LATITUDINAL DIVERSITY GRADIENTS: HOSTS AND CLIMATE SHAPE PARASITE DIVERSITY PATTERNS

A Dissertation

by

WHITNEY CLAIRE PREISSER

Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

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August 2019

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

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 novel investigations of the LDG of parasitic helminths (nematodes, trematodes and cestodes) of cricetid rodents (Rodentia: Cricetidae). Using published host-parasite records from 175 parasite communities and field-collected data from 294 rodent hosts, I tested for the presence and direction of a latitudinal pattern of total helminth richness, as well as latitudinal patterns of nematode, cestode, and trematode richness. Additionally, I explored climate- and host-associated variables as potential correlates of parasite richness. The analyses were performed with and without phylogenetic comparative methods, as necessary. Across both studies and all levels of community organization, all helminths and nematodes followed the traditional LDG of increasing species richness with decreasing latitude, while trematodes showed no relationship with latitude. Cestodes exhibited both a reverse LDG and no latitudinal pattern, depending on the study. Across both studies, helminth 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. Host diet was significantly correlated with cestode and trematode species richness, while host body mass was significantly correlated with helminth, nematode, and cestode species

richness. Helminth β-diversity was high between and within most communities and was primarily driven by species turnover. Geographic distance, climate, and host β-diversity may predict patterns of helminth turnover in this system. Changes in helminth community composition and rates of turnover may contribute to the detected latitudinal patterns. Results of this study support a complex association between parasite richness and latitude, and indicate that researchers should carefully consider a variety of factors when trying to understand diversity gradients in parasitic organisms.

ACKNOWLEDGEMENTS

I would like to thank my committee chair, Dr. Light, and my committee members, Dr. Dronen, Dr. Hamer, and Dr. Lawing, for their guidance and support throughout the course of this research. I also thank my friends, colleagues, and the department faculty and staff for making my time at Texas A&M University a great experience. Finally, thanks to my family and friends outside of TAMU for their love and encouragement.

CONTRIBUTORS AND FUNDING SOURCES

Contributors

This work was supervised by a dissertation committee consisting of Dr. Jessica Light and Dr. Norman Dronen of the Department of Wildlife and Fisheries Sciences, Dr. Sarah Hamer of the Department of Veterinary Integrative Biosciences, and Dr. Michelle Lawing of the Department of Ecosystem Science and Management.

The data for Chapters 3 and 4 were collected with the assistance of undergraduate field assistants Katelyn Lasater, Ashley Sloan, Bonner Watson, and Gabby Green; Dr. Eugenio Gonzalez and staff at the Soltis Center; Dr. Jesús A. Fernández; Dr. Gil Rosenthal and the staff at CICHAZ; Texas Ecolab program and property owners; Dr. Jillian Detwiler and her lab; and the staff at the Churchill Northern Studies Centre. The data for Chapters 2 and 3 were analyzed with the assistance of Dr. Michelle Lawing, Adrian Castellanos, and Dr. Friedrich Keppeler. All other work conducted for the dissertation was completed by the student independently.

Funding Sources

Graduate study was supported by the Excellence, Willie May Harris, and Tom Slick Graduate Research fellowships and a Wildlife and Fisheries Sciences graduate student scholarship from Texas A&M University.

This work was also made possible in part by the Texas A&M University's Ecology and Evolutionary Biology program, Office of Graduate and Professional Studies, MSC L.T. Jordan Fellowship, and the Tom Slick Development Grant; American Society of Parasitologists; Texas Ecolab program; Churchill Northern Studies Centre; American Museum of Natural History Theodore Roosevelt Memorial Fund; and the Macroecology of Infectious Disease Research

Coordination Network, funded by a joint NSF/NIH/USDA grant (DEB 1316223). This work is solely the responsibility of the authors and does not necessarily represent the official views of the awarding offices.

TABLE OF CONTENTS

Page

LIST OF FIGURES

LIST OF TABLES

1. INTRODUCTION

A primary objective in the field of macroecology is describing biodiversity, including understanding the patterns of biodiversity across space and time and the factors that drive these patterns across large spatial scales. One of the most recognized macroecological patterns is the latitudinal diversity gradient (LDG), or the pattern of higher species richness at lower latitudes. To date, hundreds of studies have searched for a latitudinal pattern of diversity in free-living organisms (e.g., Dobzhansky 1950, Janzen 1970, Kaufman 1995, Hillebrand 2004, Condamine et al. 2012, Rolland et al. 2014, Andam et al. 2016), with most taxa following the traditional LDG of higher species diversity in the tropics compared to temperate and polar regions (Rohde 1992). Over 30 hypotheses have been proposed to explain the LDG (reviewed in Rohde 1992, Willig et al. 2003, and Fine 2015), with abiotic factors that affect multiple taxa simultaneously, like such as geographic area, ecological and evolutionary time, and climate stability, have received support as potential influential drivers of the LDG (Pianka 1966, Rohde 1992, Chown & Gaston 2000, Willig et al. 2003, Fine 2015). For example, climate stability can encourage higher diversity through decreased range sizes, increased specializations, and decreased extinction rates (Fine 2015); climate is further supported as a major cause of latitudinal patterns as over the past few hundred million years, tropical peaks in diversity are often found during cold climatic periods, while temperate diversity peaks or no latitudinal pattern is often seen during warmer periods (Mannion et al. 2014). In conjunction with abiotic factors, biotic factors might help maintain diversity patterns; species interactions, like competition, predation, and mutualism, and biotic characteristics, like population growth rate, can encourage higher diversity (Rohde 1992, Pianka 1966, Huston 1979).

Even though parasitism is one of the most common life history strategies (Dobson et al. 2008), the LDG has been less studied in parasitic taxa, with approximately 20 studies published to date (reviewed in Preisser 2019). These studies, conducted across various geographic scales and within different host and parasite taxa, failed to converge on a general relationship between latitude and parasite diversity; most studies found a positive or no relationship, while few found the expected negative relationship. These mixed results may emerge because they represent true patterns that vary across taxa, or they may be a consequence of the varying scales used across the studies. Previous recommendations suggest using a globally distributed host species (Poulin 2014) or phylogenetic group (Salkeld et al. 2008) to investigate diversity patterns like the LDG, though not all previous studies followed these recommendations. An additional potential source of variation in the demonstrated patterns is the chosen taxonomic scale of the parasites. Fourteen of the previous 19 LDG studies investigated latitudinal patterns of helminths, an informal grouping of organisms that includes parasitic nematodes (Nematoda), cestodes (Platyhelminthes: Cestoda), trematodes (Platyhelminthes: Trematoda), and acanthocephalans (Acanthocephala). Though these taxa have been evolving independently for hundreds of millions of years (Wang et al. 1999) and have different life cycles and methods of reproduction, nutrient acquisition, and host use, they are often grouped together in LDG studies. Given their evolutionary and ecological differences, these taxa may follow different latitudinal patterns and grouping them together may obscure disparate patterns.

To address this gap in our knowledge and explore the importance of parasite taxonomic scale, I analyze latitudinal patterns of helminth diversity in cricetid rodents (Rodentia: Cricetidae), a single host group with a geographically widespread distribution. I analyze all helminths together, to allow for comparisons with previous LDG helminth studies, and repeat all

analyses separating helminths into nematodes, cestodes, and trematodes; acanthocephalans were not analyzed due to their low prevalence of infection in these hosts. Given that biodiversity patterns are shaped by both abiotic and biotic pressures (Rohde 1992, Fine 2015), I also analyze climate and host-associated variables for their potential correlation with diversity patterns. Climate, in conjunction with other abiotic factors, may help shape LDG patterns in parasitic taxa; however, because climate varies predictably with latitude, other factors that vary with latitude may shape diversity patterns more strongly.

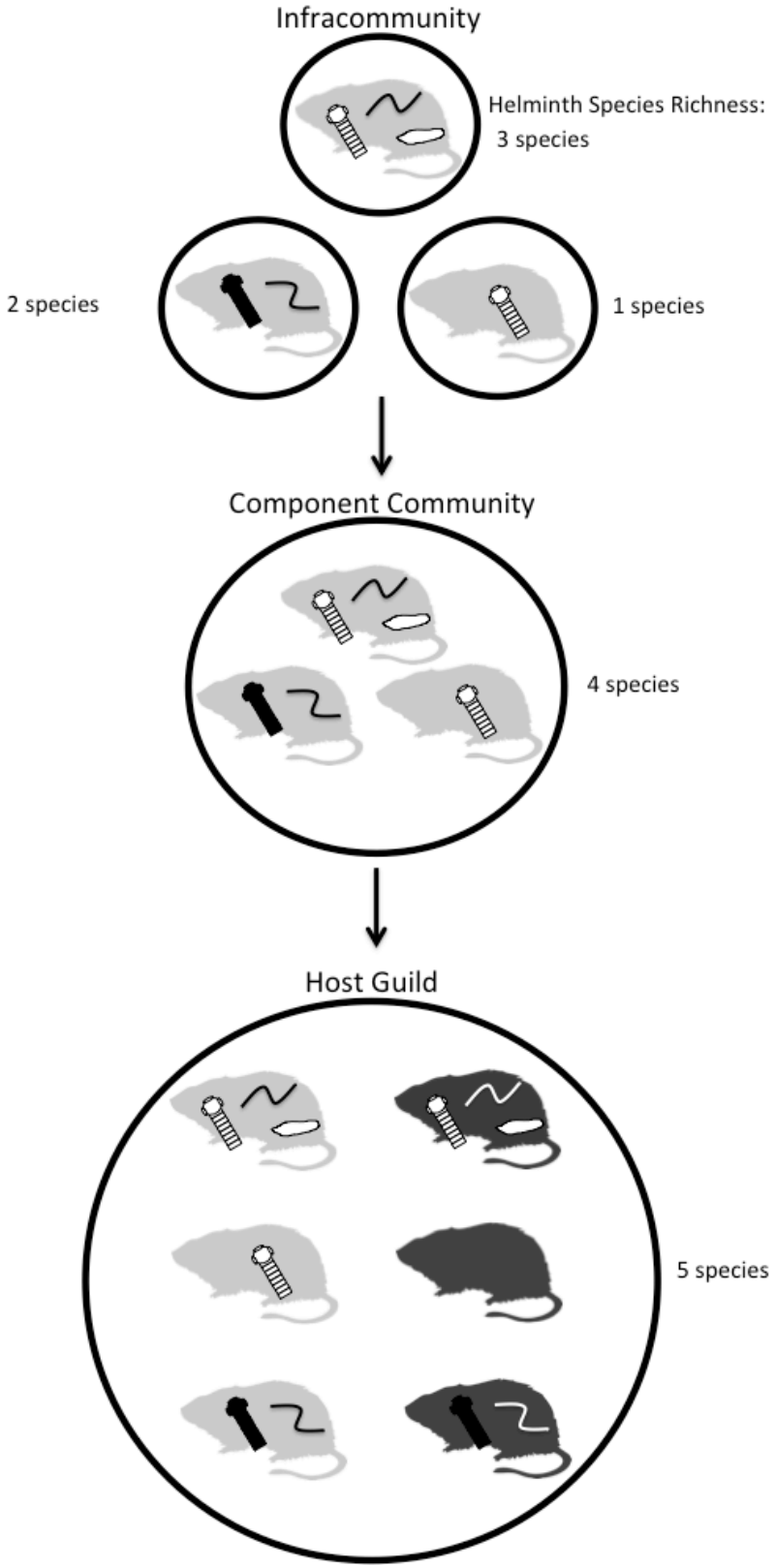
First, following past investigations of the LDG of parasitic taxa using existing literature, I aggregate data from previously published helminth surveys of cricetid rodents from around the world to investigate the presence and direction of a latitudinal pattern of species richness of all helminths, as well as nematode, cestode, and trematode taxa separately. I explore the potential influence of climate and host body mass and diet in shaping richness patterns. Next, I investigate the LDG within the same parasite and host taxa as described above, but at a different geographic scale and across different levels of community organization. Following Bush et al. (1997) and Zander (2001), I analyze latitudinal diversity patterns across infracommunities, component communities, and host guilds along a latitudinal gradient in North and Central America. An infracommunity is all of the parasites within a single host individual, a component community is all of the parasites within a sample population of a single host species at a given locality, and a host guild is all of the parasites within a group of functionally similar hosts, like cricetid rodents, at a given locality (Figure 1.1). Within each community analysis, I again examine the potential effects of climate and host body mass on helminth species richness.

Finally, to explore how changes in helminth communities may contribute to the latitudinal patterns, I analyze β-diversity, or the changes in helminth species composition

between communities (i.e., community dissimilarity), across community scales along the same latitudinal gradient described above. I partition β-diversity between infracommunities, component communities, and host guilds into its two components of species turnover (i.e., loss of some species and gain of others) and nestedness (i.e., smaller communities are subsets of more species-rich assemblages) (Baselga 2010). Additionally, I investigate the influence of geographic distance, climate, and host β-diversity on helminth β-diversity across all three levels of community organization using a novel method to account for the nonlinearity of changes in β-diversity along geographic and ecological gradients.

This work will contribute to the knowledge of LDG of parasites and of potential contributing factors to helminth diversity. Additionally, I provide updated helminth biodiversity surveys for cricetid rodents in North and Central America. Through the investigation of the LDG at different taxonomic scales and levels of community organization, I also provide new insights into the importance of considering scales of study and analyzing helminth taxa independently.

Figure 1.1 Levels of parasite community organization. Latitudinal diversity gradients were investigated at the level of infracommunity, component community, and host guild. Each host represents an infracommunity; at each locality, a population of hosts of the same species represents a component community; together, all of the cricetid species at each locality represent a host guild. Species richness varies with community scales, and macroecological patterns of richness may differ with on the community scale used. Three different parasites (nematodes, cestodes, and trematodes) are indicated with different shapes and in this simple example, different host and parasite colors indicate different species. The rodent graphic is by Natasha Vitek and is freely available on PhyloPic.


Infracommunity
Helminth Species Richness:
3 species
2 species
1 species
Component Community
4 species
Host Guild
5 species

1.1. References

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2. LATITUDINAL GRADIENTS OF PARASITE RICHNESS: A REVIEW AND NEW INSIGHTS FROM HELMINTHS OF CRICETID RODENTS*

2.1. 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 (e.g., Hutchinson 1959, Fischer 1960, Pianka 1966, Rohde 1992, Rohde 1998, Rohde 1999, Chown & Gaston 2000, Gaston 2000, Hillebrand & Azovsky 2001, Lyons & Willig 2002, Mittelbach et al. 2007, Brown 2014). Over 30 hypotheses have been proposed to explain the LDG (Table 2.1; see Pianka 1966, Rohde 1992, Willig et al. 2003, and 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 & Gibson 1983, Rohde 1992, Chown & Gaston 2000, Willig et al. 2003, Condamine et al. 2012, Fine 2015, Valentine & 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

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Table 2.1. Factors hypothesized to cause and/or maintain latitudinal diversity gradients, with original citations provided (when available); table adapted with permission from Preisser (2019). These factors are adapted from Pianka (1966), Rohde (1992), and Willig et al. (2003).

Factor/Hypothesis	**References**
Environmental harshness*	Thiery 1982, Brown & Gibson 1983
Environmental stability°	Klopfer 1959, Klopfer & MacArthur 1961
Environmental predictability°	Slobodkin & 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 & McCoy 1979, Currie 1991 Colwell & Hurtt 1994, Colwell & 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 & Conner 1980
Temperature dependence of chemical reactions	Alekseev 1982
Energy	Hutchinson 1959, Currie 1991
Abiotic-biotic	Kaufman 1995, Kaufman 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 1998, Brown & Gibson 1983
Epidemics*	
Mutualism*	Brown & Gibson 1983
Population size*	Boucot 1975, Rohde 1978
Niche width*	Ben-Eliahu & Safriel 1982, Brown & 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) 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 & Jablonski 2015; see also

temperature correlations with the evolutionary speed hypothesis, Table 2.1, Rohde 1992, Willig et al. 2003, and 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 & Willig 1998, Buckley et al. 2010, Rolland et al. 2014, Rolland et al. 2015), fish (Hobson 1994, Macpherson & Duarte 1994, Hanly et al. 2017), insects (Condamine et al. 2012, Fattorini & Baselga 2012, Heino et al. 2015), aquatic invertebrates (France 1992, Yasuhara et al. 2012a, Yasuhara et al. 2012b), bacteria (Pommier et al. 2007, Fuhrman et al. 2008, Andam et al. 2016), and plants (Dobzhansky 1950, Janzen 1970, Heino & 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 & Baltzer 2015), ectomycorrhizal fungi (Sánchez-Ramírez et al. 2015), Chilean mollusks (Kiel & Nielsen 2010), New World Lampropeltini snakes (Pyron & Burbrink 2009), galling insects (Price et al. 1998), parasitoid wasps (Janzen 1981, Skillen et al. 2000), aquatic mosses (Heino & Toivonen 2008), pelagic

seabirds (Chown et al. 1998), pinnipeds (Procheş 2001), lagomorphs (Rolland et al. 2014), and many parasitic taxa (Poulin 1995, Poulin & 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 & 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.

2.1.1. 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) and 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 & Krasnov 2013). While rodent surveys have been incorporated in previous large-scale investigations of the LDG of parasites (e.g., Poulin 1995 and Poulin & 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 & Leung 2011); considering rodents comprise 39.3% of all mammal species (2,552 species out of 6,495 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.

2.2. Materials and Methods

2.2.1. The Search for New Insights into the Parasite LDG

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 (Figure 2.1), 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 & Heap 1998, Calvete et al. 2003, Guernier et al. 2004, and Linardi & 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 & 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.

