patterns and correlates of helminth diversity in cricetid rodents.

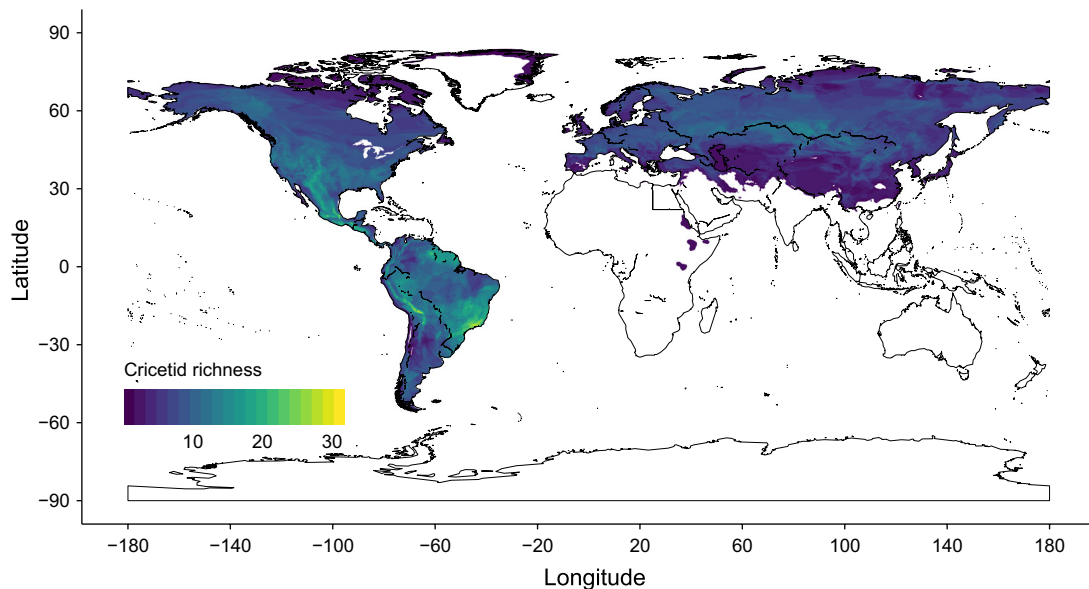


Figure 1. A heat map of cricetid species richness around the world. Data from digital distribution maps on the IUCN Red List of threatened species (IUCN 2016).

Literature search

A thorough literature search was conducted to find surveys of parasitic helminths infecting wild rodents in the family Cricetidae. Surveys were collected from the Web of Science database using generic names, species names and synonyms of each cricetid species, according to the International Union for Conservation of Nature (IUCN) Red List and Burgin et al. (2018), as primary search terms, with 'parasit*', 'helminth*', 'nematod*', 'trematod*', and 'cestod*' used within primary searches to narrow search results. Recently extinct cricetid species were included in the literature search. The search was conducted in November 2017, and no publishing date limits were specified. Only surveys with sample sizes of at least four rodents per species and reporting helminth infections (nematodes, trematodes and cestodes) were collected; as data on acanthocephalans were rare, they were not used in these analyses. Surveys examining the whole host body and alimentary tract surveys were included. Surveys reporting only ectoparasites, microparasites, blood parasites, or extra-intestinal parasites were excluded, as were those using non-invasive methods for surveying parasites (such as fecal egg counts), searching for a particular type of parasite, or without collection localities or sample sizes.

Data collection

From each survey, host species, sample size, latitude and longitude of the sampling locality, nematode species richness (NSR), cestode species richness (CSR), trematode species richness (TSR), and total helminth species richness (HSR; the total number of nematode, cestode and trematode species) were recorded. If multiple sites were sampled within one survey for a species, the latitude and longitude of the approximate center of the collection sites were used, as HSR was not always specified for each specific site. If the latitude and longitude of sites were not provided in the text, they were estimated using the approximate center of the described collection locality as visualized on Google maps. The absolute value of the latitude was used in the models as distance from the equator is the measure of interest when investigating the LDG. Unlike many previous studies of the LDG, this study used specific latitudes and longitudes of the collection localities to correlate with HSR, rather than using species richness within latitudinal bands or regions.

Climate data were downloaded from WorldClim at the lowest spatial resolution, 30 seconds or approximately one square kilometer (Hijmans et al. 2005). As the WorldClim data are in the WGS84 geographic coordinate system, the latitude and longitude of the collection localities were translated onto this system. Annual precipitation (AP), mean annual temperature (MAT) and annual temperature range (ATR) for each latitude and longitude point were extracted from the WorldClim data. Annual precipitation range (APR) was not directly provided and was instead calculated by subtracting the precipitation of the driest month from the precipitation

of the wettest month. Climate data were unavailable for two collection localities (one in Canada and one in Japan); the nearest points with associated climate data were used instead. Temperature data were converted from Celsius to Fahrenheit to remove negative data for transformation. For each of the host species, biotic data on host mass (g) were obtained from the PanTHERIA database (Jones et al. 2009) and additional sources described in the Metadata of Dataset D175 (Supplementary material Appendix 4). Host diet data, presented as proportions of different food types (invertebrates, birds and mammals, reptiles and amphibians, fish, unknown vertebrates, scavenge, fruit, nectar, seeds and other plant material), were obtained from Wilman et al. (2014). These proportions were used to create a variable informative of the animal (invertebrates, vertebrates and scavenge) and plant (fruit, nectar, seeds and other plant material) compositions of the diet. This variable had potential scores of zero to one, with the score representing the percent of the plant composition of the diet; scores closer to zero represent a more carnivorous/insectivorous diet, while scores closer to one represent a more herbivorous diet.