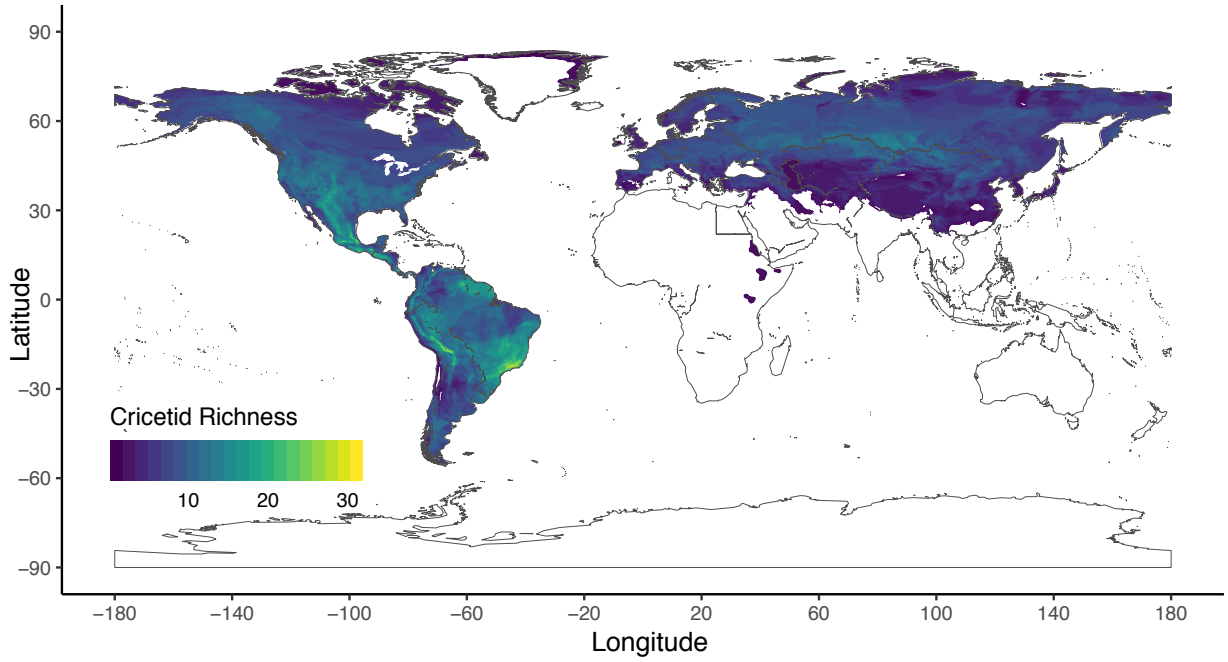

Figure 2.1. A heat map of cricetid species richness around the world; reprinted with permission. Data from digital distribution maps on *The IUCN Red List of Threatened Species* (IUCN 2016). This figure is reprinted with permission from "Latitudinal gradients of parasite richness: a review and new insights from helminths of cricetid rodents" by W. Preisser, 2019. Ecography, 42: 1315–1330, 2019 by Ecography.

2.2.2. 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.

2.2.3. 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 (available upon request). 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.

2.2.4. Data Analysis

All analyses were performed in R version 3.3.3 (R Core Team 2017). All continuous data were tested for normality using the Shapiro-Wilk test (Shapiro & 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, Walther et al. 1995, Poulin 1997), 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 (R code available upon request).

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; Appendix 2.1, Table A2.1). Methodologies and results for these analyses are included in the Appendix 2.1. 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, Poulin 2014) and host-parasite records may not be independent data points (Gittleman & 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 Appendix 2.1. 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 (Appendix 2.1, Table A2.3), 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 2.4) using a single survey for each host species, as detailed in the Appendix 2.1. For all analyses, the function 'vif' from the package 'car' (Fox & 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 - (residual deviance/null deviance).

2.3. Results

2.3.1. Literature Search and Data Collection

A total of 114 published surveys were collected, representing 175 unique helminth communities of 60 cricetid species (see Figure 2.2 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 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 Appendix 2.1, Tables A2.1 and A2.2 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 upon request; the references for the dataset are provided in the Appendix 2.2.

2.3.2. Data Analysis

All PCA results are listed in Table 2.2 and model results are reported in Tables 2.3 and 2.4 and Appendix 2.1, Table A2.4. Both HSR and NSR were significantly and negatively correlated with distance from the equator (Table 2.3, Figure 2.3). 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 2.4 and Appendix 2.1, Table A2.4; Figure 2.3). As abiotic variables were collinear in all analyses (using the standard cutoff of vif >

4; Appendix 2.1, Figures A2.1 and A2.2), 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 2.2). Only PC loadings over 0.3 and significant results of the model are discussed.

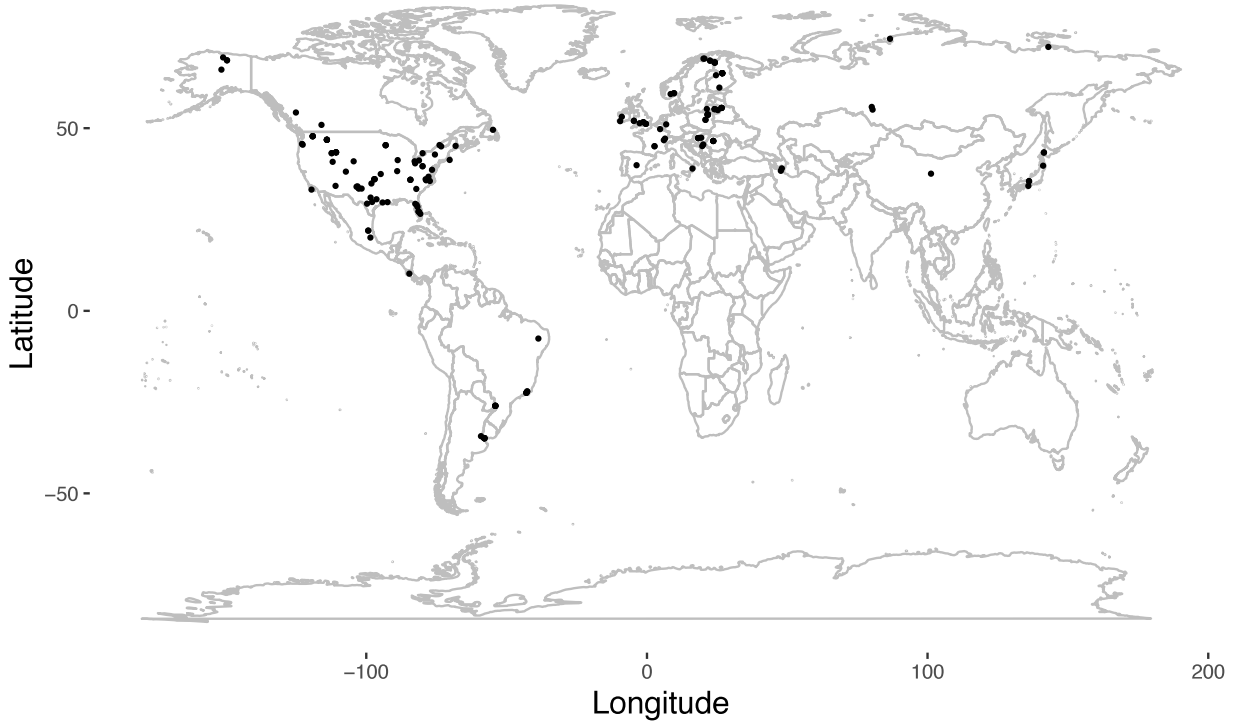

Figure 2.2. A map of the locations of the 175 parasite communities from 60 host species collected from published literature sources and used in this study; reprinted with permission. Each dot represents a survey locality. This figure is reprinted with permission from "Latitudinal gradients of parasite richness: a review and new insights from helminths of cricetid rodents" by W. Preisser, 2019. Ecography, 42: 1315–1330, 2019 by Ecography.

Table 2.2. PCA axes used in the various analyses to account for collinearity; table adapted with permission from Preisser (2019). 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.

Model 175					
	PC1	**PC2**	**PC3**	**PC4**	**PC5**
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, NP[1] Models Cestodes and Trematodes					
	PC1	**PC2**	**PC3**	**PC4**	**PC5**
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

[1]Non-phylogenetic

Model Cestodes					
	PC1	**PC2**	**PC3**	**PC4**	**PC5**
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					
	PC1	**PC2**	**PC3**	**PC4**	**PC5**
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

Table 2.3. Results of the final non-phylogenetic GLMs with helminth and nematode richness (refer to Table 2.2 for loadings and cumulative proportion of the PC axes); table adapted with permission from Preisser (2019). 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 - residual deviance/null deviance). Bolded rows represent significant variables in the models.

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

Table 2.4. Results of the final PGLS models with cestode and trematode richness (refer to Table 2.2 for loadings and cumulative proportion of the PC axes); table adapted with permission from Preisser (2019). 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 ±SE	t Value	*P* Value	Effect	λ	R^2
Latitudinal Model Cestodes	**Intercept**	**-0.393238 ±0.139333**	**-2.8223**	**0.006521****	**-**	0.136	0.146
	Latitude	**0.066150 ±0.021004**	**3.1493**	**0.002586****	+		
Latitudinal Model Trematodes	Intercept	0.354912 ±0.188824	1.8796	0.06519	+	0.000	0.05928
	Latitude	-0.056694 ±0.029656	-1.9117	0.06086	-		
Model Cestodes	**Intercept**	**-0.166352 ±0.082093**	**-2.0264**	**0.04750***	**-**	0.017	0.353
	Diet	**0.144306 ±0.066700**	**2.1635**	**0.03478***	+		
	PC1	**0.034923 ±0.014176**	**2.4635**	**0.01686***	+		
	PC3	**-0.085707 ±0.038307**	**-2.2374**	**0.02926***	**-**		
Model Trematodes	**Intercept**	**0.261533 ±0.105051**	**2.4896**	**0.01573***	+	0.000	0.1399
	Diet	**-0.222978 ±0.084960**	**-2.6245**	**0.01112***	**-**		
	PC4	0.115472 ±0.076786	1.5038	0.13815	+		

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 2.2). When analyzing cestode richness, both the non-phylogenetic (Appendix 2.1, Table A2.4) and the phylogenetic analyses (Table 2.4) 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 ~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 2.4) and non-phylogenetic (Appendix 2.1, Table A2.4) 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.

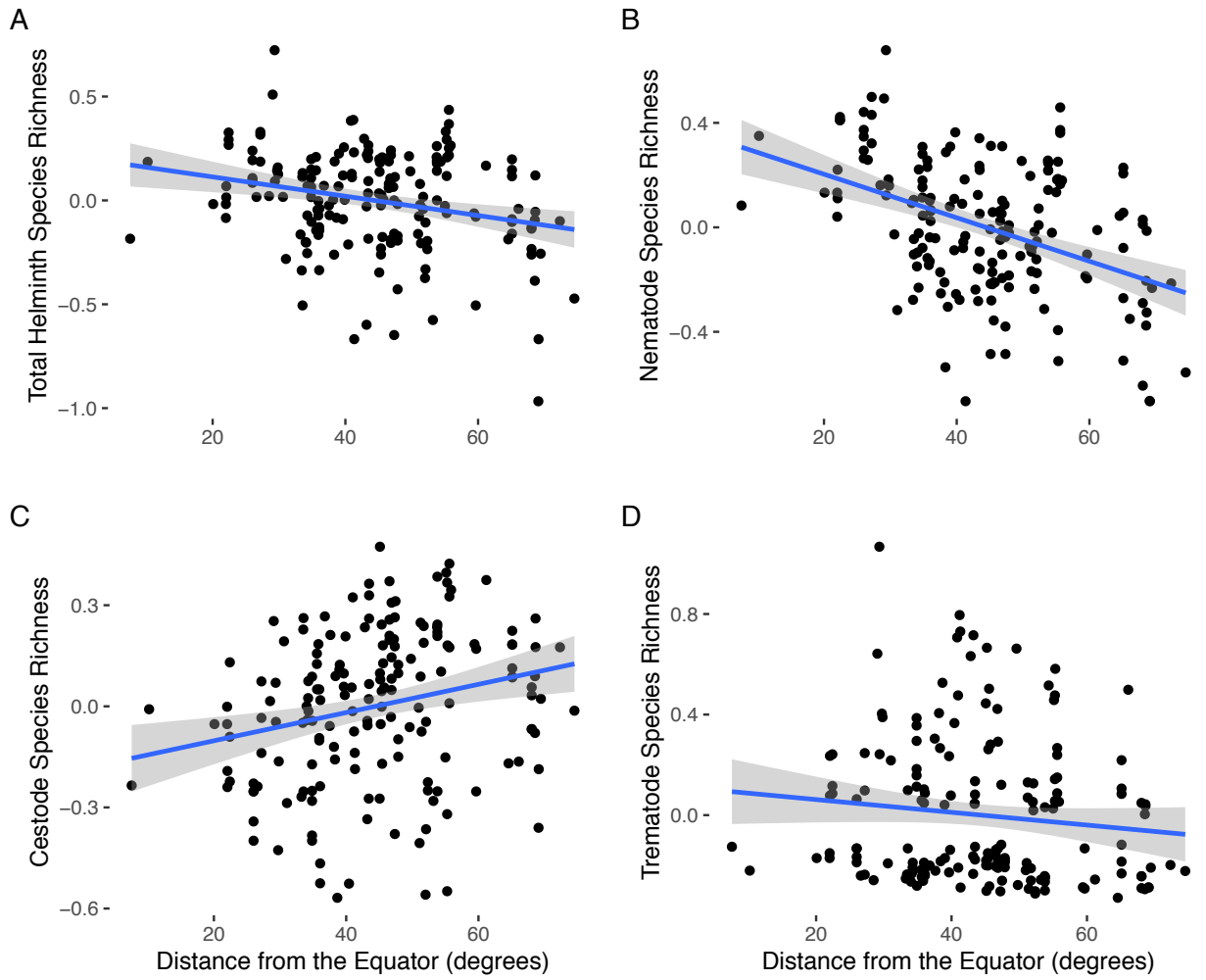

Figure 2.3. The relationship between A) HSR, B) NSR, C) CSR, and D) TSR, controlled for sampling effort, and distance from the equator from the latitudinal models; reprinted with permission (Tables 2.3 and 2.4). HSR, NSR, CSR, and TSR were controlled for sampling effort by regressing the number of species 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 – -0.001981333, R^2 = 0.06405. NSR: y = 0.370126 - 0.008332x, 95% CI -0.01099484 – -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 – 0.0007550201, R^2 = 0.0133. This figure is reprinted with permission from "Latitudinal gradients of parasite richness: a review and new insights from helminths of cricetid rodents" by W. Preisser, 2019. Ecography, 42: 1315–1330, 2019 by Ecography.

2.4. 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 (Figure 2.3). 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 & 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. 2002), 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 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 2.1) and previous research supporting the role of climatic factors in influencing richness in free-living organisms (see Hawkins et al. 2003, Wang et al. 2009, Tittensor et al. 2010, Mayhew et al. 2012, Fergnani & Ruggiero 2017) and parasitic taxa (Guernier et al. 2004, Dunn et al. 2010, Froeschke et al. 2010, Vhora & 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 (Appendix 2.1, Figure A2.1). 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 (e.g., Møller et al. 2013, Goedknegt 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 & 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 & Poulin 1998, Sasal & Morand 1998, Vitone et al. 2004, Nunn et al. 2003, Nunn et al. 2005, 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 & Poulin 1998), data on this relationship while controlling for host phylogeny have been contradictory (for a lack of a relationship, see Poulin 1995, Morand & Poulin 1998, Nunn et al. 2003; see Sasal & Morand 1998 and Lindenfors et al. 2007 for significant positive relationships), although positive relationships are often seen in non-phylogenetic models (Poulin 1995, Morand & 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 & Nadler 1988, Dybdahl & Lively 1998, Hoberg & 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 (Appendix 2.1, Table A2.1). 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 & 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 (Figure 2.1) 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 (Figure 2.1). 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 (e.g., Choudhury & 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.

2.5. 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.

2.6. References

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3. LATITUDINAL PATTERNS OF PARASITE SPECIES RICHNESS ACROSS COMMUNITY SCALES

3.1. Introduction

The latitudinal diversity gradient (LDG), or the trend of increasing species diversity with decreasing latitude, is one of the most well-known, large scale patterns in ecology. Much of the past work on the LDG centers around surveying free-living taxa that adhere to or deviate from this gradient (e.g., Janzen 1970, 1981, Kaufman 1995, Hillebrand 2004) and exploring the potential abiotic and biotic factors that drive the observed patterns (e.g., Pianka 1966, Rohde 1992, Lyons & Willig 2002, Brown 2014). Although it has been estimated that upwards of 75,000 helminth species (parasitic nematodes, cestodes, trematodes, and acanthocephalans) parasitize vertebrate hosts and there are at least 50% more helminth species than vertebrate species (Poulin & Morand 2000, 2004, Dobson et al. 2008), much less is known about the LDG patterns and processes of helminths than of free-living taxa. Although parasites should follow the latitudinal patterns of their host taxa (Poulin 2014), mixed relationships between species diversity and latitude have been found across diverse parasite and host taxa and various geographic scales (reviewed in Preisser 2019); most commonly, a positive or no relationship was found between latitude and helminth species richness, with the traditional negative relationship only detected in three studies (Calvete et al. 2003, Guernier et al. 2004, Preisser 2019). These mixed results suggest that generalizations of latitudinal diversity patterns of helminths may not be realistic, particularly given the lack of standardized scales of investigation in parasite LDG studies.

The LDG may be geographically scale dependent (Lyons & Willig 2002), and this dependency on scale may also extend to taxonomic (for both host and parasite) and community scales. “Helminth” is not a taxonomic classification, but an informal grouping of diverse parasitic taxa spanning three phyla (Nematoda, Acanthocephala, Platyhelminthes). These phyla have been evolving independently for hundreds of millions of years (Wang et al. 1998) and have evolved diverse and often complex strategies of nutrient acquisition, reproduction, and host use (for general overviews, see Wardle & McLeod 1968, Fried & Graczyk 1997, Anderson 2000), including the evolution of different life cycles (Parker et al. 2003, Benesh et al. 2014). Nematodes, cestodes, trematodes, and acanthocephalans may vary widely in their responses to other parasites, their hosts, and the environment; consequently, these taxa may respond to the factors that shape the LDG in different ways, resulting in varying latitudinal patterns among the groups.

Few previous LDG studies have analyzed nematodes, cestodes, trematodes, and acanthocephalans separately (e.g., Poulin & Leung 2011, Preisser 2019), as most previous LDG studies grouped all helminths together in their analyses (e.g., Blaylock et al. 1998, Choudhury & Dick 2000, Guernier et al. 2004). Even analyzing these taxa separately did not clarify the conflicting latitudinal patterns. Poulin & Leung (2011) found no relationship between latitude and any of the helminth taxa, although the helminth communities came from 650 bird, mammal, and fish host species; Poulin (2014) recommends searching for LDG patterns at a low host taxonomic level. Within a single host family, Preisser (2019) found that helminth taxa followed different latitudinal patterns: nematodes had higher diversity at lower latitudes, cestodes had lower diversity at lower latitudes, and trematodes had no relationship with latitude (acanthocephalan diversity was not included due to the lack of acanthocephalans in the data);

when all helminths were grouped together, richness was negatively correlated with latitude, suggesting that nematode richness drove this pattern and masked the latitudinal patterns of cestodes and trematodes when these taxa were combined. Given the likely differential responses of these taxa to a suite of biotic and abiotic factors, latitudinal patterns may be obscured if the grouped helminth taxa follow different latitudinal patterns. Parasite taxonomic scale may therefore be an important consideration in LDG studies, in addition to geographic and host taxonomic scales discussed previously in Preisser (2019).

Following Bush et al. (1997), parasite communities are divided into infracommunities, component communities, and supracommunities (Figure 1.1): infracommunities are at the level of host individual and comprise all parasite populations within or on a single host, component communities contain all infracommunities within a subset of a host species, and supracommunities are comprised of all component communities within a habitat, including parasite communities within both intermediate and definitive hosts and free-living parasitic stages. While data are commonly collected at the infracommunity scale, most parasite surveys publish summaries of richness, abundance, and prevalence at the level of the component community (Bush et al. 1997). Similarly, most investigations of the LDG of helminths have been conducted at the component community scale (e.g., Poulin 1995, Nunn et al. 2005, Lindenfors et al. 2007, Preisser 2019), with fewer being conducted at the level of infracommunities (Rohde & Heap 1998, Calvete et al. 2003) and none at the level of supracommunities. Incorporating variability in infracommunity richness may allow researchers to better understand how local diversity patterns and the factors that regulate them (e.g., inter- and intraspecific competition, disturbance, predation, and environment conditions like habitat complexity and temperature) produce larger scale patterns like the LDG.

Here, I investigate latitudinal patterns of helminth diversity at varying community and parasite taxonomic scales to determine if the observed latitudinal patterns differ with the scale used. As climate has been suggested to shape LDGs (Erwin 2009, Yasuhara et al. 2012, Mannion et al. 2014, Fine 2015) and both climate and host-associated traits to influence parasite diversity (Arneberg 2002, Ezenwa et al. 2006, Dunn et al. 2010, Froeschke et al. 2010), I investigate the potential effects of temperature, precipitation, and host body mass on helminth diversity. Since the same host and parasite taxa were examined in a previous study using the component community (Preisser 2019), I also explore the robustness of the LDG and the relationships with climate and host-associated variables across different datasets and geographic scales within the same general host-parasite system.

3.2. Methods

3.2.1. Parasite Collection

Cricetid rodents (family Cricetidae) were chosen as the target host species as they are distributed across North and Central America and represent one of the lowest host taxonomic groups suitable for continental scale investigations of the LDG of parasites. I selected six field sites set approximately every ten degrees in latitude across North and Central America (Figure 3.1, Table 3.1). I spent one to eight weeks at each site collecting rodents and their helminths (catalog data available upon request). At each field site, I set baited Sherman live traps in the evenings and checked them each morning for captures. Adults of cricetid species were euthanized according to the guidelines established by the American Society of Mammalogists for humane treatment of wild mammals (Sikes et al. 2016), the American Veterinary Medical Association (AVMA 2001, 2007), and the Texas A&M University (TAMU) Institutional Animal

Care and Use Committee. All collecting permits were approved prior to beginning field work (available upon request). Rodents were weighed with a Pesola scale, measured (lengths of total body, tail, hind foot, and ear), and dissected for parasite collection. The majority of host specimens were dissected fresh, shortly after collection. A few specimens from Texas were frozen before dissection and in a few cases at field sites in Texas and Winnipeg, organs were split open and stored in 70-80% ethanol prior to helminth collection. Ectoparasites were collected opportunistically. Rodent specimens were prepared for museum installation and were installed into Texas A&M University's Biodiversity Research and Teaching Collections (TCWC), College Station, TX, USA and various collections in their respective countries (data available upon request).

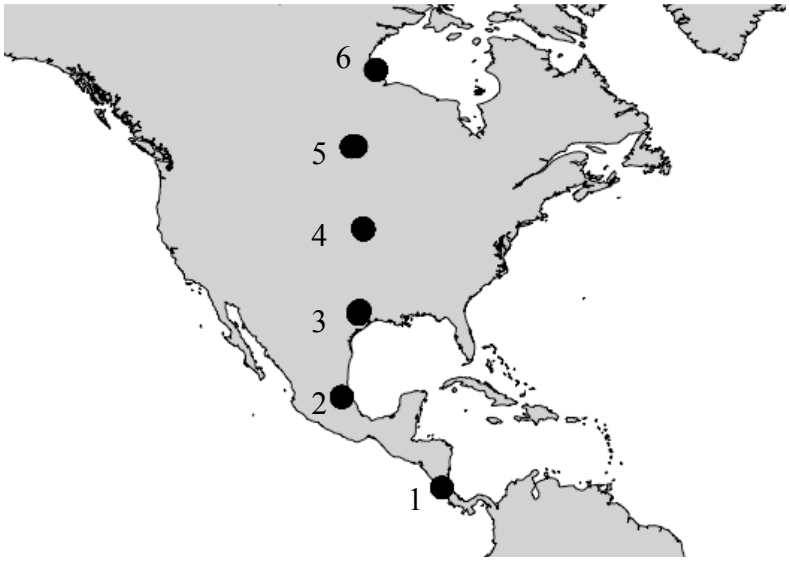

Figure 3.1. Map of sampling sites across North and Central America. Sampling sites were set approximately every 10 degrees in latitude, from north central Costa Rica (~10° N) to northern Manitoba, Canada (~58° N). See Table 3.1 for the specific location of each sampling site.

Internal body cavities and organs (excluding muscle, brain, eyes, bladder, and reproductive organs) were examined for helminths using a dissecting scope. Collected helminths were preserved for morphological identification using standard techniques (Cable 1977). Specifically, nematodes were stored in 70% ethanol and cleared in lacto-phenol or 80% phenol. Cestodes and trematodes were heat fixed in 10% ethanol or AFA (acetic acid, formalin, and ethanol), stained with Semichon's carmine, and mounted on slides with Canada balsam. No acanthocephalans were found. Specimens were identified and keyed out to the lowest taxonomic level possible by myself and collaborators. After the completion of this research, parasite specimens will be deposited into various collections, including the Harold W. Manter Laboratory of Parasitology Collection (HWML), University of Nebraska, Lincoln, Nebrask, USA; the United States National Parasite Collection (USNPC), Smithsonian National Museum of Natural History, Washington, D.C., USA; and various collections in their respective countries of origin.

3.2.2. Data Analysis

All analyses were performed in R ver. 3.5.1 (R Core Team). For each host individual, I assembled data on parasite species richness (including all helminths and nematodes, cestodes, and trematodes separately), host species, host body mass, and latitude and longitude of the collection site. Species richness was tallied for each level of community organization: infracommunity, component community, and host guild (i.e., a group of functionally similar hosts, intermediate between component communities and the supracommunity; Zander 2001, Marcogliese 2005). A host guild of cricetid rodents is used here in place of the supracommunity, as I did not sample all hosts and parasite life stages that comprise a supracommunity at these localities.

As helminth species richness can increase with host sample size (Walther et al. 1995), I used generalized linear models (GLMs) to test for a relationship between species richness counts (all helminths and nematodes, cestodes, and trematodes separately) and sample size for the component communities and host guilds. If no significant relationship was found, raw counts were used in all analyses; if there was a significant relationship between sample size and species richness for a particular richness measure and level of community organization, extrapolation and interpolation methods were used to control for differences in sample sizes between host species and localities. I created a site by species incidence matrix (with host individuals representing sites and the presence or absence of each parasite species marked for each site) and used it to extrapolate or interpolate species richness to one, two, and three times the lowest component community or host guild sample size, as extrapolations to more than three times a sample size are less accurate (Colwell et al. 2012a). Host species with only one or two individuals at each locality were removed from the component community analyses, and host component communities with no parasites could not be extrapolated and were assumed to have no parasites at the larger sample size. I extrapolated or interpolated species richness (Hill number $q=0$, H_0) using the iNEXT package (Chao et al. 2014, Hsieh et al. 2016).

I chose climate variables that captured information on average temperature, precipitation, and seasonality. Climate data were downloaded from WorldClim at the lowest resolution (Hijmans et al. 2005); latitude and longitude of the collection localities were translated onto the WGS84 geographic coordinate system and used to extract climate data specific to each locality. Relationships between diversity and latitude, host body mass, mean annual temperature (MAT), annual temperature range (ATR), annual precipitation (AP), and annual precipitation range

(APR; calculated as the difference between the wettest month and the driest month) were investigated in these analyses.

As more closely related host species might be expected to harbor more similar parasite faunas (Poulin 2009), I tested for phylogenetic signal (Felsenstein 1985, Revell et al. 2008) in the infracommunity, component community, and host guild species richness measures. Since I sampled multiple individuals of each host species and had multiple component communities with the same host species, I used phylogenetic comparative methods incorporating within-species variation (Ives et al. 2007, Goolsby et al. 2016) of the trait of interest (parasite species richness) for the infracommunity and component community analyses. A rooted rodent phylogeny with branch lengths from Fabre et al. (2012) was trimmed to include only the species collected using the 'geiger' package (Harmon et al. 2008), and polytomies were randomly resolved using the function 'multi2di' in the package 'ape' (Paradis et al. 2004). Using the package 'Rphylopars' (Goolsby et al. 2016), I fit two models, one assuming complete Brownian motion and one fit with a star phylogeny, for each of the helminth species richness measures and compared them using a likelihood ratio test to test for phylogenetic signal. For richness measures with significant signal, I used phylogenetic comparative linear regressions incorporating within-species variation (Goolsby et al. 2016) to control for the influence of host relatedness when investigating potential correlates of helminth diversity. For richness measures where a phylogenetic signal was not present, generalized linear models (GLMs) were used. In the host guild analyses, helminth richness was combined from all hosts within each locality and phylogenetic comparative methods were not employed. Individual host mass was used for infracommunity analyses, while the average host mass of each species was used in component community analyses; host mass was not included in host guild analyses. In all analyses, the predictor variables (latitude, climate

variables, and host mass) were transformed as necessary to meet the assumptions of normality. In the phylogenetic comparative linear regressions, the richness measures were log transformed as ($\log_{10}[x+1]$); in the GLMs, richness was left untransformed (O'Hara & Kotze 2010).

For each level of community organization and for each helminth group, I evaluated the relationships between species richness and latitude and species richness and the climate variables and host mass. As the climate variables used have previously been demonstrated to be multicollinear (Preisser 2019), I ordinated the climate data using a principal component analysis (PCA) and used the first axis in place of the original climate variables, as it explained over 85% of the variation in the data. Models with the lowest AIC were retained as the final model. R^2 values for each model were calculated as 1-(residual deviance/null deviance).

3.3. Results

3.3.1. Infracommunity

I collected 294 cricetid rodents representing 23 species across the six field sites (Table 3.1; catalog data available upon request). Seventy-five helminth species, including 50 nematode, 12 cestode, and 13 trematode species, were recovered from these 294 infracommunities; approximately 43% of the hosts harbored no helminths (Figure 3.2). I was unable to identify three host individuals from two species in Costa Rica to the species level; these host individuals (and their parasite data) were therefore excluded from the infracommunity and component community analyses, as phylogenetic comparative methods require knowledge of host species identity. Significant phylogenetic signal was detected in the all helminth, nematode, and cestode species richness (Table 3.2). Thus, phylogenetic comparative linear regressions with intraspecific

variation were used for these groups. As no phylogenetic signal was found in the trematode species richness, GLMs were used.

Table 3.1. The number of infracommunities (individual hosts) and component communities (host species) collected at each locality; all of the host individuals at each field site represent a host guild. Reported are the total number and ranges of helminth species and the number of nematode, cestode, and trematode species collected per community. Host specimen catalog information, individual-level data for helminth species richness, and the site by species matrix used to extrapolate and interpolate species richness are available upon request.

Locality	Degrees Latitude	Scale	Number of Communities	Helminth Species	Nematode Species	Cestode Species	Trematode Species
1. San Juan de Peñas Blancas, Costa Rica	10.38 N	Infracommunities	14	1 – 5	1 – 4	0 – 1	0 – 1
		Component Communities	6	1 – 13	1 – 10	0 – 1	0 – 2
		Host Guild	1	22	17	1	4
2. Calnali, Hidalgo, Mexico	20.89 N	Infracommunities	57	1 – 4	1 – 3	0 – 1	0 – 1
		Component Communities	8	2 – 7	2 – 6	0 – 1	0 – 1
		Host Guild	1	19	16	1	2
3. College Station, Texas, United States	30.64 N	Infracommunities	64	0 – 5	0 – 4	0 – 3	0 – 1
		Component Communities	4	1 – 9	1 – 6	1 – 3	0 – 2
		Host Guild	1	18	12	4	2
4. Brownsville, Nebraska, United States	40.38 N	Infracommunities	81	0 – 2	0 – 1	0 – 1	0 – 1
		Component Communities	7	0 – 4	0 – 3	0 – 1	0 – 1
		Host Guild	1	7	4	2	1
5. Winnipeg, Manitoba, Canada	49.87 N	Infracommunities	43	0 – 2	0 – 2	0 – 1	0 – 1
		Component Communities	3	0 – 5	0 – 2	0 – 3	0 – 1
		Host Guild	1	8	4	3	1
6. Churchill, Manitoba, Canada	58.73 N	Infracommunities	35	0 – 3	0 – 2	0 – 1	0 – 2
		Component Communities	2	1 – 8	0 – 2	1 – 3	0 – 2
		Host Guild	1	8	2	3	3

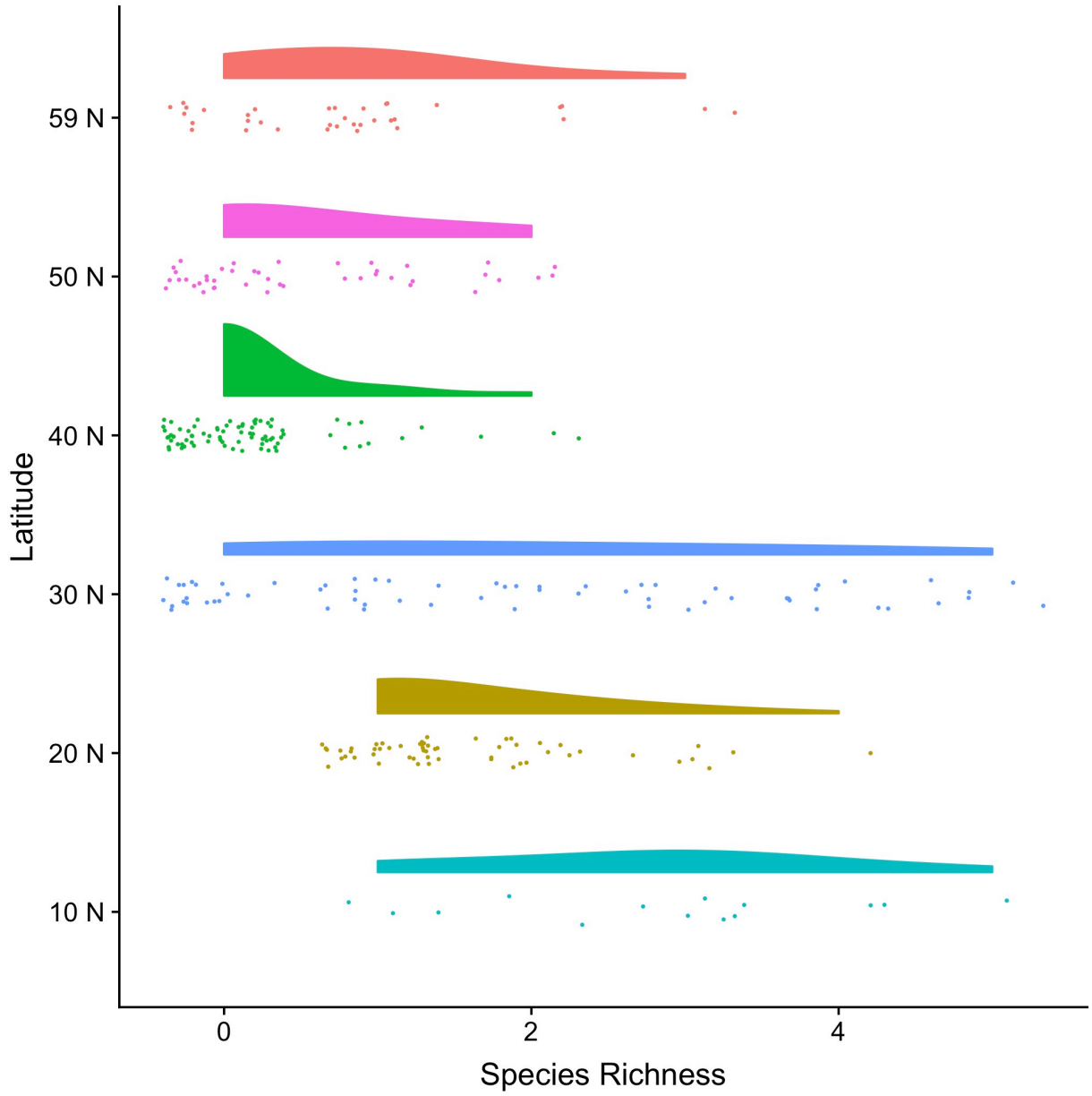

Figure 3.2. Raincloud plot showing the distribution of infracommunity helminth species richness for each sampled locality. Each point represents an infracommunity, with the thickness of the clouds representing the number of hosts with that richness value. Species richness per infracommunity ranged from zero to six. Richness values were 10% jittered to prevent clumping. Raincloud plots were developed by Allen et al. (2018a, 2018b).

All helminth and nematode richness were significantly and negatively correlated with latitude, while cestode and trematode richness were not significantly correlated with latitude (Table 3.2, Figure 3.3). Species richness for all groups except trematodes was significantly and positively correlated with host body mass (Table 3.3). All helminth and nematode richness were significantly and negatively correlated with PC1, which was negatively related to AP, APR, and MAT and positively related to ATR (Table 3.4), suggesting that helminth and nematode species richness are higher in areas of higher annual precipitation, annual precipitation range, and mean annual temperature, and lower annual temperature range, characteristics that typify lower latitudes (Figure 3.4). Cestode richness was significantly and positively correlated with PC1, suggesting that richness is higher in areas of lower annual precipitation, annual precipitation range, and mean annual temperature, and higher annual temperature range. Trematode species richness was not significantly correlated with any of the predictor variables (Table 3.3).

3.3.2. Component Community

After removing species with fewer than three individual hosts at a locality, I analyzed species richness across 20 component communities (each host species at each locality). Helminth and cestode species richness were significantly and positively correlated with component community sample size; species richness for these two taxa were extrapolated or interpolated. Relationships between latitude and species richness for each of the three sample sizes (one, two, and three times the lowest component community sample size) were identical; as such, only results from the largest sample size are reported here and used in subsequent analyses. As nematode and trematode species richness were not significantly correlated with sample size, raw values were used in all analyses. Helminth and nematode species richness were negatively and significantly correlated with latitude, while cestode and trematode species richness were not

Table 3.2. Results of the infracommunity analyses, correlating all helminth, nematode, cestode, and trematode species richness with latitude. For the component community models, species richness (Hill number q=0, H_0) for each community were obtained by extrapolating or interpolating observed species richness to a sample size of three times the lowest sample size. When significant phylogenetic signal was detected, phylogenetic comparative linear regressions with intraspecific variation were used; when no significant phylogenetic signal was found, negative binomial or Poisson generalized linear models (GLM) were used. The adjusted R^2 is reported for the phylogenetic analyses, while R^2 for the GLM was calculated as 1-(residual deviance/null deviance). Significant results are in bold. Significance codes: '*' ≤ 0.05, '**' ≤ 0.01, '***' ≤ 0.001.