Data analysis

All analyses were performed in R ver. 3.3.3 (R Core Team). All continuous data were tested for normality using the Shapiro–Wilk test (Shapiro and Wilk 1965). If data were not normally distributed, they were transformed and visualized with a histogram to confirm normality. Because multiple studies have determined that sampling effort is often significantly correlated with parasite species richness (Gregory 1990, Poulin 1995, 1997, Walther et al. 1995), sampling effort was controlled by regressing the HSR on the number of hosts examined for each survey, with both variables log transformed before the regression. The residuals were used in place of HSR values as the dependent variable in all analyses using HSR. NSR, CSR and TSR values were similarly controlled for sample size (but were transformed as $\log[x + 1]$), and were used as the dependent variables in their respective analyses. Distance from the equator (latitude), longitude, AP, MAT, APR, ATR, host body mass and host diet were used as candidate explanatory variables. In all analyses, variables were transformed as appropriate (see R code in Supplementary material Appendix 2 for specific transformations).

The data were checked for spatial autocorrelation and pseudoreplication, as multiple surveys were used per host species. An analysis of variance was run to determine if HSR significantly differed between the different dissection areas when survey authors collected helminths (alimentary tract, alimentary tract and some other organs, whole body, or not specified; Supplementary material Appendix 1 Table A1). Methodologies and results for these analyses are included in the Supplementary material Appendix 1. As I detected no spatial autocorrelation in the residuals of any latitudinal models, no evidence of pseudoreplication and no differences

in HSR among dissection types, no corrections were made to the data or further analyses.

Parasite communities are characteristics of the host; closely related hosts might be expected to have more similar parasite communities (Poulin 2009, 2014) and host–parasite records may not be independent data points (Gittleman and Kot 1990, Revell et al. 2008). Pagel's λ (Pagel 1999) was used to determine if there was a phylogenetic signal in the HSR, NSR, CSR and TSR data. Methodologies and detailed results for these analyses are included in the Supplementary material Appendix 1. HSR and NSR had no significant phylogenetic signal in the data and were analyzed using only generalized linear models (GLMs); although a phylogenetic signal was detected in the CSR and TSR data (Supplementary material Appendix 1 Table A3), non-phylogenetic GLMs were also run for these data. First, latitudinal GLMs were run using the residuals of HSR, NSR, CSR and TSR as the dependent variables and distance from the equator (latitude) as the independent variable. Separate GLMs with HSR, NSR, CSR and TSR as the dependent variables and all abiotic and biotic variables (except latitude), including interactions between the abiotic variables, were also employed. Since significant phylogenetic signals were detected in the CSR and TSR data, phylogenetic generalized least squares (PGLS) were run using the residuals of CSR and TSR as the dependent variables with distance from the equator (latitudinal models cestodes and trematodes) and the abiotic and biotic variables (model cestodes and trematodes, Table 4) using a single survey for each host species, as detailed in the Supplementary material Appendix 1. For all analyses, the function 'vif' from the package 'car' (Fox and Weisberg 2011) was used to test for collinearity between the abiotic variables. Principal component analyses

(PCA) were run with all collinear variables to correct for collinearity, using the package 'vegan' (Oksanen et al. 2017), in each model. The first few axes that explained at least 95% of the variation were used in place of the collinear variables in the GLMs and PGLSs. The best fit models were found using the 'dredge' and 'model.sel' functions in the package 'MuMIn' (Bartoń 2018) using the lowest AICc value, and only the first returned model was explored in this study; these functions try all possible combinations of variables and return the models in ascending order based on their AICc value. As this is exploratory work, with no previous studies investigating latitudinal gradients of diversity using large geographic- and taxonomic-scale datasets of rodents and their helminths, using model selection functions that try all possible combinations of variables is appropriate. R^2 values for each final model were calculated as $1 - (\text{residual deviance}/\text{null deviance})$.

Data deposition

Data available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.js4s24f>> (Preisser 2019).

Results

Literature search and data collection

A total of 114 published surveys were collected, representing 175 unique helminth communities of 60 cricetid species (Fig. 2 for a map of the collection localities of the surveys). Surveys were published between 1931 and 2017. Twenty-eight surveys reported helminth records for more than one host species, and up to 26 surveys were reported for each

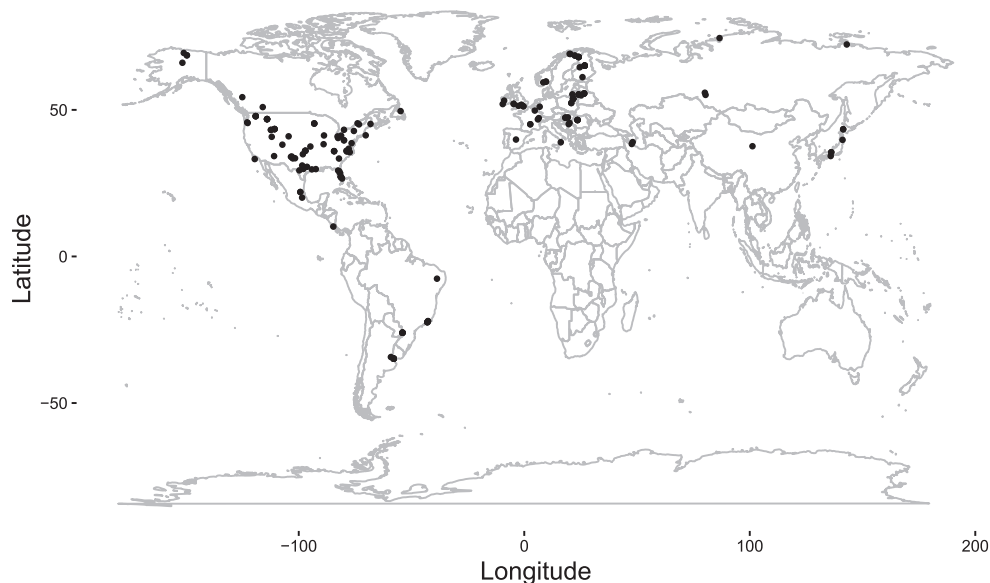


Figure 2. A map of the locations of the 175 parasite communities from 60 host species collected from published literature sources and used in this study. Each dot represents a survey locality.

Table 2. PCA axes used in the various analyses to control for collinearity. Collinear variables included longitude, annual precipitation (AP), annual precipitation range (APR), mean annual temperature (MAT) and annual temperature range (ATR). Model identification is in the top row of the table, with the cumulative proportion of the variation explained in each axis in the last row of the table. Only the first four axes were used for each analysis, as they explained over 95% of the variation in each case.

	PC1	PC2	PC3	PC4	PC5
Model 175					
Longitude	0.01417643	−0.90223387	0.1559472	−0.1070179	−0.3872993
AP	0.52170207	−0.09716489	0.2168989	0.8121559	0.1083681
APR	0.49435553	0.05672121	0.634634	−0.5182486	0.2846988
MAT	0.51638609	0.31448359	−0.2037456	−0.1386038	−0.7574445
ATR	−0.46538586	0.27279259	0.6959618	0.2028728	−0.4283457
Cum. Prop.	0.5594	0.7938	0.9009	0.96159	1
Model nematodes, NP¹ models cestodes and trematodes					
Longitude	0.01677898	−0.90392844	0.155968	−0.1073422	−0.3831233
AP	0.52128638	−0.09524686	0.217239	0.8125644	0.1083278
APR	0.49379684	0.05898477	0.6347672	−0.5176948	0.2859163
MAT	0.51687621	0.31228212	−0.2035222	−0.1395347	−0.75791
ATR	−0.46581397	0.26989272	0.6957949	0.201839	−0.4304716
Cum. Prop.	0.5603	0.794	0.9011	0.96189	1
Model cestodes					
Longitude	−0.1781991	−0.939002	0.0395933	−0.23622218	0.1707389
AP	−0.5026932	−0.08156017	−0.1849284	0.81652101	0.199355
APR	−0.4837937	0.10015089	−0.7211084	−0.37613376	−0.3073102
MAT	−0.4838994	0.31852739	0.2740768	−0.36844316	0.6734339
ATR	0.4973225	−0.0115448	−0.6075512	0.01629608	0.6189936
Cum. Prop.	0.6706	0.8698	0.93304	0.97193	1
Model trematodes					
Longitude	−0.1859695	−0.92805509	0.07636985	−0.24192746	−0.1994188
AP	−0.5008358	−0.11345923	−0.27236926	0.80867418	−0.09028593
APR	−0.4856667	0.11585052	−0.67555413	−0.48490093	0.24331909
MAT	−0.4810512	0.33437691	0.30871973	−0.22677105	−0.71417704
ATR	0.4972891	−0.02472847	−0.60687838	0.03103452	−0.61873061
Cum. Prop.	0.6678	0.8688	0.93253	0.97067	1

¹Non-phylogenetic.

host species. There were no surveys reporting a HSR of zero for any species with a sample size larger than four rodents. Dataset D175 contained 175 records of 60 species of cricetid rodents and had data on sample size, HSR, NSR, CSR, TSR, latitude, longitude, AP, MAT, APR, ATR, host body mass and host diet. See Supplementary material Appendix 1 Table A1, A2 for the number and type of surveys and the HSR, NSR, CSR and TSR for each host species. Dataset D175 is available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.js4s24f> (Preisser 2019) and the Supplementary material Appendix 4; the R code and the references for the dataset are provided in the Supplementary material Appendix 2, 3, respectively.