Helminth Group	Phylogenetic Signal	Coefficient	Estimate ±Std. Error	Z Value	*P* Value	R^2
Infracommunity Species Richness						
All Helminths	***P* = 0.00189****	Intercept	3.16			0.330
		Latitude	**-0.0523 ±0.0159**	**-3.29**	**0.00384****	
Nematodes	***P* = 0.000241*****	Intercept	2.79			0.494
		Latitude	**-0.0500 ±0.0110**	**-4.53**	**0.000228*****	
Cestodes	***P* = 0.0278***	Intercept	0.0802			-0.0170
		Latitude	0.00447 ±0.00548	0.815	0.425	
Trematodes	*P* = 1	**Intercept**	**-2.49 ±0.684**	**-3.65**	**0.000267*****	0.00139
		Latitude	-0.00645 ±0.0180	-0.359	0.719	
Component Community Species Richness (H_0)						
All Helminths	*P* = 0.151	**Intercept**	**2.65 ±0.289**	**9.14**	**<2e-16*****	0.337
		Latitude	**-0.0436 ±0.0101**	**-4.33**	**1.49e-05*****	
Nematodes	*P* = 0.217	**Intercept**	**2.46 ±0.329**	**7.48**	**7.65e-14*****	0.414
		Latitude	**-0.0465 ±0.0116**	**-4.00**	**6.34e-05*****	
Cestodes	*P* = 0.530	**Intercept**	**-2.00 ±0.985**	**-2.03**	**0.0426***	0.117
		Latitude	0.0381 ±0.0238	1.60	0.109	
Trematodes	*P* = 1	Intercept	-1.10 ±0.870	-1.27	0.206	0.0161
		Latitude	0.0147 ±0.0230	0.640	0.522	
Host Guild Species Richness (H_0)						
All Helminths		**Intercept**	**3.42 ±0.227**	**15.1**	**<2e-16*****	0.820
		Latitude	**-0.0253 ±0.00697**	**-3.64**	**0.000277*****	
Nematodes		**Intercept**	**3.44 ±0.264**	**13.1**	**<2e-16*****	0.881
		Latitude	**-0.0412 ±0.00918**	**-4.49**	**7.14e-06*****	
Cestodes		Intercept	0.155 ±0.724	0.214	0.831	0.374
		Latitude	0.0184 ±0.0168	1.10	0.274	
Trematodes		**Intercept**	**1.206 ±0.603**	**2.00**	**0.0453***	0.190
		Latitude	-0.0130 ±0.0169	-0.767	0.443	

Table 3.3. Results investigating relationship between species richness, climate (via PC axes; Table 3.4), and host body mass at the infracommunity and component community scales. For the component community models, species richness (Hill number q=0, H_0) for each total helminth and cestode community were obtained by extrapolating or interpolating observed species richness to a sample size of three times the lowest sample size. Phylogenetic comparative linear regressions with intraspecific variation were used when phylogenetic signal was detected (Table 3.2); when no phylogenetic signal was found, negative binomial or Poisson generalized linear models (GLM) were used. Only relationships between species richness and climate were assessed at the host guild scale. The adjusted R^2 is reported for the phylogenetic analyses, while R^2 for the GLM was calculated as 1-(residual deviance/null deviance). Significant results are in bold. Significance codes: '*' ≤ 0.05, '**' ≤ 0.01, '***' ≤ 0.001.

Helminth Group	Coefficient	Estimate ±Std. Error	Z Value	*P* Value	R^2
Infracommunity Species Richness					
All Helminths	Intercept	-1.61			0.723
	Mass	**2.03 ±0.418**	**4.87**	**0.000124*****	
	PC1	**-0.232 ±0.0705**	**-3.30**	**0.00402****	
Nematodes	Intercept	-0.643			0.677
	Mass	**1.15 ±0.363**	**3.15**	**0.00549****	
	PC1	**-0.258 ±0.0611**	**-4.22**	**0.000514*****	
Cestodes	Intercept	-0.876			0.614
	Mass	**0.795 ±0.139**	**5.73**	**1.96e-05*****	
	PC1	**0.0724 ±0.0232**	**3.12**	**0.00591****	
Trematodes	**Intercept**	**-4.371 ±1.19**	**-3.68**	**0.000236*****	0.0198
	Mass	1.12 ±0.774	1.45	0.146	
Component Community Species Richness (H_0)					
All Helminths	Intercept	-1.36 ±0.734	-1.85	0.0644	0.582
	Mass	**1.77 ±0.479**	**3.69**	**0.000226*****	
	PC1	**0.218 ±0.0634**	**3.44**	**0.000591*****	
Nematodes	Intercept	-0.892 ±0.831	-1.07	0.283	0.529
	Mass	**1.28 ±0.553**	**2.31**	**0.0207***	
	PC1	**0.236 ±0.0732**	**3.23**	**0.00123****	
Cestodes	**Intercept**	**-5.83 ±1.94**	**-3.01**	**0.00260****	0.451
	Mass	**3.37 ±1.17**	**2.89**	**0.00388****	
	PC1	**-0.441 ±0.205**	**-2.16**	**0.0311***	
Trematodes	**Intercept**	-2.00 ±1.77	-1.13	0.258	0.0261
	Mass	0.975 ±1.19	0.822	0.411	
Host Guild Species Richness (H_0)					
All Helminths	**Intercept**	**2.54 ±0.119**	**21.4**	**<2e-16*****	0.757
	PC1	**-0.222 ±0.0622**	**-3.57**	**0.000356*****	
Nematodes	**Intercept**	**2.03 ±0.159**	**12.7**	**<2e-16*****	0.796
	PC1	**-0.348 ±0.0784**	**-4.44**	**9.1e-06*****	
Cestodes	**Intercept**	**0.788 ±0.284**	**2.77**	**0.00555****	0.472
	PC1	0.204 ±0.169	1.21	0.228	
Trematodes	**Intercept**	**0.745 ±0.285**	**2.61**	**0.00898****	0.241
	PC1	-0.136 ±0.156	-0.872	0.383	

Table 3.4. PCA axes used in the infracommunity, component community, and host guild analyses to control for multicollinearity. Collinear variables included annual precipitation (AP), annual precipitation range (APR), mean annual temperature (MAT) and annual temperature range (ATR). Only the first axis was used for each analysis, as it explained over 85% of the variation in each case.

Infracommunity PC Axes				
Variables	**PC1**	**PC2**	**PC3**	**PC4**
AP	-0.522	-0.00914	0.743	-0.418
APR	-0.457	0.810	-0.116	0.348
MAT	-0.496	-0.562	0.0159	0.661
ATR	0.521	0.166	0.659	0.517
Cumulative Proportion	0.878	0.978	0.995	1.00
Component Community PC Axes				
Variables	**PC1**	**PC2**	**PC3**	**PC4**
AP	0.513	-0.0545	-0.838	-0.177
APR	0.478	0.748	0.152	0.434
MAT	0.488	-0.661	0.232	0.521
ATR	-0.520	0.0136	-0.469	0.713
Cumulative Proportion	0.899	0.976	0.995	1.00
Host Guild PC Axes				
Variables	**PC1**	**PC2**	**PC3**	**PC4**
AP	-0.516	0.0979	-0.413	0.744
APR	-0.490	0.635	-0.229	-0.551
MAT	-0.478	-0.766	-0.235	-0.361
ATR	0.515	-0.00705	-0.850	-0.113
Cumulative Proportion	0.906	0.976	0.990	1.00

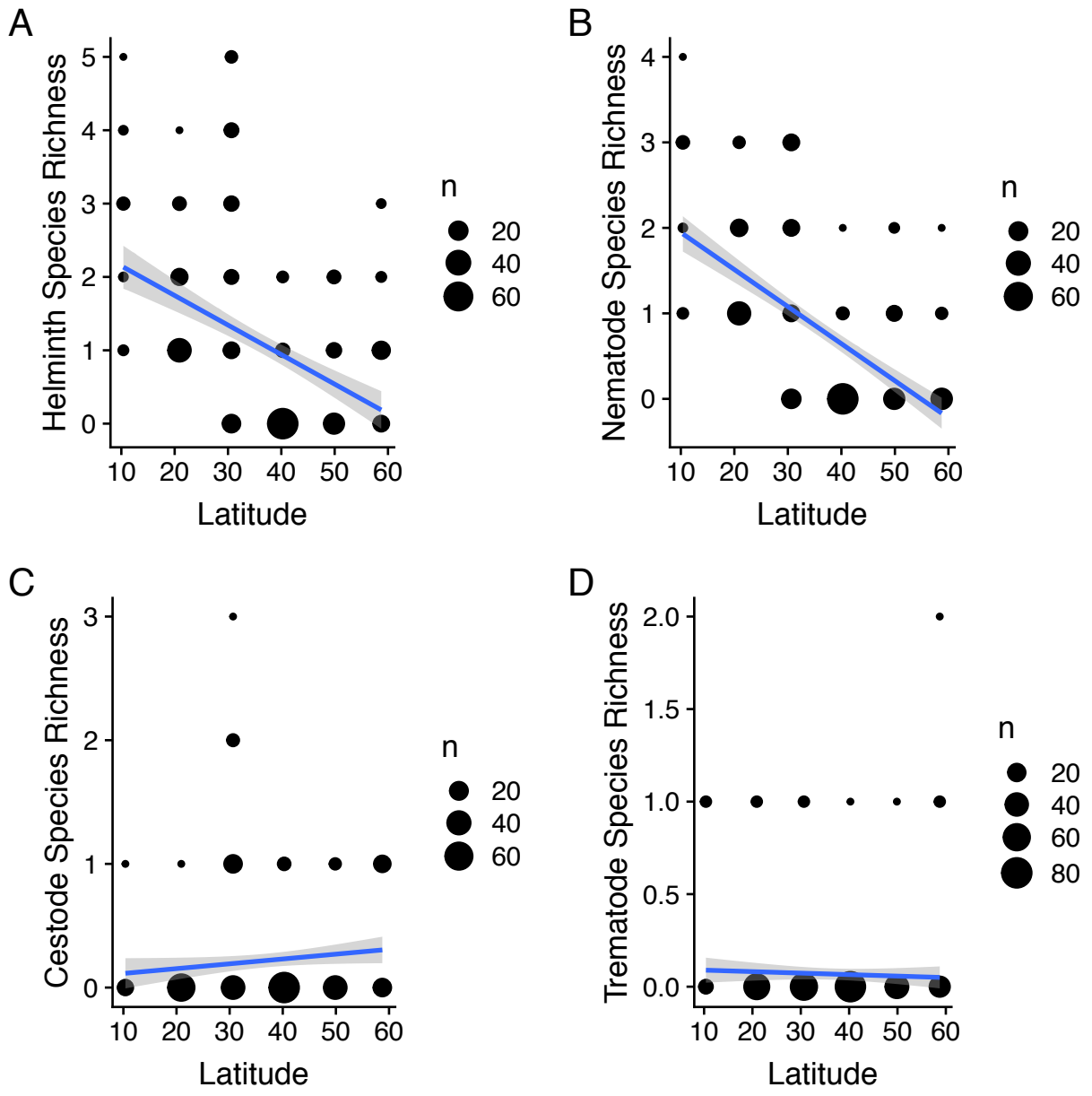

Figure 3.3. Graphs of the relationships between latitude and A) helminth, B) nematode, C) cestode, and D) trematode species richness at the infracommunity level. Circle size corresponds with the number of infracommunities. Helminth and nematode species richness were significantly and negatively correlated with latitude, while cestode and trematode species richness showed no significant relationship with latitude (Table 3.2).

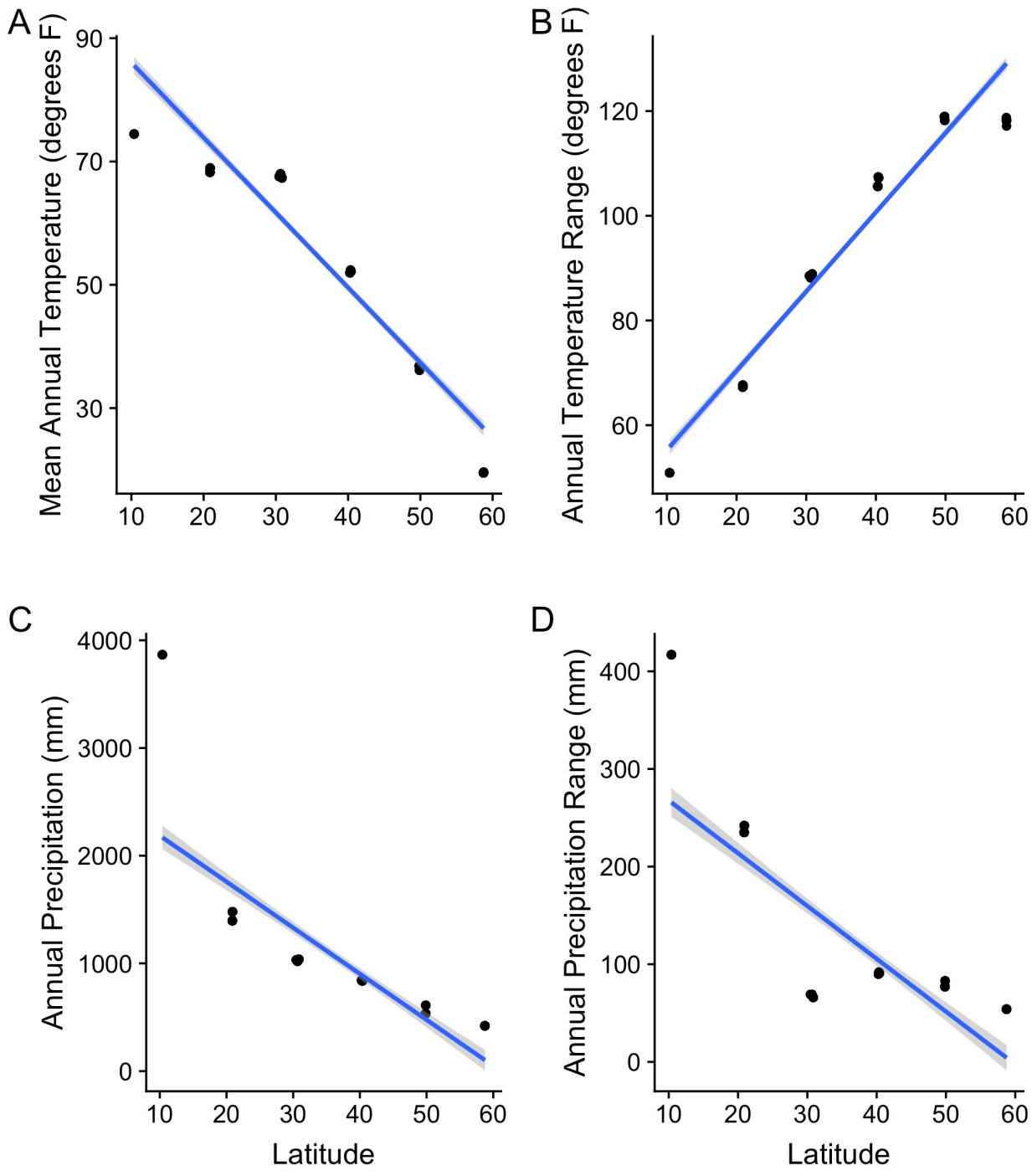

Figure 3.4. Relationships between latitude of the six sampling sites examined in this study and the climate variables A) mean annual temperature (MAT), B) annual temperature range (ATR), C) annual precipitation (AP), and D) annual precipitation range (APR).

significantly correlated with latitude (Table 3.2; Figure 3.5). Host body mass was significantly and positively correlated with helminth, nematode, and cestode richness (Table 3.3). PC1 was positively related to AP, APR, and MAT and negatively related to ATR, significantly and positively correlated with all helminth and nematode richness, and significantly and negatively correlated with cestode richness (Tables 3.3, 3.4). Trematode richness was not significantly correlated with either host body mass or climate (Table 3.3).

3.3.3. Host Guild

I analyzed six host guilds (Figure 1.1) and all host species were included in these analyses, regardless of sample sizes. None of the species richness measures were significantly correlated with sample size ($P > 0.1$). Latitude was significantly and negatively correlated with helminth and nematode richness and not significantly correlated with cestode or trematode richness (Table 3.2; Figure 3.6). PC1 was negatively related to AP, APR, and MAT and positively related to ATR (Table 3.4) and significantly and negatively correlated with helminth and nematode richness (Table 3.3). Cestode and trematode richness were not significantly correlated with the climate variable (Table 3.3).

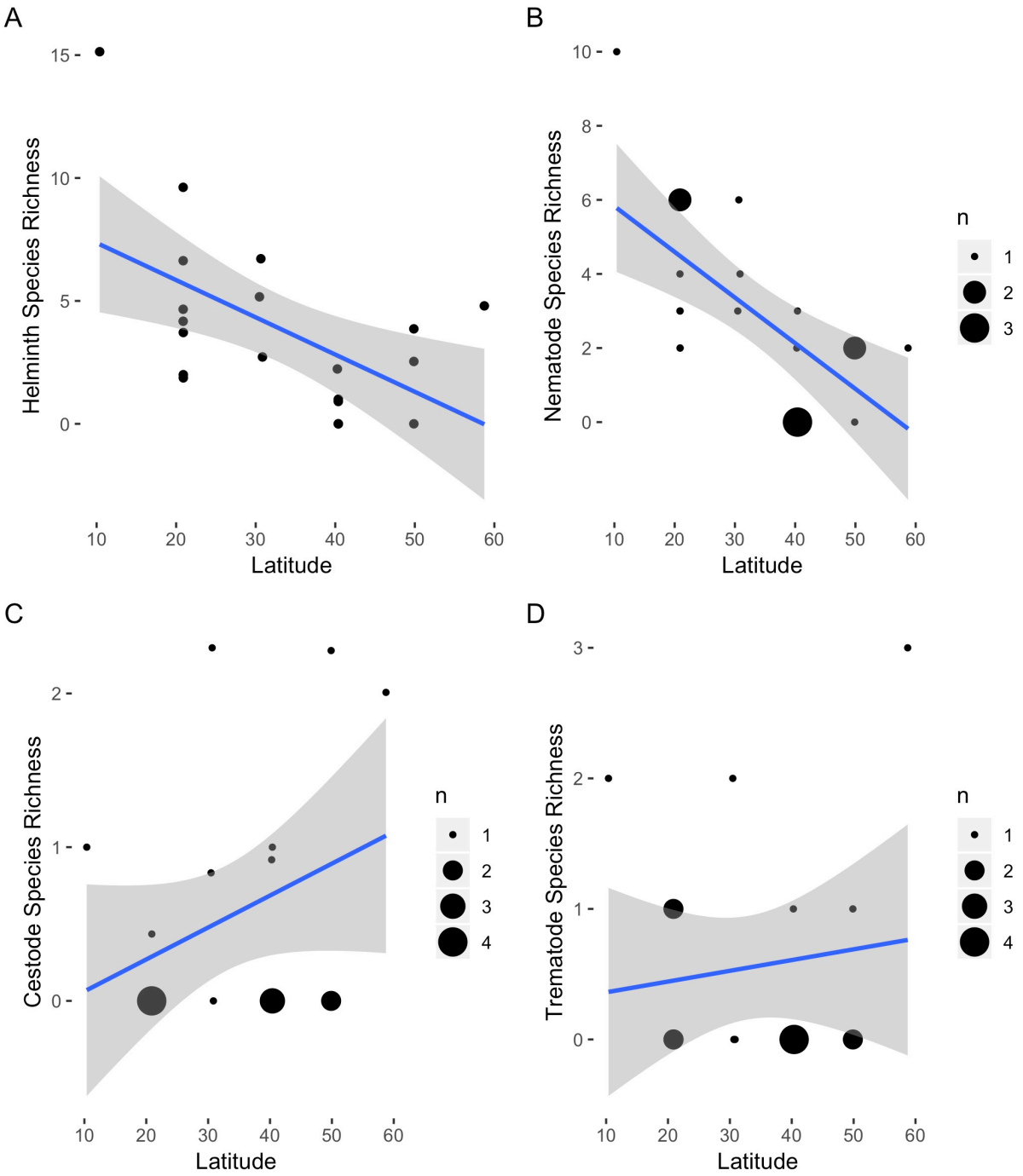

Figure 3.5. Graphs of the relationships between latitude and A) helminth, B) nematode, C) cestode, and D) trematode species richness at the component community level. For cestodes and trematodes, circle size corresponds with the number of component communities. Species richness were extrapolated or interpolated to a sample size of 10 hosts for all helminths and cestodes. Helminth and nematode species richness were significantly and negatively correlated with latitude, while cestode and trematode species richness showed no significant relationship with latitude (Table 3.3).