Data analysis

All PCA results are listed in Table 2 and model results are reported in Table 3, 4 and Supplementary material Appendix 1 Table A4. Both HSR and NSR were significantly and negatively correlated with distance from the equator (Table 3, Fig. 3). In both the non-phylogenetic and phylogenetic analyses, CSR was significantly and positively correlated with latitude, while TSR was not significantly correlated with latitude (Table 4 and Supplementary material Appendix 1

Table A4; Fig. 3). As abiotic variables were collinear in all analyses (using the standard cutoff of $vif > 4$; Supplementary material Appendix 1 Fig. A1, A2), PCA axes were used to replace collinear abiotic variables. The first four PC axes of all PCAs captured at least 95% of the variation in the data and were included in the models (Table 2). Only PC loadings over 0.3 and significant results of the model are discussed.

In model 175, helminth richness was significantly and positively correlated with PC axis 1. In model nematodes, nematode richness was significantly and positively correlated with PC axis 1 and negatively correlated with host body mass. The climatic variables had similarly-sized loadings on both PC axes 1, which explained ~56% of the variation and were positively related to AP, APR and MAT, and negatively related to ATR (Table 2). When analyzing cestode richness, both the non-phylogenetic (Supplementary material Appendix 1 Table A4) and the phylogenetic analyses (Table 4) returned the same relationships between variables. Cestode richness was significantly and positively correlated with host diet. CSR was positively correlated with PC axis 1 (negatively related to AP, APR and MAT and positively to ATR and explained ~67% of the variation in the data) in the phylogenetic model and negatively correlated with PC axis 1 (positively related to AP, APR and MAT and negatively to ATR and explained

Table 3. Results of the final non-phylogenetic GLMs with helminth and nematode richness (refer to Table 2 for loadings and cumulative proportion of the PC axes). Final models were chosen based on lowest AICc scores using model selection functions in R. Significance codes: '*' ≤ 0.05 , '**' ≤ 0.01 , '***' ≤ 0.001 . R^2 values were calculated as $(1 - \text{residual deviance}/\text{null deviance})$. Bolded rows represent significant variables in the models.

Final model	Predictor	Coefficient \pm SE	t value	p value	Effect	R^2
Latitudinal model 175	Intercept	0.206076 \pm 0.062452	3.30	0.001175**	+	0.06405
	Latitude	-0.004648 \pm 0.001351	-3.44	0.000728***	-	
Latitudinal model nematodes	Intercept	0.370126 \pm 0.062463	5.926	1.66e-08***	+	0.1815
	Latitude	-0.008332 \pm 0.001349	-6.177	4.58e-09***	-	
Model 175	Intercept	1.252e-17 \pm 0.01764	0	1	+	0.0729
	PC1	0.0333 \pm 0.01058	3.151	0.00192**	+	
Model nematodes	PC3	0.04579 \pm 0.02418	1.894	0.05992	+	0.2844
	Intercept	0.246016 \pm 0.056488	4.355	2.29e-05***	+	
	PC1	0.069047 \pm 0.009943	6.944	7.72e-11***	+	
	PC3	0.037609 \pm 0.023059	1.631	0.105	+	
	Mass	-0.138787 \pm 0.030463	-4.556	9.92e-06***	-	

~56% of the variation in the data) in the non-phylogenetic model. CSR was also negatively correlated with PC axis 3 (negatively related to APR and ATR and explained ~6% of the variation in the data) in the phylogenetic model and positively correlated with PC axis 3 (positively related to AP and ATR and explained ~11% of the variation in the data) in the non-phylogenetic model. The phylogenetic (Table 4) and non-phylogenetic (Supplementary material Appendix 1 Table A4) analyses of trematode richness returned different results. In the phylogenetic model, TSR was significantly and negatively related to diet; in the non-phylogenetic model, TSR was significantly and positively related to body mass and PC axis 4, which was positively related to AP and negatively related to APR.