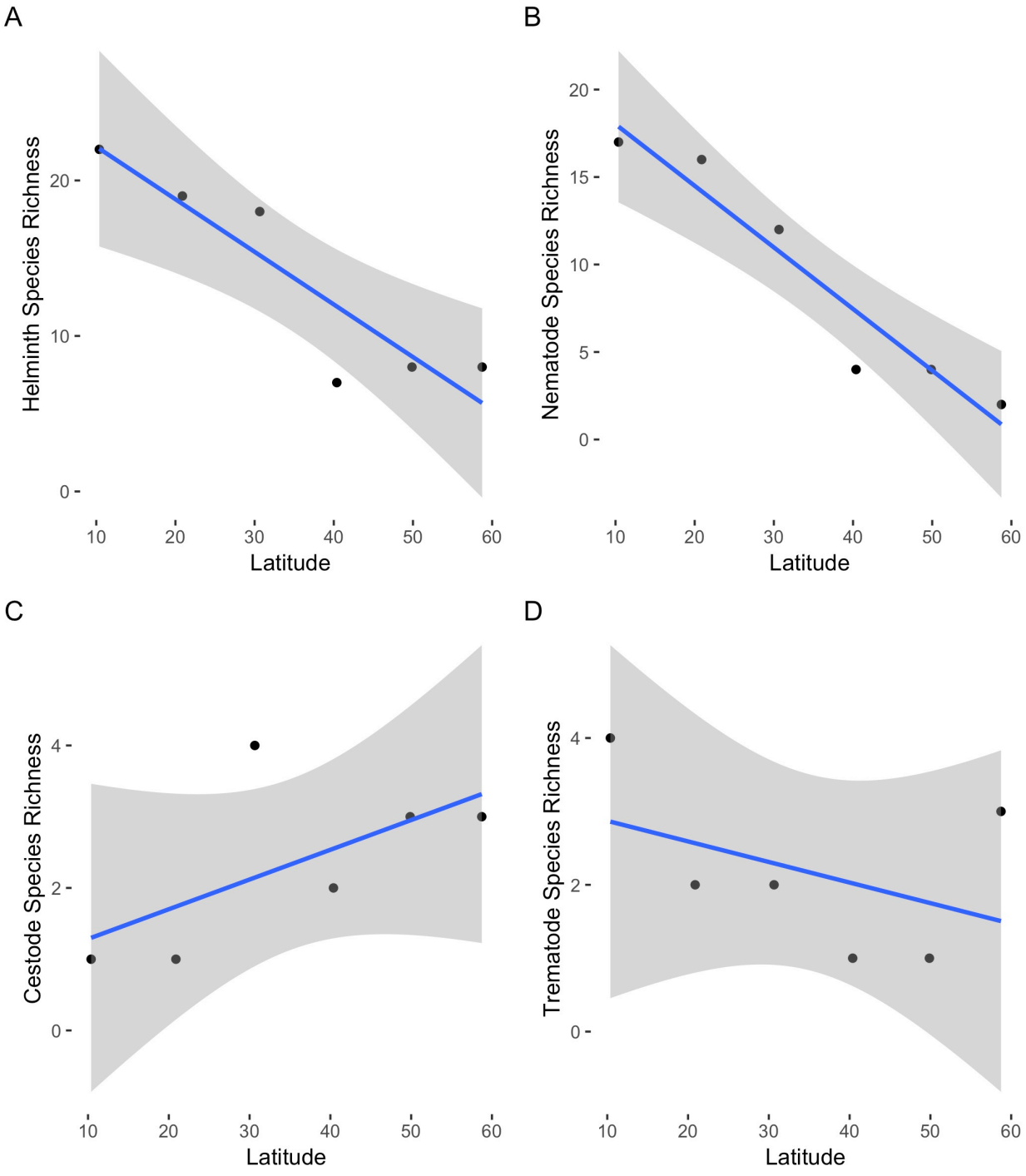

Figure 3.6. Graphs of the relationships between latitude and A) helminth, B) nematode, C) cestode, and D) trematode species richness at the level of host guild. Helminth and nematode species richness were significantly and negatively correlated with latitude, while cestode and trematode species richness showed no significant relationship with latitude (Table 3.3).

3.4. Discussion

3.4.1. Latitudinal Gradients and Potential Causes

For these helminths of cricetid rodents, the LDG appears to be robust to different scales of community organization, with trends consistent across infracommunity, component community, and host guild scales for all helminth, nematode, cestode, and trematode species richness. Nematodes followed the traditional LDG of increasing species richness with decreasing latitude (Table 3.2; Figures 3.3, 3.5, 3.6). As nematodes likely dominate the helminth communities of many mammals (Poulin & Leung 2011) and were around four times more species in these hosts than cestodes or trematodes, they drove the latitudinal pattern seen when all helminths were combined. Cestode and trematode species richness did not demonstrate a relationship with latitude at any community scale.

Similar relationships with climate were also seen across community analyses. Nematode richness was higher in areas of higher annual precipitation, annual precipitation range, and mean annual temperatures, and lower annual temperature ranges across all levels of community organization, and again likely drove the relationships between all helminths and climate (Table 3.3). Cestode richness demonstrated the opposite pattern, with higher richness in areas of lower annual precipitation, annual precipitation range, and mean annual temperatures, and higher annual temperature ranges at the infracommunity and component community scales, although this relationship was not significant at the level of host guild. Trematode richness showed no relationship with climate at any community scale.

While significant relationships with climate were found for most of the examined diversity, causative relationships cannot be determined. Although climate varies predictably with latitude, it may not be driving patterns of helminth diversity; instead, other factors that also vary

with latitude may be shaping these gradients. Disentangling the contributions of various factors is problematic, even in the LDG studies of free-living organisms (Rohde 1992). An added difficulty in studies of parasite ecology is the influence of the host: for example, host body size, population density, and geographic range size are all known to affect both parasite species richness and abundance (Gregory 1990, Ezenwa et al. 2006, Poulin 2014). One or more of these host-related factors may enhance or reduce the effect of other biotic or environmental variables shaping diversity patterns. Additional research is necessary to understand if or how the host environment mediates the relationship between helminths and their external environment.

To explore potential host factors, I examined the effect of host body mass on helminth species richness. Previous research suggests that parasite diversity should increase with body size through the increased availability of niches (Morand & Poulin 1998), although this relationship often has mixed support, particularly when phylogenetic comparative methods are used (Poulin 1995, Nunn et al. 2003, Sasal & Morand 1998, Lindenfors et al. 2007). In this study, mass was significantly and positively correlated with all helminth, nematode, and cestode richness at both the infracommunity and component community scales, using both phylogenetic comparative and non-phylogenetic methods. These helminth taxa are indeed more diverse in larger cricetid rodents, likely due to larger hosts having more and larger habitats for parasites to occupy. Ad hoc phylogenetic comparative linear regressions incorporating within-species variation demonstrated no significant relationship between individual host body mass and latitude (estimate = -0.0097, std. error = 0.0050, Z = -1.937, $P = 0.068$), but a significant and negative relationship between average host body mass and latitude at the component community level (estimate = -0.0152631, std. error = 0.0061482, Z = -2.4825, $P = 0.02256$). As there are

larger-bodied host populations at lower latitudes and higher nematode diversity in larger hosts, host body mass may help shape the LDG of nematodes at the component community level.

Given that Nematoda and Platyhelminthes have been evolving independently for hundreds of millions of years (Wang et al. 1998), it is perhaps unsurprising that these taxa may exhibit different macroecological patterns. These taxa likely respond differently to the abiotic (e.g., climate) and biotic (e.g., host-associated) factors that shape latitudinal gradients. Indeed, the helminth groups showed different relationships with latitude and climate, with trematodes also differing in their relationship with host mass (Table 3.5). These taxa vary widely in their host use, life cycles, reproduction, and transmission. For example, most trematodes use snails as intermediate hosts (i.e., host where some development occurs) to reach their definitive host (i.e., host where maturation and reproduction occurs); cestodes can use rodents as their intermediate or definitive host, depending on cestode species, while nematodes primarily use them as definitive hosts, with or without the use of intermediate hosts. Nematodes and trematodes may have their developmental life stages travel through the external environment before reaching their hosts, while cestodes may only come in contact with the external environment while they are in eggs. These different life histories likely influence how these taxa respond to the local, regional, and global pressures that shape latitudinal gradients. Further work should explore how parasite taxa with these different life histories respond to various abiotic and biotic factors.

Table 3.5. Comparisons of the results of the infracommunity, component community, and host guild analyses in this study with a previous investigation of the LDG of helminths at the component community level (Preisser 2019). Significant negative relationships (−), positive relationships (+), or no relationship ("None") are marked for the results of each analysis. Climate variables included annual precipitation (AP), annual precipitation range (APR), mean annual temperature (MAT) and annual temperature range (ATR).

Helminth Group	Infracommunity			Component Community			Host Guild		Preisser (2019) Component Community		
	Latitude	Mass	Climate	Latitude	Mass	Climate	Latitude	Climate	Latitude	Mass	Climate
All Helminths	−	+	+ AP +APR + MAT − ATR	−	+	None	−	+ AP +APR + MAT − ATR	−	None	+ AP +APR + MAT − ATR
Nematodes	−	+	+ AP +APR + MAT − ATR	−	+	+ AP +APR + MAT − ATR	−	+ AP +APR + MAT − ATR	−	−	+ AP +APR + MAT − ATR
Cestodes	None	+	− AP −APR − MAT + ATR	None	+	− AP −APR − MAT + ATR	None	None	+	None	− AP −APR − MAT + ATR
Trematodes	None	None	None	None	None	None	None	None	None	None	None

3.4.2. LDGs Across Studies and Scales

This is not the first study to investigate latitudinal patterns of helminths of cricetid rodents. Preisser (2019) explored the LDG of these taxa using host and parasite data acquired from previously published parasite surveys, similar to most helminth LDG studies. Comparing these two studies may provide some insight into the mixed results seen across previous LDG studies when studies are performed at variable scales. First, relationships between all helminth, nematode, and trematode richness and latitude and climate were consistent between these studies (Table 3.5). These correlations were robust to different geographic scales (worldwide versus North America), different data sources (literature- versus field-based), and different cricetid host species, as only six species out of the 60 in Preisser (2019) and 23 (sampled here; catalog data available upon request) were shared between the studies. The congruence suggests that these latitudinal gradients are likely real patterns, given our current knowledge of the helminth fauna of these hosts, and not a consequence of geographic or host sampling bias. However, as only approximately 10% of cricetid rodent species have been sampled for their helminth communities and were included in these two studies (~77 of 792 species; Burgin et al. 2018), additional sampling of the other 90% of these hosts is needed to confirm this pattern.

There is a discrepancy in patterns of cestode richness across these component community analyses. While Preisser (2019) found that cestode richness had a significant and positive relationship with latitude, no relationship was found in this study across any of the community levels, including across component communities (Table 3.5). These dissimilar latitudinal relationships may be a consequence of using a subset of the true helminth biodiversity present in this host family. Klibansky et al. (2017) found that analyses of subsets of true data may return patterns that are weaker, absent, or opposite of true trends. These two subsets of data,

representing our best, but incomplete, knowledge of the cestodes of cricetid rodents, returning different latitudinal relationships suggests these subsets are not representative of the true cestode biodiversity of these hosts. Further sampling of the other 90% of cricetid rodents and inclusion of their helminth fauna in LDG studies is necessary before latitudinal patterns of cestode diversity can be understood. However, given the agreement between Preisser (2019) and the present study on the latitudinal gradients (or lack thereof) for all helminth, nematode, and trematode species richness using non-overlapping datasets, these may be the true patterns for these taxa in this host system. Similar problems of subsetting true diversity likely plague other LDG helminth studies and may help explain differences in latitudinal patterns across investigations. Further exploration of the current helminth biodiversity is needed, particularly given increasing anthropological threats and extinction risks (Dunn et al. 2009, Colwell et al. 2012b, Carlson et al. 2017, Cizauskas et al. 2017), before macroecological patterns can be confirmed.

Interestingly, the relationships with mass seen here also contradict the findings in Preisser (2019), where host mass was negatively correlated with nematode richness and not significantly related to all helminth or cestode richness (Table 3.5). This discrepancy may be a result of the coarse resolution of the body mass variable used in Preisser (2019). Preisser (2019) collected data from published sources (e.g., PanTHERIA; Jones et al. 2009) because information on host body mass for individual rodents or populations were not available. Preisser (2019) then analyzed these data for each component community record, similar to previous LDG studies investigating host characteristics (e.g., Nunn et al. 2005, Lindenfors et al. 2007). In the present study, the component communities were associated with averages of the specific, measured, individual host body masses making up each component community, providing a much finer resolution for analyses and likely demonstrating a result closer to the true relationship. In

analyses including host characteristics, these more individual host-based variables may be more informative than approximations at the species-level. Helminth surveys often only include component community-level summaries of host and parasite data (Bush et al. 1997), and are not always published with data for individual hosts. I would encourage future parasite surveys to publish individual host-level data, including host characteristics, to allow for these finer-scale analyses.

Another advantage of using individual host data is the ability to better account for uneven sampling across host populations and species. With the uneven sampling between species and localities here and with parasite species richness generally increasing with the number of hosts examined (Walther et al. 1995), extrapolation and interpolation of helminth species richness allowed for comparisons between equally-sized component communities in the parasite taxa where species richness increased with host sample size. While extrapolation introduces sources of error, particularly when extrapolating small samples, it is an appropriate method for controlling for differences in host sampling effort, and is preferable to alternative methods (e.g., regressing parasite richness with the number of hosts examined or citation counts).

Overall, a specific level of community organization for investigations of the LDG and potential correlating factors may not be necessary for some helminth taxa, a positive finding when investigations of macroecological patterns of parasites are often limited by the data. While most of the previous parasite LDG studies were limited to component community-level analyses given their use of host population summaries of parasite richness, future studies of macroecological patterns should investigate trends across community scales to determine if these findings are consistent across other host and helminth taxa. Also, results here confirm previous work (Preisser 2019) suggesting helminth taxa may respond to the pressures that shape

latitudinal gradients in different ways, resulting in different diversity patterns among the taxa. With few LDG studies investigating helminth taxa individually, LDG patterns within these taxa may be missed, particularly if the parasite fauna of the host is dominated by a particular host group that masks the patterns of other taxa (as seen here). Future investigations of the LDG should separate helminth taxa when possible. Finally, surveying the parasite fauna of new host species and localities should be a priority, to both increase our knowledge of the biodiversity of parasites and to allow for further exploration of the problem of scale in investigations of macroecological patterns.

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4. CLIMATE, HOST B-DIVERSITY, AND GEOGRAPHIC DISTANCE PREDICT SPECIES TURNOVER OF HELMINTHS IN CRICETID RODENTS

4.1. Introduction

A central theme in ecology is focused on describing patterns of biodiversity and discerning the processes that shape them. In particular, patterns of alpha (α), beta (β), and gamma (γ) diversity have been a major topic in ecology since Whittaker (1960) coined the terms and their use in ecology over half a century ago (e.g., Sepkoski 1988, Lu et al. 2007, Mori et al. 2018, Willig & Presley 2019). The regional diversity of a landscape (γ-diversity) is comprised of the diversity of local assemblages or communities (α-diversity) and the changes in species composition between them (β-diversity). β-diversity can be estimated between communities and can also be partitioned into two phenomena, species turnover and nestedness (Baselga 2010). Species turnover encompasses the species replacement between two dissimilar communities (loss of some species and gain of others), whereas nestedness describes the pattern of smaller communities being comprised of subsets of more species-rich assemblages (Baselga 2010). β-diversity has been estimated at different geographic or taxonomic scales in free-living organisms (Gambi et al. 2014, Pavoine et al. 2016). Evaluating patterns of β-diversity in parasitic taxa, however, lends an added layer of complexity. Assemblages of different parasite species in or on a host are similar to those of free-living organisms in that they are products of interactions with other species and environmental pressures. The additional layer of difficulty is that many parasites are often subjected to 'dual' environments (Maestri et al. 2017, Krasnov et al. 2019), occupying both the outside environment and the environment of the body of their host. In the case of the latter, parasites are affected by factors such as host immunity, antiparasite behavior,

nutrient availability, and the availability of suitable hosts in the environment for transmission and persistence.

The β-diversity of ectoparasite and helminth (parasitic nematodes, cestode, trematodes, and acanthocephalans) communities has been explored in some host systems, including fish (Poulin & Morand 1999, Aguilar-Aguilar & Salgado-Maldonado 2006, Timi & Lanfranchi 2013), bats (Warburton et al. 2016), and rodents (Brouat & Duplantier 2007, Krasnov et al. 2010, van der Mescht et al. 2016, Maestri et al. 2017, Krasnov et al. 2019). In particular, distance-decay, or the increase in community dissimilarity (i.e., β-diversity) with geographic, ecological, or host phylogenetic distance, has been a popular topic of study for parasite ecologists (e.g., Poulin & Morand 1999, Poulin 2003, 2009, Locke 2013). These studies compared parasite community dissimilarities with corresponding dissimilarities in geography, parasite ecology, or host relatedness and found signatures of distance-decay, or higher parasite β-diversity with farther distances. In contrast, other studies have not supported the expected distance-decay relationship (e.g., Poulin 2009, Warburton et al. 2016, Williamson et al. 2019). These mixed findings may be due to actual variation in β-diversity patterns across host or parasite taxa, or may be affected by investigator-defined choices of taxonomic scale, geographic scale, community scale, or even analysis methods. In the case of analysis methods, traditional linear methods (e.g., linear regressions) are often used to analyze β-diversity patterns, but these methods can be problematic as relationships between β-diversity and predictor variables (e.g., geographic distance) and the rate of change in β-diversity across a landscape may not be linear. The use of generalized dissimilarity models (GDMs) has allowed researchers to overcome problems with assumptions of linearity (Ferrier et al. 2007). GDMs are an extension of matrix regressions and have an advantage over traditional linear analyses when investigating spatial patterns of

community dissimilarity or turnover in that they accommodate two sources of non-linearity often present in ecological community datasets: 1) the curvilinear relationship between distance and the dissimilarity in community composition, and 2) the variation in species turnover rate along geographic and ecological gradients (see Ferrier et al. 2007, Maestri et al. 2017). While GDMs have been in use for over a decade (Ferrier et al. 2007), they have only recently been used to explore β-diversity patterns in parasite taxa (e.g., Maestri et al. 2017, van der Mescht et al. 2018, Williamson et al. 2019).