Discussion

This study is the first to support an LDG in parasitic helminths of non-human animals using a geographically large-scale dataset, with helminth richness increasing closer to the equator (Fig. 3). Out of the 19 investigations of latitudinal patterns of parasite diversity reviewed above, only five found

a significant negative relationship between richness and latitude, or the classic LDG. Three of these five studies found this pattern in ectoparasites or microparasites (Rohde and Heap 1998, Cumming 2000, Nunn et al. 2005). The other two studies (Calvete et al. 2003, Guernier et al. 2004) corroborated the classic LDG in helminths; however, Calvete et al. (2003) sampled a narrow latitudinal range (encompassing approximately six degrees in latitude) and Guernier et al. (2004) sampled parasites and pathogens of humans, with disease patterns potentially confounded by variables such as socioeconomic status, sanitation practices and availability of medical care (Poulin 2014). There is an overall lack of support for the LDG in parasitic helminths; Poulin (2014) asserts that parasite species richness should track host species richness, which as previously discussed largely increases with decreasing latitude (with some exceptions). However, the majority of LDG studies, including this one, use parasite richness per host species to investigate patterns, rather than parasite richness per unit area (but see Guilhaumon et al. 2012), as is commonly used in LDG studies of free-living organisms (Poulin 2014). Future studies of latitudinal patterns of parasite richness should consider parasite richness per area in addition to per host species, which may reveal patterns

Table 4. Results of the final PGLS models with cestode and trematode richness (refer to Table 2 for loadings and cumulative proportion of the PC axes). Final models were chosen based on lowest AICc scores using model selection functions in R. Significance codes: '*' ≤ 0.05 , '**' ≤ 0.01 , '***' ≤ 0.001 . R^2 values were provided in the model summary. λ is an estimate of the phylogenetic signal in the analysis and ranges from 0 (no phylogenetic signal in data) to 1 (Brownian motion). Bolded rows represent significant variables in the models.

Final model	Predictor	Coefficient \pm SE	t value	p value	Effect	λ	R^2
Latitudinal model cestodes	Intercept	-0.393238 \pm 0.139333	-2.8223	0.006521**	-	0.136	0.146
	Latitude	0.066150 \pm 0.021004	3.1493	0.002586**	+		
Latitudinal model trematodes	Intercept	0.354912 \pm 0.188824	1.8796	0.06519	+	0.000	0.05928
	Latitude	-0.056694 \pm 0.029656	-1.9117	0.06086	-		
Model cestodes	Intercept	-0.166352 \pm 0.082093	-2.0264	0.04750*	-	0.017	0.353
	Diet	0.144306 \pm 0.066700	2.1635	0.03478*	+		
	PC1	0.034923 \pm 0.014176	2.4635	0.01686*	+		
	PC3	-0.085707 \pm 0.038307	-2.2374	0.02926*	-		
Model trematodes	Intercept	0.261533 \pm 0.105051	2.4896	0.01573*	+	0.000	0.1399
	Diet	-0.222978 \pm 0.084960	-2.6245	0.01112*	-		
	PC4	0.115472 \pm 0.076786	1.5038	0.13815	+		