Here, I seek to understand continental-scale patterns of β-diversity of helminth parasites (Nematoda and Cestoda and Trematoda within Platyhelminthes) of cricetid rodents (Rodentia: Cricetidae) and how environmental factors and host communities impact helminth community turnover. From previous work, helminths from these hosts follow the traditional latitudinal diversity gradient, with increasing species richness at lower latitudes (Preisser 2019, chapter two). However, the mechanisms shaping this pattern are less well understood. Potentially, changes in helminth β-diversity might contribute to this gradient. Higher turnover between communities at lower latitudes might result in higher diversity, and helminth communities at higher latitudes may be subsets of more species rich communities at lower latitudes.

Secondly, I aim to determine if the chosen level of helminth community organization may influence observed β-diversity patterns and their predictors. Parasites have 'dual' environments (Maestri et al. 2017, Krasnov et al. 2019), both the environment within their host and the external environment outside their host; parasites have additional levels of community organization when considering their host as a habitat. Community terms follow Bush et al. (1997) and Zander (2001). Briefly, infracommunities include all parasites within a single host individual (i.e., all helminths in an individual rodent), component communities include all

parasites within a host species at a given locality (i.e., all helminths in all of the rodent individuals belonging to a single species sampled at a particular locality), and host guilds include all parasites within a group of functionally similar hosts (i.e., all helminths in all of the rodent individuals and species sampled at each locality; Figure 1.1). As different factors can influence helminth communities at different spatial and community scales (Warburton et al. 2016), investigating β-diversity patterns and predictors at various scales may shed light on the local and regional processes shaping β-diversity in this system.

4.2. Methods

4.2.1. Data Collection and Organization

Rodents and parasites were collected along a latitudinal gradient in North and Central America as previously detailed in chapter two. Data on helminth species, host species, and latitude and longitude of the locality were recorded for each host individual (data available upon request). All analyses were performed in R ver. 3.5.1 (R Core Team). Multiple site by species matrices using presences/absences were assembled; the presence or absence of each helminth species was marked for each site, with sites representing host individuals (infracommunities), host species at each locality (component communities), and the six localities (host guilds). I introduced a dummy variable in all matrices to allow for the inclusion of infracommunities and component communities where no helminths were found; communities with helminths were marked with a "0", while communities with no helminths were given a "1". I assessed geographic distance (Poulin 2003), climate (Warburton et al. 2016, Maestri et al. 2017), and host β-diversity (Maestri et al. 2017, Williamson et al. 2019) as potential predictors of helminth β-diversity between infracommunities, component communities, and host guilds. Climate data

were downloaded from WorldClim at the 30s resolution (Hijmans et al. 2005) and extracted for each locality using its coordinates. Specifically, mean annual temperature (MAT), annual temperature range (ATR), annual precipitation (AP), and annual precipitation range (APR; calculated as the difference between the wettest month and the driest month) were recorded for each locality. As the climate variables used have previously been shown to be multicollinear (Preisser 2019), I ordinated the climate data using a principal component analysis (PCA) and used the first two axes in place of the raw climate variables in the GDMs.

4.2.2. β-diversity, Turnover, and Nestedness

I calculated the total β-diversity and the species turnover and nestedness components of helminths between each infracommunity and within and between each component community and host guild using the Sørensen index in the package 'betapart' (Baselga et al. 2018). Within component community β-diversity was calculated for component communities with two or more host individuals. I calculated β-diversity using both average pairwise and multiple site dissimilarities because average pairwise dissimilarity is less biased when community sample sizes are lower than the true number of communities present (Marion et al. 2017), yet multiple site dissimilarity can better quantify overall heterogeneity, as it accounts for patterns of co-occurrence across all sites (Baselga 2013). Values of total β-diversity and both species turnover and nestedness range from 0 to 1, where '0' represents no community dissimilarity, species turnover, or nestedness and '1' represents complete dissimilarity, species turnover, or nestedness.

4.2.3. Factors Affecting β-diversity

I used GDMs (Ferrier et al. 2007) to examine the influence of geographic distance, host β-diversity, community sample size, and climate (using the PC axes) on helminth β-diversity. I included host community sample size to account for uneven sampling across the study sites. I-

splines are created for each predictor variable. Along the x-axis is the geographic or ecological gradient (e.g., for precipitation, low to high rainfall); along the y-axis is the amount of community dissimilarity associated with only that gradient (hence "partial" ecological distance). The height of an I-spline (corresponding to the sum of coefficients) indicates the total amount of helminth turnover associated with the specific gradient holding the other predictor variables constant; the slope of the I-spline indicates the rate of turnover and how this rate changes along the variable gradient (where steeper slopes indicate higher rates of turnover; Ferrier et al. 2007). Overall, these I-splines inform the importance of each predictor in its contribution to community turnover, and how the rate of community turnover might change along the gradients of each predictor, as rates of turnover are not always constant along geographic and ecological gradients (Ferrier et al. 2007).

Using the 'gdm' package (Manion et al. 2018), I fit three GDMs using the Bray-Curtis dissimilarity with incidence data, one at each level of community organization: infracommunities (using host individuals as the sites in the site by species matrix), component communities (using host species at each locality), and host guilds (using each of the six localities). Geographic distance among localities was computed within the GDM function using their coordinates. To investigate the influence of host β-diversity on helminth β-diversity, I created a site by species matrix using the six localities and the presence or absence of all host species, calculated the pairwise dissimilarities using the package 'betapart' (Baselga et al. 2018), and included this dissimilarity matrix as a predictor variable in the host guild model.

4.3. Results

4.3.1. β-diversity, Turnover, and Nestedness

Total β-diversity and its two components, species turnover and nestedness, were calculated between 294 infracommunities, within 22 and between 30 component communities, and within and between six host guilds, using both multiple site and pairwise dissimilarities (Table 4.1). One hundred twenty-six infracommunities and five component communities had no helminths. β-diversity was high for all between-community calculations and species turnover was between one and two orders of magnitude higher than nestedness (Table 4.1). Among host individuals within component communities, the β-diversity ranged from zero to almost one, with the contributions from species turnover and nestedness varying between component communities; total β-diversity was most often driven by species turnover. Component communities with a β-diversity of zero (complete similarity between communities) were often small communities with few host individuals or communities with no parasites found (data available upon request). Among individuals within host guilds, β-diversity was high and species turnover was much higher than nestedness, suggesting that species turnover is the main contributor to β-diversity in this system. Overall, multiple site analyses often reported higher dissimilarities than the pairwise analyses.

4.3.2. Factors Affecting β-diversity

In the infracommunity model, the predictor variables were geographic distance and climate variables; in the component community model, the predictor variables were geographic distance, climate variables, and component community sample size. Finally, in the host guild model, the predictor variables were geographic distance, climate variables, host β-diversity, and host guild sample size. Across all three levels of community organization (infracommunity, component

community, and host guild), PC1 was a better predictor than PC2 (i.e., larger sum of coefficients and taller I-spline; Table 4.2) and explained between 82 – 87% of the variation in the data (versus 10 – 13% in PC2; Table 4.3). The infracommunity GDM explained approximately 28% of the deviance in the data (Table 4.4). The high β-diversity seen between infracommunities (Table 4.1) might explain the zero and low slope of geographic distance (Figure 4.1A); compositional turnover is consistently high across geography, therefore the rate of change is low. PC1 had almost 10 times the amount of helminth turnover associated with its gradient (sum of coefficients and height of I-spline) than with the other two predictor variables (Table 4.2) and was therefore the best predictor of helminth community dissimilarity. A higher rate of turnover (i.e., steeper slope) was associated with higher MAT, AP, APR and lower ATR, and the rate slowed and eventually became zero at lower measurements of MAT, AP, and APR and higher measurements of ATR (Figure 4.1B). The rate of turnover did not vary much across the gradient of PC2 (Figure 4.1C).

The component community GDM explained around 34% of the deviance (Table 4.4). Unlike the β-diversity among infracommunities, the rate of change in β-diversity among component communities did increase with geographic distance (Figure 4.2A), and the highest amount of species turnover was associated with geographic distance, followed by PC1, sample size, and PC2 (Table 4.2). Rates of turnover increased with increasing component community sample sizes (Figure 4.2B). Greater rates of change are seen at higher MAT, AP, APR, and lower AT on PC1 (Figure 4.2C) and higher MAT and lower AP and APR on PC2 (Figure 4.2D).

Table 4.1. Total helminth β-diversity and its two components, species turnover and nestedness, between infracommunities and between and within component communities and host guilds. β-diversity estimates range from 0 (no difference in community composition) to 1 (communities are completely dissimilar). Similarly, values of both species turnover and nestedness also range from 0 to 1, where '0' represents no species turnover or nestedness and '1' represents complete species turnover or nestedness. Both multiple site and average pairwise dissimilarities were calculated for each community. A range of dissimilarities was reported for the within component communities and host guilds analyses, as β-diversity was estimated for 22 component communities and six host guilds. Full dissimilarity results within the component communities and host guilds are available upon request.

Between Infracommunities, Component Communities, and Host Guilds						
Community	**Multiple Site Dissimilarity**			**Average Pairwise Dissimilarity**		
	Species Turnover	**Nestedness**	**Total Beta Diversity**	**Species Turnover**	**Nestedness**	**Total Beta Diversity**
Infracommunities	0.990	0.00312	0.993	0.782	0.00711	0.789
Component Communities	0.966	0.0146	0.981	0.946	0.0135	0.960
Host Guilds	0.951	0.0143	0.965	0.922	0.0173	0.940
Within Component Communities and Host Guilds						
	Multiple Site Dissimilarity			**Average Pairwise Dissimilarity**		
Community	**Species Turnover**	**Nestedness**	**Total Beta Diversity**	**Species Turnover**	**Nestedness**	**Total Beta Diversity**
Component Communities	0 - 0.930	0 - 0.5	0 - 0.943	0 - 0.803	0 - 0.25	0 - 0.803
Host Guilds	0.909 - 0.934	0.00874 - 0.0333	0.929 - 0.962	0.270 - 0.886	0.00123 - 0.0943	0.271 - 0.909

Table 4.2. The I-spline coefficients and their sums for the gradient of each predictor variable (geographic distance, sample size, PC1, PC2, and host β-diversity). These sums are reflected in the height of the I-splines in Figures 4.1, 4.2, and 4.3, and represent the total amount of helminth turnover associated that variable, holding the other variables constant.

Infracommunity				
Gradient	**I-Spline Coefficients**			**Sum of Coefficients**
	1	**2**	**3**	
Geographic Distance	0	0	2.06	2.06
PC1	19.6	0	0.00568	19.6
PC2	0.369	0	1.19	1.56
Component Communities				
Gradient	**I-Spline Coefficients**			**Sum of Coefficients**
	1	**2**	**3**	
Geographic Distance	0	4.09	0	4.09
Sample Size	0	1.64	0.231	1.87
PC1	0	0.171	2.17	2.34
PC2	1.41	0	0	1.41
Host Guild				
Gradient	**I-Spline Coefficients**			**Sum of Coefficients**
	1	**2**	**3**	
Geographic Distance	0.00973	0	0	0.00973
Sample Size	0	0.713	0.414	1.13
PC1	0	1.45	0	1.45
PC2	0.372	0	0	0.372
Host β-diversity	0	1.20	0.917	2.12

Table 4.3. The principal component (PC) axes for each generalized dissimilarity model (GDM), used to control for collinearity between the climate variables (mean annual temperature, MAT; annual temperature range, ATR; annual precipitation, AP; annual precipitation range, APR) for infracommunity, component community, and host guild analyses.

Infracommunity				
	PC1	**PC2**	**PC3**	**PC4**
MAT	-0.457	-0.751	0.201	0.432
ATR	0.531	0.190	0.496	0.661
AP	-0.510	0.365	0.738	-0.249
APR	-0.500	0.517	-0.411	0.561
Cumulative Proportion	0.828	0.959	0.990	1.00
Component Community				
	PC1	**PC2**	**PC3**	**PC4**
MAT	0.464	-0.762	0.329	0.311
ATR	-0.524	0.174	0.541	0.635
AP	0.499	0.475	0.666	-0.286
APR	0.511	0.405	-0.394	0.648
Cumulative Proportion	0.875	0.978	0.996	1.00
Host Guild				
	PC1	**PC2**	**PC3**	**PC4**
MAT	-0.460	-0.779	-0.297	-0.304
ATR	0.523	0.148	-0.620	-0.566
AP	-0.507	0.410	-0.664	0.366
APR	-0.507	0.450	0.294	-0.674
Cumulative Proportion	0.877	0.979	0.994	1.00

Table 4.4. The null deviance, generalized dissimilarity model (GDM) deviance, and the percent deviance explained by each GDM model at the infracommunity, component community and host guild scales.

	Infracommunity	*Component Community*	*Host Guild*
Null Deviance	42977.39	116.42	1.82
GDM Deviance	31121.64	76.83	0.94
% Deviance Explained	27.59	34.01	48.29

Around 48% of the deviance was explained by the host guild GDM (Table 4.4). Host β-diversity explained the largest amount of turnover, followed by PC1, sample size, PC2, and geographic distance (Table 4.2). A low amount of turnover was associated with geographic distance, and the rate of change along this gradient appears to be zero (Figure 4.3A) although the rate of species turnover increased with increasing host sample size (Figure 4.3B). The greatest rate of change in turnover (i.e., steepest slope) was associated with intermediate measurements of MAT, ATR, AP, and APR on PC1 (Figure 4.3C) and a small increase in the rate of change is also associated with higher MAT and lower AP and APR on PC2 (Figure 4.3D). Increasing host β-diversity was accompanied by an increasing rate of change in turnover (Figure 4.3E).

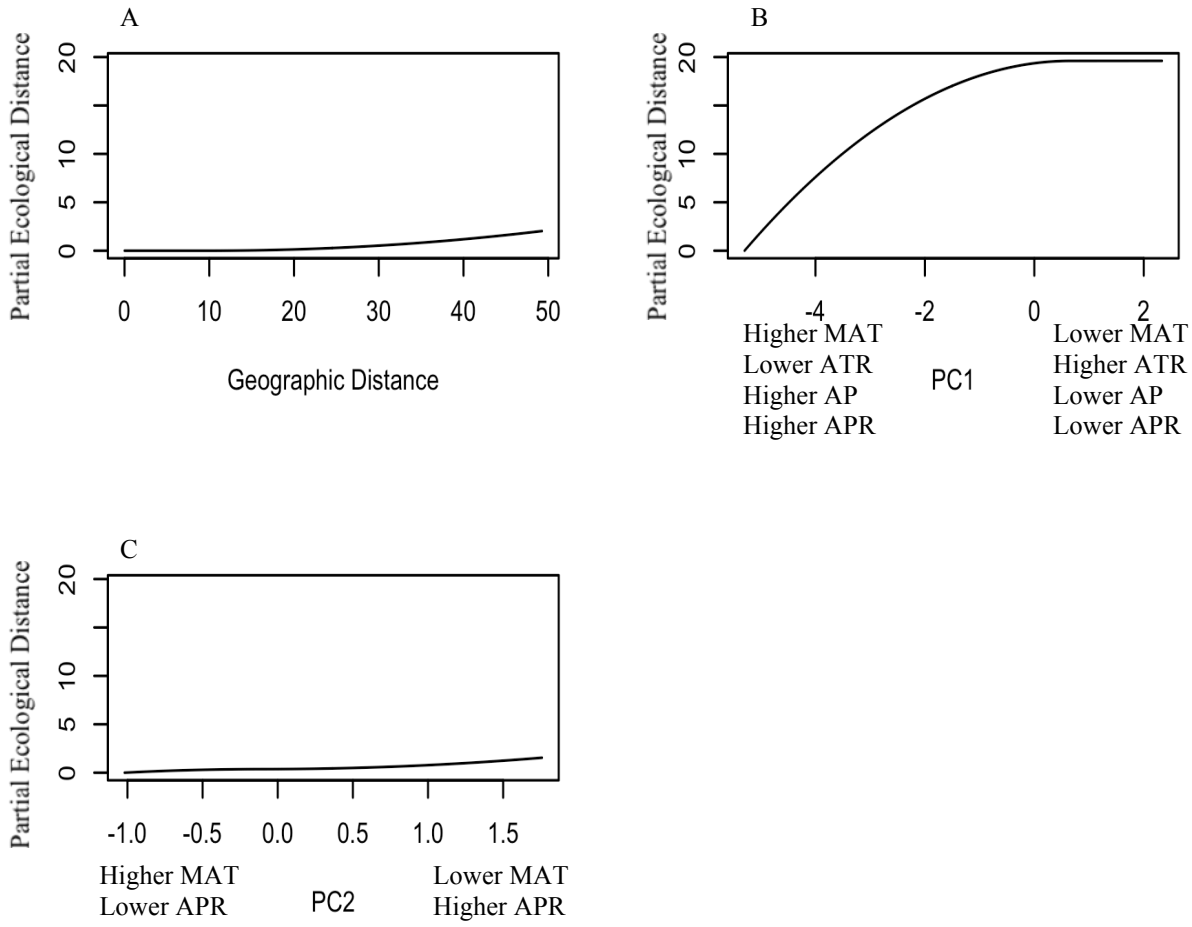

Figure 4.1. For the generalized dissimilarity model (GDM) analyzing β-diversity across all infracommunities. The fitted I-splines of each predictor variable: A) geographic distance, B) PC1, and C) PC2, where the maximum height of the I-splines represents the total amount of helminth species turnover associated with each gradient while holding all other variables constant (i.e., the partial ecological distance) and the slope represents the rate of helminth species turnover, which can change along the gradient. Relationships between PC1 and PC2 and the climate variables are shown in Table 4.2. Abbreviations for climate variables are as follows: MAT - mean annual temperature; ATR - annual temperature range; AP - annual precipitation; APR - annual precipitation range.