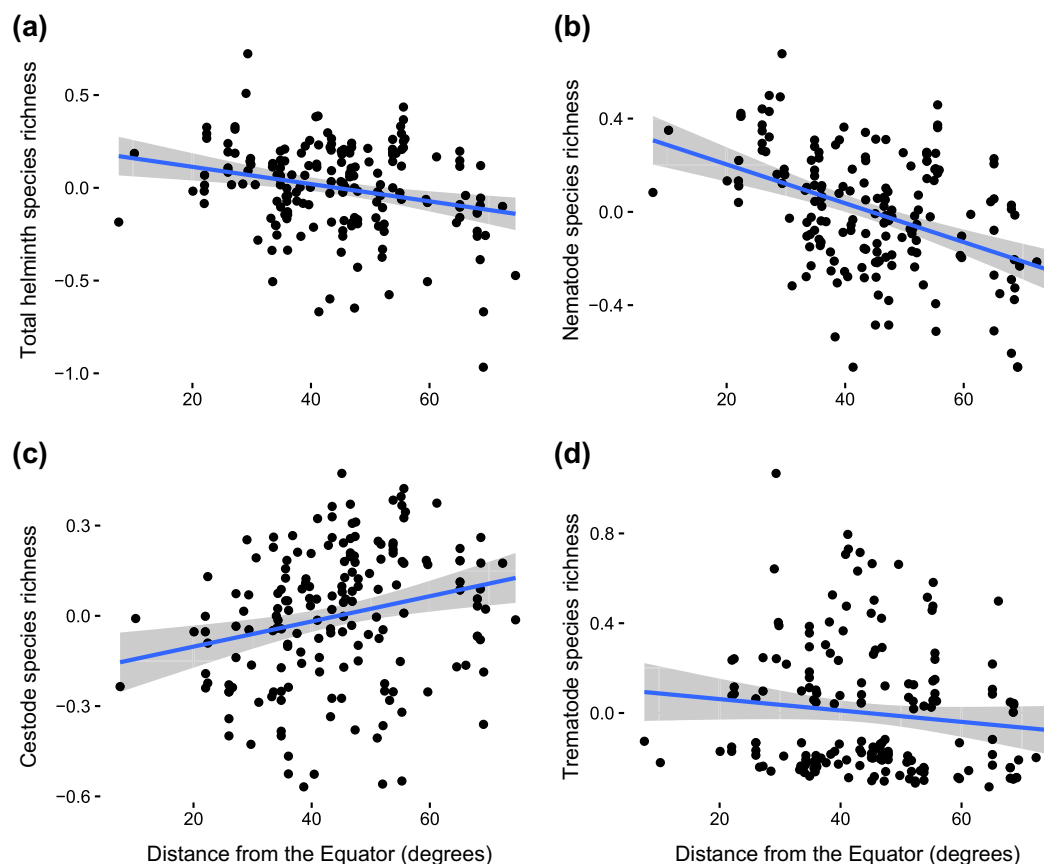


Figure 3. The relationship between (a) HSR, (b) NSR, (c) CSR and (d) TSR, controlled for sampling effort, and distance from the equator from the latitudinal models (Table 3, 4). HSR, NSR, CSR and TSR were controlled for sampling effort by regressing the number of species collected from each survey on the number of hosts examined, with all variables log transformed before the regression. The residuals were used as the dependent variable. HSR: $y = 0.206076 - 0.004648x$, 95% CI -0.007314348 to -0.001981333 , $R^2 = 0.06405$. NSR: $y = 0.370126 - 0.008332x$, 95% CI -0.01099484 to -0.005669577 , $R^2 = 0.1815$. CSR: $y = -0.186005 + 0.004187x$, 95% CI $0.001660668 - 0.006713963$, $R^2 = 0.0586$. TSR: $y = 0.112654 - 0.002536x$, 95% CI -0.005827097 to 0.0007550201 , $R^2 = 0.0133$.

similar to those of free-living organisms. Host species richness of the area should also be included in future analyses to determine the extent to which parasite richness tracks host richness (although until more host species and geographical areas are sampled for parasite richness, the true relationship may be difficult to accurately assess).

This study revealed a complex association between latitude and species richness. While latitude was significantly and negatively correlated with overall helminth richness in this host-study system, investigations into the relationships between latitude and nematode, cestode and trematode species richness revealed mixed gradients: only NSR was negatively correlated with latitude, while the relationships between latitude and CSR and TSR were significantly positive and not significant, respectively. Given these results, it appears that NSR is driving the LDG demonstrated when all helminth groups are combined. Differences in how these helminths respond and have adapted to environmental conditions may underlie the conflicting latitudinal diversity patterns among taxa. The significant correlations between PC axes with information on climatic variables and species richness suggest that

climate factors influence patterns of helminth, nematode and cestode richness, in consensus with multiple LDG hypotheses (Table 1) and previous research supporting the role of climatic factors in influencing richness in free-living organisms (Hawkins et al. 2003, Wang et al. 2009, Tittensor et al. 2010, Mayhew et al. 2012, Fergnani and Ruggiero 2017) and parasitic taxa (Guernier et al. 2004, Dunn et al. 2010, Froeschke et al. 2010, Vhora and Bolek 2015). Nematode richness appears to also drive the relationship between total helminth richness and climatic factors, with both total helminth and nematode species richness suggested to be higher in areas of higher mean annual temperature, annual precipitation and annual precipitation ranges and lower annual temperature ranges – climatic conditions that often typify environments closer to the equator (Supplementary material Appendix 1 Fig. A1). Cestode richness has the opposite relationship with climate variables, with potentially higher richness in areas of lower mean annual temperature, annual precipitation and annual precipitation ranges and higher annual temperature ranges, characteristics of higher latitudes. Lastly, accounting for host phylogeny reveals no relationship

between trematode richness and climate (although the non-phylogenetic model suggests TSR may be higher in areas with higher annual precipitation and lower precipitation ranges). The mechanisms by which these helminths are influenced by climate are less clear: climatic conditions can influence the helminth during environmental stages (e.g. when eggs are deposited in the environment for transmission or during free-living larval or adult stages) and can independently affect the host species, which in turn can influence host exposure and susceptibility to infection by helminths. Disentangling these influences is the topic of previous and ongoing research (Møller et al. 2013, Goedknecht et al. 2015, Mignatti et al. 2016, Gehman et al. 2018).

Parasite diversity is also influenced by host-associated factors (Poulin 2014), such as host range size (Nunn et al. 2005, Lindenfors et al. 2007), population density (Morand and Poulin 1998, Lindenfors et al. 2007) or size (Nunn et al. 2005), diet (Morand et al. 2000, Vitone et al. 2004) and body mass (Poulin 1995, Morand and Poulin 1998, Sasal and Morand 1998, Nunn et al. 2003, 2005, Vitone et al. 2004, Lindenfors et al. 2007). Both host-associated variables explored here, host body mass and diet, were significantly correlated with species richness in different helminth groups. Body mass was negatively correlated with nematode richness suggesting that nematode richness is higher in smaller host species. While a positive relationship between parasite species richness and body size has been hypothesized (Morand and Poulin 1998), data on this relationship while controlling for host phylogeny have been contradictory (for a lack of a relationship, see Poulin 1995, Morand and Poulin 1998, Nunn et al. 2003; see Sasal and Morand 1998 and Lindenfors et al. 2007 for significant positive relationships), although positive relationships are often seen in non-phylogenetic models (Poulin 1995, Morand and Poulin 1998, Nunn et al. 2003; present study for TSR). Bergmann's rule posits that body size is positively correlated with latitude in endotherms (Bergmann 1847), with smaller hosts at lower latitudes; given that nematode richness is higher at lower latitudes, the relationship may be a consequence of the latitudinal gradient, with other factors, such as climate, more important in shaping richness patterns than the availability of niches within a host. While this study and previous LDG studies using published helminth surveys use helminth richness of host populations and average body mass of each host species, future investigations should examine the relationship between helminth richness and body mass of individual hosts to investigate this relationship in more detail.

Host diet was positively correlated with cestode richness and negatively correlated with trematode richness, suggesting cestode richness is higher in more-herbivorous rodents while trematode richness is higher in more-carnivorous/insectivorous rodents. In past studies, higher parasite diversity was found with omnivorous diets (Morand et al. 2000) and folivorous diets (Vitone et al. 2004). Rodents often acquire cestode infections through the ingestion of eggs in

the environment or invertebrate intermediate hosts (where parasite intermediate life stages grow, but do not mature or reproduce), with these routes often differing among cestode species; the eggs may be ingested with herbivorous feeding and may represent the transmission route of the majority of the cestode species infecting these hosts. Due to the lack of cestode species identifications in the surveys and incomplete knowledge of all life cycles, the effect of transmission route cannot be tested with this dataset. Rodents often acquire trematode infections through the ingestion of a snail intermediate host, leading to a potentially higher trematode richness in rodent species that ingest more snails (i.e. with a more carnivorous/insectivorous diet). Future investigations should further explore influences of diet on cestode richness, and also determine whether diet impacts parasite composition, in addition to richness, as different diets may expose hosts to different parasites.

Life cycle differences may mediate climatic and biotic effects. Nematodes have both direct (one host for development and reproduction) and indirect (more than one host required for development and reproduction) life cycles, and the majority (if not all; some life cycles are unknown) of the nematode species reported in these surveys use rodents as their definitive hosts, in which they reach maturity and reproduce. Cestodes have primarily indirect life cycles and use rodents as both intermediate and definitive hosts; for example, some *Taenia* species encyst in rodent livers and use these rodents as intermediate hosts to reach their definitive hosts (usually carnivorous birds or mammals that consume rodents) while some *Hymenolepis* species use rodents as their definitive hosts (having infected the rodent when it ate an intermediate host, such as an insect) and often occupy the small intestine. The surveyed trematode species also have an indirect life cycle and use rodents as definitive hosts. While the type of life cycle and the use of these rodents as either intermediate or definitive hosts were factors not included in these analyses (but see Lindenfors et al. 2007), there are likely taxon-specific factors that drive the different patterns seen, and exploring life cycle differences might further our understanding of these factors.

Like some previous studies (Ezenwa et al. 2006, Lindenfors et al. 2007), this study found no phylogenetic signal in overall helminth or nematode species richness, suggesting that while some parasites are co-evolving with or alongside their hosts (Hafner and Nadler 1988, Dybdahl and Lively 1998, Hoberg and Brooks 2008), for nematodes, the number of species infecting a host species in a region is likely influenced by environmental and/or biotic factors more than parasite–host evolutionary history. A phylogenetic signal was found in both cestode and trematode species richness data, suggesting that more closely related host species have more similar cestode and trematode richness values. While the non-phylogenetic and phylogenetic analyses returned identical correlations between cestode richness and the abiotic and biotic variables, the non-phylogenetic and phylogenetic models of trematode richness returned different results. As

host evolutionary history can play a major role in parasite patterns, it is essential to test for the presence of a phylogenetic signal in species richness data before analysis to determine if correcting for host phylogeny through the use of phylogenetic comparative methods is necessary. Doing so will facilitate a better understanding of abiotic and biotic factors affecting parasite diversity.