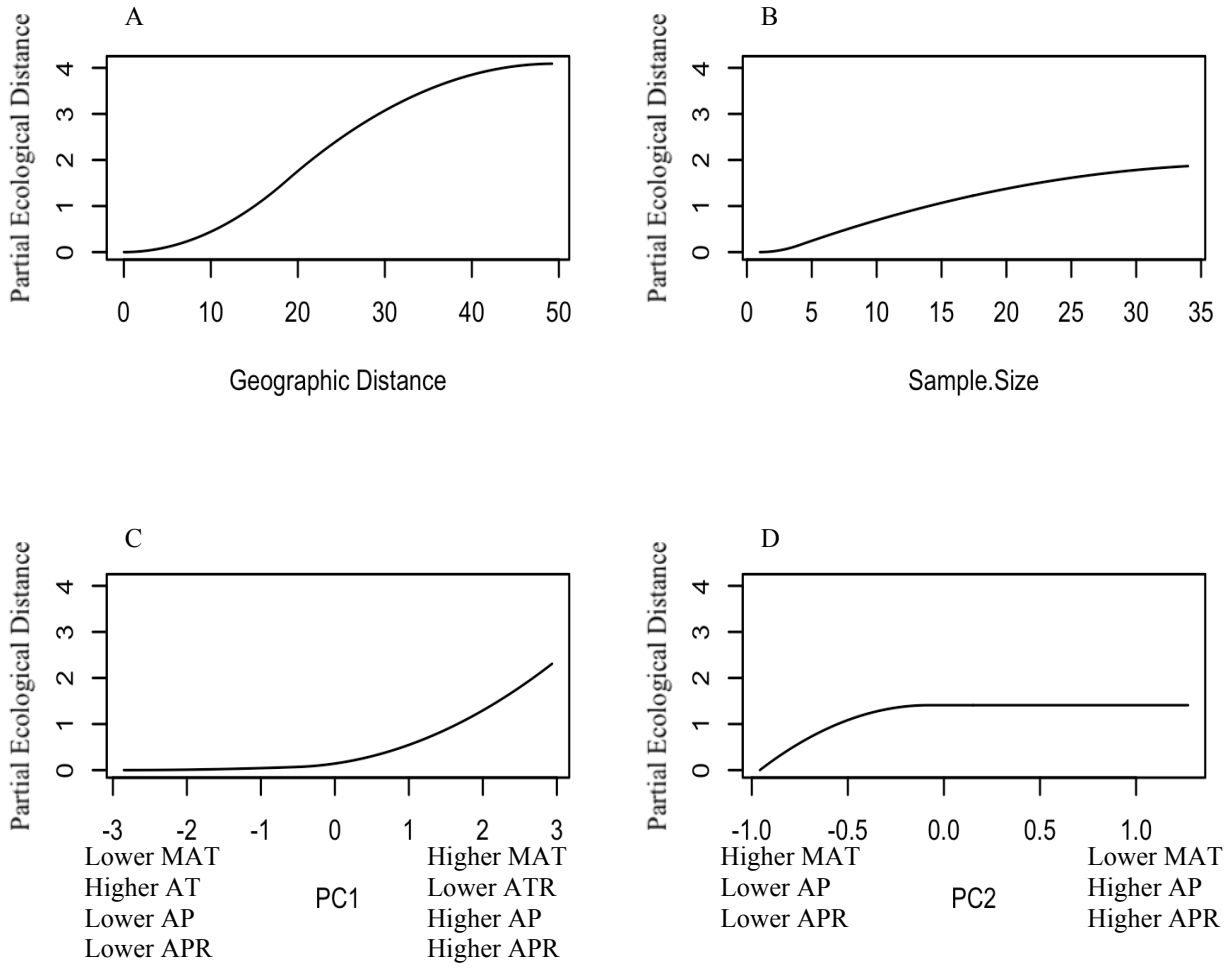

Figure 4.2. For the GDM analyzing β-diversity across all component communities. The fitted I-splines of each predictor variable: A) geographic distance, B) component community sample size, C) PC1, and D) PC2 , where the maximum height of the I-splines represents the total amount of helminth species turnover associated with each gradient while holding all other variables constant (i.e., the partial ecological distance) and the slope represents the rate of helminth species turnover, which can change along the gradient. Relationships between PC1 and PC2 and the climate variables are shown in Table 4.2. Abbreviations for climate variables are as follows: MAT - mean annual temperature; ATR - annual temperature range; AP - annual precipitation; APR - annual precipitation range.

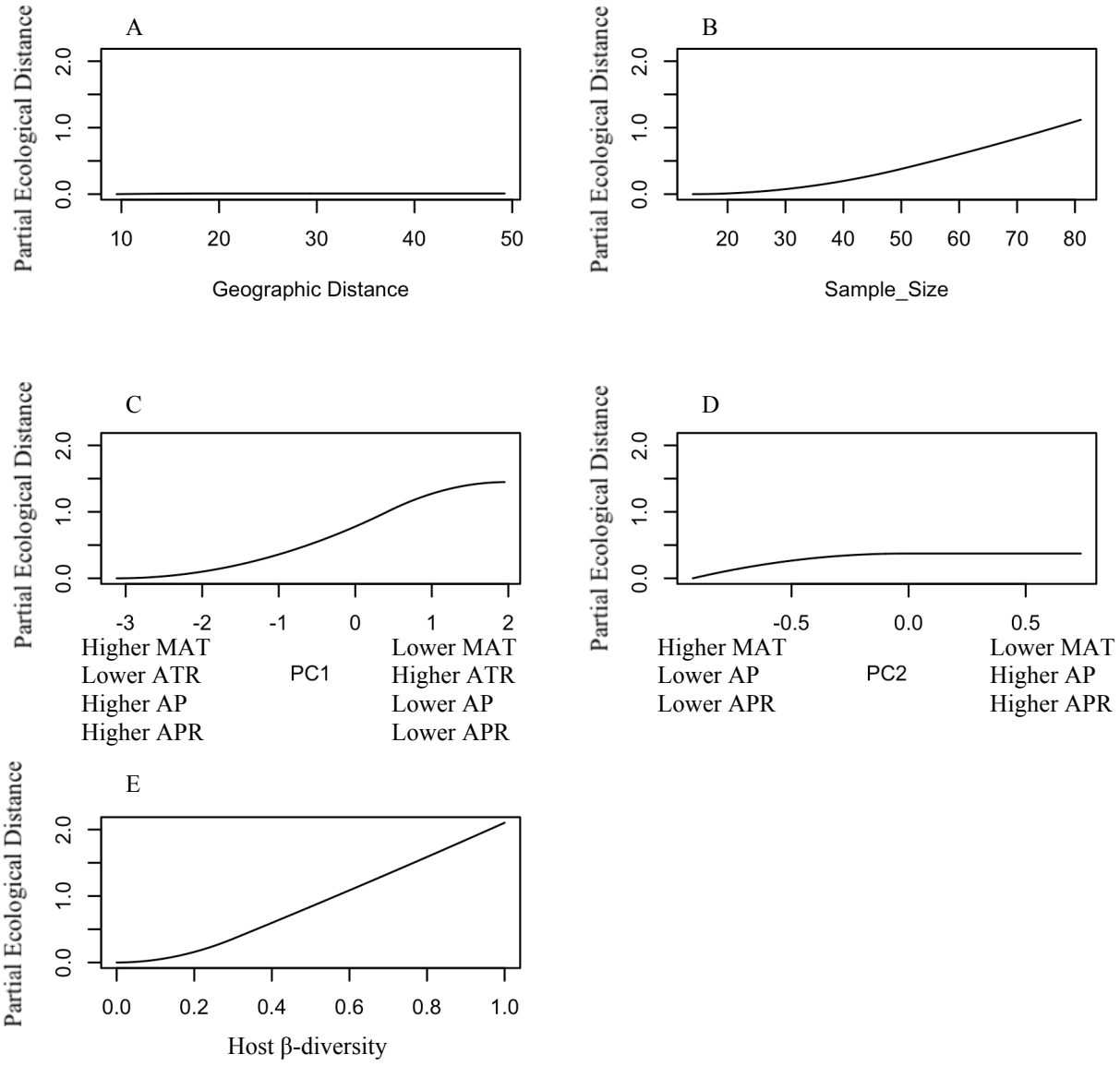

Figure 4.3. For the GDM analyzing β-diversity across the six host guilds. The fitted I-splines of each predictor variable: A) geographic distance, B) component community sample size, C) PC1, D) PC2, and E) host β-diversity, where the maximum height of the I-splines represents the total amount of helminth species turnover associated with each gradient while holding all other variables constant (i.e., the partial ecological distance) and the slope represents the rate of helminth species turnover, which can change along the gradient. Relationships between PC1 and PC2 and the climate variables are shown in Table 4.2. Abbreviations for climate variables are as follows: MAT - mean annual temperature; ATR - annual temperature range; AP - annual precipitation; APR - annual precipitation range.

4.4. Discussion

To understand macroecological patterns of diversity, β-diversity should be incorporated alongside traditional γ- and α-diversity metrics to investigate not only if species diversity changes across landscapes, but how specific changes in community composition may contribute to these patterns. Along a latitudinal gradient across North and Central America, helminth β-diversity was primarily driven by species turnover, or species replacement, and changes in geographic distance, climate, and host β-diversity were accompanied by changes in helminth community composition. Climate and host diversity, in particular, have been implicated in shaping latitudinal patterns of parasite diversity (Poulin 2014, Fine 2015). Given the large amounts of turnover associated with climate and host β-diversity, these factors are likely affecting patterns of helminth β-diversity of cricetid rodents, which in turn may contribute to the observed latitudinal gradients of parasite diversity (Preisser 2019, chapter two).

Climate was the best predictor of helminth β-diversity in the infracommunity GDM and the second best predictor in the component community and host guild GDMs, as it had the highest amount of helminth turnover associated with its gradient (tallest I-spline; Figures 4.2, 4.3, and 4.4, Table 4.2). In the infracommunity and component community models, the rate of change in helminth species turnover decreased with decreasing mean annual temperature, annual precipitation, and annual precipitation ranges and increasing annual temperature ranges (Figures 4.1 and 4.2). Given that these climate variables are closely tied to latitude (Preisser 2019, chapter two), with lower latitudes characterized by higher mean annual temperatures, annual precipitation, annual precipitation ranges, and lower annual temperature ranges, this relationship may be extended to suggest community composition changes at a greater rate (i.e., steeper slope) at lower latitudes than at higher latitudes. In the host guild GDM comparing the helminth

communities of each of the six localities, the rate of change was higher at intermediate climates, decreasing at both extremes, suggesting that the helminth turnover rate is highest at middle latitudes (Figure 4.3).

Host β-diversity was the best predictor of helminth species turnover in the host guild model (Table 4.2). Host communities shape helminth communities, and helminth community turnover is higher with higher host dissimilarity. These results are in congruence with previous work demonstrating a relationship between host β-diversity and parasite β-diversity (Maestri et al. 2017, Dallas & Poisot 2018, Williamson et al. 2019). Given that some parasite species are host specific (at the level of host species or a higher taxonomic level; Costello 2016), helminth community dissimilarity should be higher between than within host species. As expected, while parasite β-diversity varied within component communities, helminth communities were overall more similar within component communities than between them (across both multiple site and pairwise dissimilarity measurements) and helminth communities were mostly unique between both host species and sampled localities.

Geographic distance was the best predictor of helminth community dissimilarity in the component community model and the second best in the infracommunity model (Table 4.2), suggesting that these helminth communities decay in similarity with increasing geographic distance. These results support previous evidence of a distance-decay in community similarity in some parasitic taxa (Poulin 2003, Oliva & González 2005, Thieltges et al. 2009, Dallas & Poisot 2018). In the infracommunity GDM, the rate of change in composition was similar across shorter geographic distances and it increased at larger geographic distances (Figure 4.1C). Similarly, the rate of change increased with increasing distance until it plateaued at larger distances at the component community scale (Figure 4.2C).

Finally, in the component community and the host guild GDMs, sample size was associated with helminth turnover, with a positive rate of change with increasing sample sizes (Table 4.2; Figures 4.2 and 4.3). Parasite diversity generally increases with host sample size (Gregory 1990); larger sample sizes here are associated with larger variation in helminth community composition between hosts (i.e., higher β-diversity). While the full infracommunity was sampled for every rodent, host sample sizes varied between component communities and host guilds, and entire communities at every locality could not be sampled. Sampling of wild hosts is often limited by permit requirements, capture success, and time and budgetary restraints. However, with the appropriate methods to account for uneven sampling included in the analyses, studies with less than ideal sampling numbers can still be useful and inform future research. For example, in the estimations of total β-diversity, turnover, and nestedness, pairwise dissimilarity may better account for uneven sampling (Marion et al. 2017), although multiple site dissimilarity accounts for helminth species co-occurrence within more than two sites where pairwise dissimilarity does not (Baselga 2013). As both dissimilarity methods have their merits, I included the results for both methods. In general, results were similar between the methods, although pairwise dissimilarity often gave lower estimates of β-diversity, turnover, and nestedness. For in-depth comparisons between these methods, see Baselga (2010, 2013) and Marion et al. (2017).

Helminth species of cricetid rodents have been demonstrated to follow the latitudinal diversity gradient, or the trend of increasing species richness with decreasing latitude, across multiple scales of helminth community organization (Preisser 2019, chapter two). Along the same latitudinal gradient explored in chapter two, helminth β-diversity was driven by helminth species turnover between communities and was consistently high between infracommunities, component communities, and host guilds in the present study; these high community

dissimilarities may contribute to the observed latitudinal richness patterns. Additionally, climate was found to be significantly correlated with helminth species richness (Preisser 2019, chapter two) and associated with a large amount of helminth species turnover (present study), suggesting that climate may help shape biodiversity patterns of helminths of cricetid rodents on a continental scale. In addition to the climate and host-associated factors examined here and in chapter two, helminth diversity is also influenced by other environmental and biotic pressures. Helminths, like other parasites, have 'dual' environments, the traditional environment encountered by free-living species as well as the environment of their host's body (Maestri et al. 2017, Krasnov et al. 2019). Helminths interact with their hosts and with other parasites inside their hosts (Jolles et al. 2008, Dillman et al. 2012) and these interactions can be mediated by environmental factors (Møller 2010, Møller et al. 2013, Torchin et al. 2015). For example, in times of drought, water sources may be smaller and more scarce, and there may be higher densities of hosts around these concentrated water sources. Higher host densities can increase host exposure to parasites and parasite transmission rates (Arneberg et al. 1998) through increased contact between infected and uninfected hosts and may increase parasite densities while reducing intraspecific competition between parasites (Lagrue & Poulin 2015).

Additionally, many helminth species encounter and infect more than one host during their lifetime through the use of intermediate and definitive hosts; together these hosts influence helminth communities and contribute to overall biodiversity patterns. While I only investigated rodent β-diversity as a potential predictor of helminth β-diversity, incorporating the α-diversity and β-diversity of the other hosts involved in the helminths' life cycles would provide a more complete picture of the factors shaping helminth diversity. Intermediate hosts can affect the diversity and similarity of parasite communities in definitive hosts (Šimková et al. 2002) and

conversely definitive hosts can drive diversity patterns in intermediate hosts (Hechinger & Lafferty 2005). Rodents can serve as both intermediate and definitive hosts to different helminth species and their helminth communities may be shaped by the many different host species involved in the helminths' life cycles. Further work should incorporate additional factors, including data from other host taxa, to better understand the pressures that shape patterns of helminth diversity.

4.5. References

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5. CONCLUSIONS

In this study system, helminths followed the traditional latitudinal diversity gradient (LDG), demonstrating a negative relationship between diversity and latitude (i.e., increasing diversity with decreasing latitude). When helminth taxa were investigated independently, nematodes also had higher diversity closer to the equator, while trematodes showed no correlation with latitude; nematodes drive the latitudinal pattern when all helminths are combined. These relationships held up across different studies (Preisser 2019, chapter two), datasets (literature versus field-based), and geography (worldwide versus North and Central America), suggesting this may be a true pattern. Cestodes were significantly and positively correlated with latitude (i.e., reverse LDG of increasing species richness with increasing latitude) in the literature-based study but were not significantly correlated with latitude in the field collection-based study at any level of community organization. As only a subsample of the current cricetid rodent diversity was sampled as part of these studies, further sampling of the cestode fauna of cricetid rodents is needed to explore the latitudinal patterns of this taxa to determine the true relationship with latitude. This work demonstrates the importance of considering helminth groups separately when searching for macroecological patterns like the LDG; patterns of some helminth taxa may be masked when all helminths are combined.

Climate was significantly correlated with the species richness of each helminth group across studies and community scales. Overall, nematode species richness was higher in areas of higher annual precipitation, precipitation ranges, mean annual temperature, and lower annual temperature ranges; again nematodes drove the relationship with climate when all helminth taxa were combined. These climatic conditions typify lower latitudes. Cestodes displayed the reverse

relationship with climate, with higher species richness in areas of lower annual precipitation, precipitation ranges, mean annual temperature, and higher annual temperature ranges at two community scales. Trematode species richness was not significantly correlated with climate.

In the third chapter, I also determined that helminth community organization did not affect the detection of latitudinal patterns in this host-parasite system. Across the three levels of community organization (infracommunity, component community, and host guild), latitudinal patterns for all helminths and nematodes, cestodes, and trematodes were the same. These results suggest that parasite community scale may not be an important consideration in detecting latitudinal patterns. The same relationships between all helminth, nematode, and trematode species richness and climate were detected across community scales; cestode richness was only significantly correlated with climate at the infracommunity and component community scales. Again, additional sampling of the cestode fauna of these hosts is needed to further explore the relationship between cestode richness and climate and understand why community scale changes this correlation.

Across all levels of community organization in the field-based study, host body mass was significantly and positively related to total helminth, nematode, and cestode species richness, suggesting that these taxa have higher species richness in larger rodents. In the literature-based study, nematode species richness was significantly and negatively correlated with body mass. However, this relationship may be a consequence of the data used and may not reflect the true relationship. The average host body mass for each species was collected from an online database (PanTHERIA; Jones et al. 2009) and assigned to each component community; in the field-based study, individual hosts were weighed and the body mass measurement was specific to each helminth community, providing a more fine resolution for analyses. Trematode species richness

was never significantly correlated with host body mass. Host diet was only explored in the literature-based study; cestode species richness was higher in more herbivorous rodents, while trematode species richness was higher in more carnivorous/insectivorous rodents.

Although both climate and host-associated factors were significantly correlated with helminth species richness, the specific mechanisms underlying these patterns are unknown. To explore the potential effects of climate and hosts on helminth communities and how changes in these communities may contribute to latitudinal patterns, I explored how helminth communities vary along geographic and ecological gradients using the data from the field-based study. In this study system, β-diversity, or the changes in helminth species composition between communities (i.e., community dissimilarity), is primarily driven by species turnover (i.e., loss of some species and gain of others) rather than nestedness (i.e., smaller communities are subsets of more species-rich assemblages) across all levels of community organization. Geographic distance, climate, and host β-diversity all potentially affect helminth β-diversity, with factors varying in importance across the different levels of community organization and along their gradients. Overall, these results suggest that climate and host-associated factors may help shape biodiversity patterns of helminths of cricetid rodents on a continental scale, with helminth species turnover across communities potentially contributing to the observed latitudinal gradients of helminth diversity.