Pseudoreplication was a concern for the dataset as it included multiple surveys per host species. However, as parasite species richness and composition vary within a host species across its range (Poulin 2003), including multiple surveys for a single host species across its range is still informative for investigations of biogeographical patterns of parasite diversity. Additionally, ad hoc modeling of the dataset with species included as a variable demonstrated a lack of a significant difference in HSR among species with one, few, or a large number of surveys, suggesting that it was acceptable to include all collected surveys in the models. Spatial autocorrelation was not a concern in this study, as the residuals of the models were not spatially autocorrelated. Another potential issue in this study is that reported HSR may be lower than the true HSR of the hosts. Some surveys reported only intestinal helminths, while others reported all helminths found in the host (Supplementary material Appendix 1 Table A1). While combining studies that surveyed only the alimentary tract with those that surveyed the whole host body is not ideal, excluding alimentary tract surveys would have further limited this investigation. As many studies did not include the location within the host where parasites were found, using only helminths known to have been collected in the alimentary tract from whole body surveys was not possible. I ran an analysis of variance to determine if dissection type (alimentary tract, alimentary tract with a few other organs, whole body, or not specified) affected HSR; there were no significant differences in the mean HSR among dissection types and whole body and intestinal helminth data were combined for the analyses performed here. Finally, using the residuals of a linear regression of helminth richness on host sample size to control for sampling effort assumes a linear relationship between the two variables. This assumption, however, is incorrect; the relationship is instead asymptotic, with helminth richness initially increasing with new hosts sampled until additional sampling reveals no new species, and the curve plateaus ('species accumulation curve' see Gotelli and Colwell 2011). Controlling for sample effort would involve the use of rarefaction or extrapolation methods to standardize the number of hosts sampled and estimate helminth richness at that host sampling level (see Colwell et al. 2012b for specific methodologies). Unfortunately, most parasite surveys summarize the parasite fauna for groups of hosts, often by host species or collection locality, which does not provide enough data to perform these rarefaction and extrapolation methods. These methods require knowledge of the parasite fauna of specific host individuals, data that are rarely available in published surveys and are often inaccessible for the older literature. Future parasite surveys should include data

at the level of host individual, rather than just at the level of host species or locality, to allow for these rarefaction and extrapolation methods to be performed, to better control for uneven sampling.

The family Cricetidae is found across the northern hemisphere and into the southern hemisphere (Fig. 1) and contains 792 species (Burgin et al. 2018); only 60 species (~8% of all cricetids) had published surveys reporting the helminth fauna in their whole body or alimentary tracts. While most of the cricetid species are distributed in North and South America (81% of the extant species), 43% of the 175 records found in the literature sampled rodents in Europe and Asia, disproportionate to the number of cricetid species found on these two continents (19% of extant species). The latitudinal range of this family in Europe and Asia is small, with the surveys taken from 34 to 75 degrees N. The other 57% of the records represented hosts in North and South America, with a range of distances from the equator of 7 to 70 degrees but only two records within 20 degrees of the equator, where rodent diversity is high (Fig. 1). Additional sampling both nearer to the equator and of additional species, as well as analyzing western and eastern hemispheres separately, may change the relationships between HSR and latitude, and may reveal relationships closer to the true pattern.

With parasitism as one of the most common life history strategies (Dobson et al. 2008), the paucity of available helminth surveys and knowledge of the parasitic helminth fauna from the second most speciose family of mammals demonstrates an alarming gap in our knowledge. Analyses using subsets of data representing much larger, but unavailable, biodiversity data (like the current limited knowledge of parasite species infecting vertebrate hosts) may return patterns weaker, absent, or even opposite of true biodiversity patterns (Klibansky et al. 2017). However, even with these biases and limitations, studies analyzing biodiversity patterns using poorly sampled fauna still represent the best available information, and efforts to increase both the knowledge of the biodiversity of these fauna and the number of studies of biodiversity patterns must be initiated.

While this investigation mimicked the approach of past investigations of latitudinal patterns of parasite diversity, using previously published data on helminth communities of the host taxa of interest (Choudhury and Dick 2000, Poulin 2001, Nunn et al. 2005, Lindenfors et al. 2007), this study is one of the few to find a negative relationship between parasite species richness and latitude, and only the third to find this pattern in parasitic helminths. Using an appropriate scale of study is important in searches for macroecological patterns, and the use of a lower taxonomic host group (within a family) and a worldwide dataset likely allowed for meaningful relationships between species richness and climatic and biotic variables to emerge. Given the low explanatory power of these models, future studies should include additional data as they become available and explore other potential correlates of parasite diversity at a global scale and within additional host–parasite systems.

Conclusion

While the latitudinal diversity gradient has been well-studied in free-living organisms, studies of latitudinal patterns of diversity in parasitic organisms are comparatively lacking. Previous investigations have explored diversity patterns and found mixed latitudinal gradients of parasite richness among different host taxa and across varying geographic scales. Investigations of parasites from lower host taxonomic groups (ideally species) that are widely distributed may represent the best study systems for identifying true latitudinal patterns; however, these investigations are limited by the lack of knowledge of parasite diversity. Here, I explored latitudinal patterns of the helminth richness of cricetid rodents to add to the current knowledge of the LDG in parasitic taxa. Helminths, as a whole, and nematodes followed the classic LDG pattern of higher species richness closer to the equator, while cestodes followed a reverse LDG and trematodes showed no significant correlation with latitude. Both climatic and biotic variables were found to be significant correlates of species richness, although additional variables should be used in future studies as these variables explained little of the variation in the data. With only a small proportion of cricetid rodents having been sampled for helminths, extensive sampling of rodents and their helminths should be conducted and included in analyses like these before strong conclusions can be made.

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Supplementary material (available online as Appendix ecog-04254 at <www.ecography.org/appendix/ecog-04254>). Appendix 1–4.