In conclusion, helminth taxa should be analyzed independently when investigating macroecological patterns like the LDG, as combining the taxa may obscure the different patterns of each group; the mixed latitudinal patterns found across previous helminth LDG studies may in part be a consequence of grouping these diverse taxa together. In this system, all helminths and nematodes had higher diversity at lower latitudes, while trematodes were not correlated with latitude; more data on the helminth fauna of cricetid hosts is needed to confirm these results and

further investigate latitudinal patterns of cestodes, as cestodes had mixed patterns across the two studies. Community scale may not affect the detection of latitudinal diversity patterns. Helminth community composition changes with geographic distance, climatic conditions, and host communities; rates of helminth turnover are higher at lower latitudes, and this may contribute to latitudinal gradients of helminth diversity. Climate was correlated with both helminth species richness and β-diversity, suggesting that climate may help shape latitudinal patterns of helminth diversity as it is suggested to do for free-living taxa (Willig et al. 2003, Mannion et al. 2014, Fine 2015). Future work should focus on the specific mechanisms behind the correlations between climate and helminth diversity.

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APPENDIX 2.1

Table A2.1. The number of surveys and the parts of the body dissected for the collection of helminth species richness (HSR) for each host species sampled.

Host Species	**Number of Surveys**	**Dissections**			
		Whole Body	**Alimentary Tract**	**Alimentary Tract + Some Organs**	**Not Specified**
Akodon azarae	2	1	0	1	0
Akodon cursor	1	0	0	1	0
Akodon montensis	2	0	0	2	0
Arvicola amphibius	5	1	0	2	2
Arvicola scherman	1	0	0	1	0
Chionomys nivalis	1	0	0	0	1
Cricetulus migratorius	1	0	0	1	0
Cricetus cricetus	1	0	0	1	0
Deltamys kempi	1	1	0	0	0
Lemmus lemmus	2	0	2	0	0
Lemmus sibiricus	2	0	2	0	0
Lemmus trimucronatus	1	0	1	0	0
Microtus agrestis	10	2	0	5	3
Microtus arvalis	5	1	0	0	4
Microtus breweri	1	0	0	0	1
Microtus cabrerae	1	0	0	0	1
Microtus longicaudus	3	3	0	0	0
Microtus mexicanus	1	0	1	0	0
Microtus miurus	1	0	0	1	0
Microtus montanus	4	3	1	0	0
Microtus montebelli	1	1	0	0	0
Microtus oeconomus	5	1	0	4	0
Microtus pennsylvanicus	3	3	0	0	0
Microtus richardsoni	1	1	0	0	0
Microtus socialis	1	1	0	0	0
Microtus subterraneus	2	0	0	0	2
Myodes andersoni	1	0	0	0	1
Myodes gapperi	2	1	0	1	0
Myodes glareolus	26	6	8	7	5
Myodes imaizumii	1	0.5*	0.5*	0	0
Myodes rufocanus	5	1	0	4	0
Myodes rutilus	2	0	0	2	0
Myodes smithii	1	0	0	0	1
Necromys lasiurus	1	0	1	0	0
Nectomys squamipes	2	1	0	0	1
Neofiber alleni	1	0	0	0	1
Neotoma cinerea	1	0	0	0	1
Neotoma floridana	2	0	1	0	1
Neotoma micropus	1	1	0	0	0
Oligoryzomys flavescens	1	1	0	0	0
Oligoryzomys nigripes	3	1	0	2	0
Ondatra zibethicus	22	4	3	3	12
Onychomys leucogaster	1	1	0	0	0
Oryzomys angouya	1	0	0	1	0

Table A2.1. (Continued)					
Host Species	**Number of Surveys**	**Dissections**			
		Whole Body	**Alimentary Tract**	**Alimentary Tract + Some Organs**	**Not Specified**
Oryzomys couesi	1	0	1	0	0
Oryzomys melanotis	1	0	1	0	0
Oryzomys palustris	2	2	0	0	0
Oryzomys russatus	1	0	0	1	0
Oxymycterus rufus	1	1	0	0	0
Peromyscus gossypinus	1	1	0	0	0
Peromyscus leucopus	5	3	1	1	0
Peromyscus maniculatus	8	2	1	3	2
Peromyscus pectoralis	1	0	0	1	0
Peromyscus polionotus	1	1	0	0	0
Phenacomys intermedius	1	1	0	0	0
Podomys floridanus	2	1	0	1	0
Reithrodontomys megalotis	1	1	0	0	0
Scapteromys aquaticus	1	1	0	0	0
Sigmodon hispidus	14	6	2	2	4
Thaptomys nigrita	1	0	0	1	0
TOTAL	175	56.5	26.5	49	43

*In one survey, whole body dissections were conducted for half of the rodents, while the small intestine was searched in the other individuals.

Table A2.2. The range of HSR and nematode, cestode, and trematode species richness across all surveys for each host species sampled.

Host Species	**HSR Range (Per survey)**	**Nematode Species Richness**	**Cestode Species Richness**	**Trematode Species Richness**
Akodon azarae	5-7	3-5	0-2	0-2
Akodon cursor	9	7	1	1
Akodon montensis	8-12	6-9	1	1-2
Arvicola amphibius	2-25	0-7	1-13	0-5
Arvicola scherman	11	4	3	4
Chionomys nivalis	6	2	4	0
Cricetulus migratorius	7	5	2	0
Cricetus cricetus	6	1	5	0
Deltamys kempi	3	1	1	1
Lemmus lemmus	1-2	0	1-2	0
Lemmus sibiricus	2-4	0-1	2-3	0
Lemmus trimucronatus	3	1	2	0
Microtus agrestis	1-11	1-7	0-8	0-1
Microtus arvalis	6-18	1-8	2-8	0-2
Microtus breweri	2	0	2	0
Microtus cabrerae	6	1	4	1
Microtus longicaudus	2-9	1-6	1-3	0
Microtus mexicanus	3	1	2	0
Microtus miurus	10	3	6	1

Table A2.2. (Continued)

Host Species	HSR Range (Per survey)	Nematode Species Richness	Cestode Species Richness	Trematode Species Richness
Microtus montanus	1-10	1-3	0-6	0-1
Microtus montebelli	6	5	1	0
Microtus oeconomus	4-7	0-3	2-5	0-1
Microtus pennsylvanicus	4-8	1-2	3-4	0-2
Microtus richardsoni	8	4	4	0
Microtus socialis	7	5	2	0
Microtus subterraneus	2-4	0-2	2	0
Myodes andersoni	8	5	3	0
Myodes gapperi	4-6	2-3	2-3	0
Myodes glareolus	2-30	1-15	0-12	0-3
Myodes imaizumii	4	2	2	0
Myodes rufocanus	4-12	1-8	1-5	0-1
Myodes rutilus	5-6	3-4	2	0
Myodes smithii	11	6	4	1
Necromys lasiurus	2	2	0	0
Nectomys squamipes	7	4-5	1	1-2
Neofiber alleni	7	6	1	0
Neotoma cinerea	7	2	5	0
Neotoma floridana	3-5	3	0-2	0
Neotoma micropus	8	4	2	2
Oligoryzomys flavescens	6	5	0	1
Oligoryzomys nigripes	4-12	3-8	0-3	0-1
Ondatra zibethicus	1-17	1-5	0-4	1-10
Onychomys leucogaster	4	2	2	0
Oryzomys angouya	5	5	0	0
Oryzomys couesi	3	2	1	0
Oryzomys melanotis	4	3	1	0
Oryzomys palustris	4-45	3-20	1-4	0-21
Oryzomys russatus	7	7	0	0
Oxymycterus rufus	8	4	1	3
Peromyscus gossypinus	13	9	2	2
Peromyscus leucopus	2-9	1-4	0-3	0-4
Peromyscus maniculatus	1-6	1-4	0-3	0-2
Peromyscus pectoralis	4	1	1	2
Peromyscus polionotus	8	6	1	1
Phenacomys intermedius	2	1	1	0
Podomys floridanus	8-14	5-11	3	0
Reithrodontomys megalotis	3	1	2	0
Scapteromys aquaticus	11	7	1	3
Sigmodon hispidus	3-25*	1-2	1-6	0-7
Thaptomys nigrita	4	4	0	0

*One of the surveys for *Sigmodon hispidus* did not identify two of the parasite species collected to the level of nematode, cestode, or trematode, so this survey was excluded from analyses of each parasite type.

Table A2.3. Estimations of Pagel's λ in helminth (HSR), nematode (NSR), cestode (CSR), and trematode (TSR) richness data, in the latitudinal models, and in the models with both biotic variables.

	HSR	NSR	CSR	TSR
λ of richness data	0.03492978 *P* = 0.825588	0.4328859 *P* = 0.09159094	0.4139217 *P* = 0.00020729	0.4151372 *P* = 0.02654237
λ from latitudinal models	0	0	0.136	0
λ from models with biotic variables	0	0	0.025	0

Table A2.4. Non-phylogenetic (NP) GLMs with cestode and trematode richness. 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 - residual deviance/null deviance). Bolded rows represent significant variables in the models.

Final Model	Predictor	Coefficient ±SE	t Value	*P* Value	Effect	R^2
NP Latitudinal Model Cestodes	**Intercept**	**-0.186005 ±0.059273**	**-3.138**	**0.00200****	-	0.0586
	Latitude	**0.004187 ±0.001280**	**3.271**	**0.00129****	+	
NP Latitudinal Model Trematodes	Intercept	0.112654 ±0.077205	1.459	0.146	+	0.0133
	Latitude	-0.002536 ±0.001667	-1.521	0.130	-	
NP Model Cestodes	Intercept	-0.07624 ±0.07862	-0.970	0.33354	-	0.1528
	PC1	**-0.02479 ±0.01106**	**-2.241**	**0.02630***	-	
	PC3	**0.04853 ±0.02227**	**2.180**	**0.03066***	+	
	Mass	-0.05370 ±0.02969	-1.808	0.07234	-	
	Diet	**0.14655 ±0.05457**	**2.685**	**0.00797****	+	
NP Model Trematodes	**Intercept**	**-0.39577 ±0.08242**	**-4.802**	**3.43e-06*****	-	0.3535
	PC4	**0.07541 ±0.03329**	**2.265**	**0.0248***	+	
	Mass	**0.28289 ±0.03328**	**8.501**	**9.24e-15*****	+	
	Diet	-0.09035 ±0.05252	-1.720	0.0872	-	

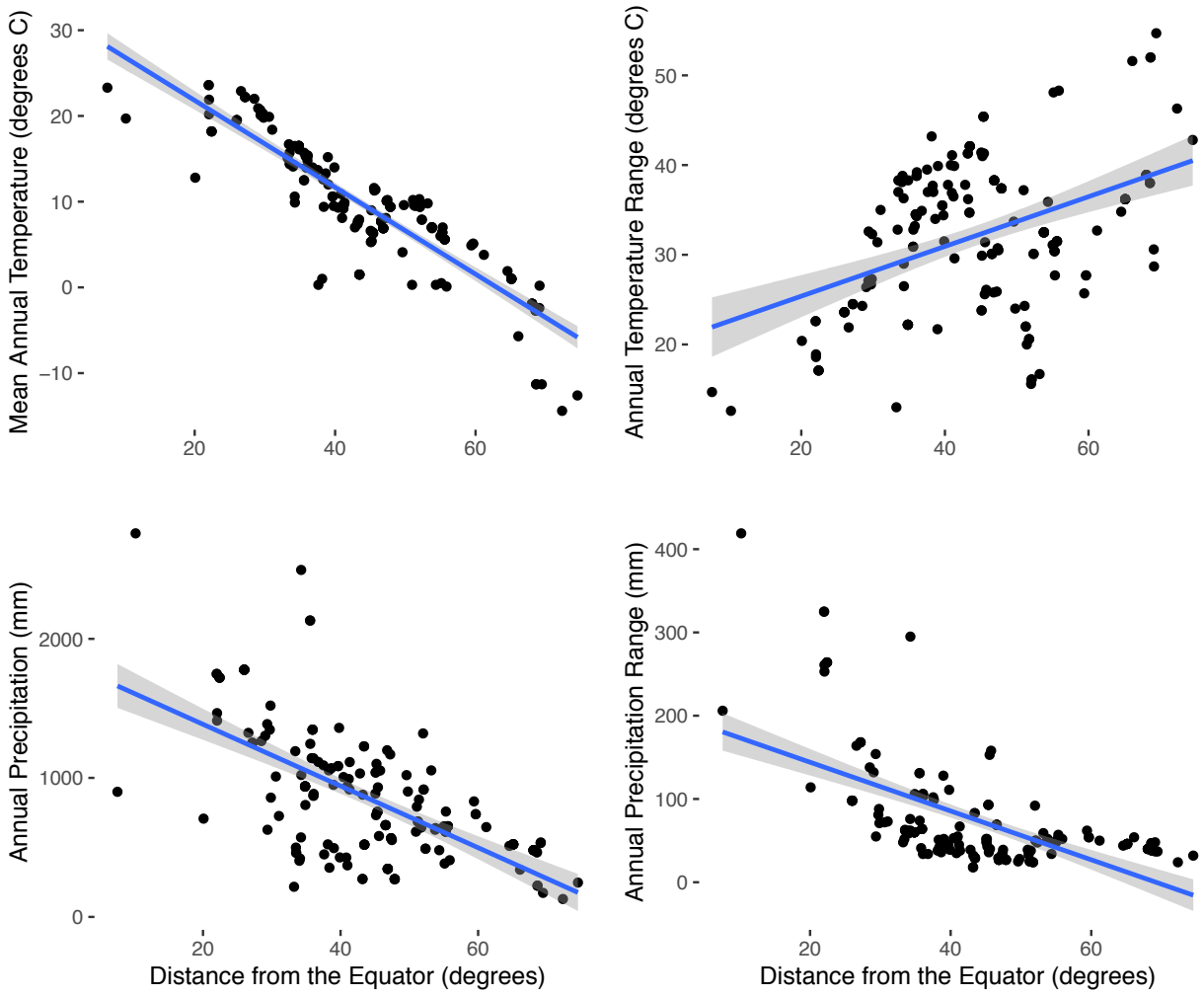

Figure A2.1. Relationships between distance from the equator and the four climatic factors analyzed with HSR: mean annual temperature (MAT), annual precipitation (AP), annual precipitation range (APR), and annual temperature range (ATR). Variables were not transformed before plotting. All climate data were downloaded from WorldClim (Hijmans et al. 2005).

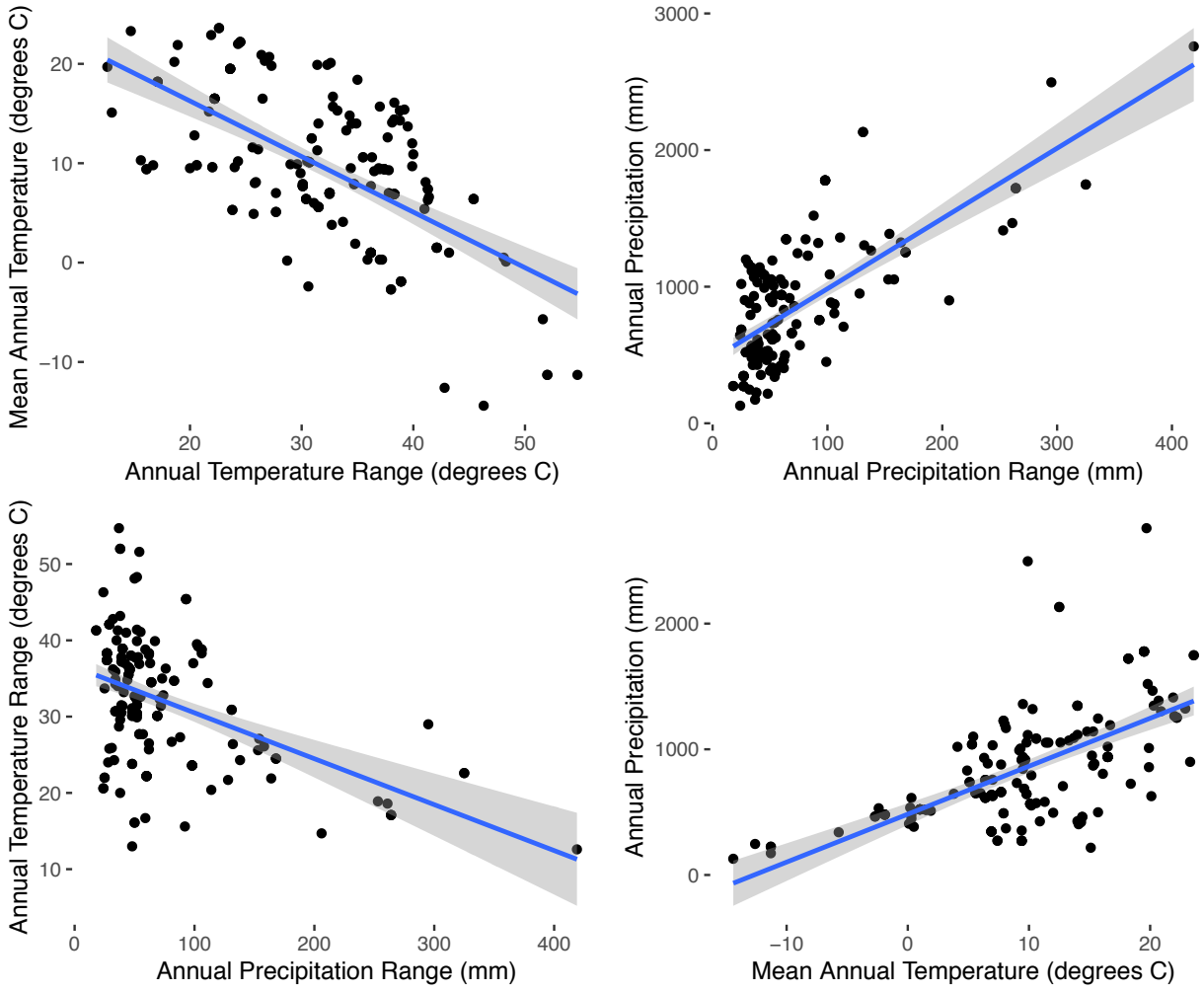

Figure A2.2. Pairwise plots between climatic factors to visualize the collinearity between variables. Variables were not transformed before plotting. All climate data were downloaded from WorldClim (Hijmans et al. 2005).

Methods and Results

Phylogenetic Signal

Pagel's λ (Pagel 1999) was calculated in two ways to determine if there was a phylogenetic signal in the helminth richness data. A rooted rodent phylogeny with branch lengths was obtained from Fabre et al. (2012). This tree was trimmed to include only species of interest (i.e., species with parasite data in the literature) using the function 'drop.tip' in the package 'geiger' (Harmon et al. 2008). Polytomies were resolved randomly using the function 'multi2di' in the package 'ape' (Paradis et al. 2004). A single parasite survey was used for each host species (a limitation to using phylogenetic generalized least squares, or PGLS). If multiple parasite surveys were found for a single host species, the survey reporting the highest HSR, NSR, CSR, or TSR, for their respective analysis, was used; if multiple surveys reported the same species richness value, the survey with the largest sample size was used. Pagel's λ was first used to test

for a phylogenetic signal in HSR, NSR, CSR, and TSR and was calculated using the function 'phylosig' in the package 'phytools' (Revell & Reynolds 2012) using the edited phylogeny and species richness, controlled for sample size. Second, PGLS was employed using the function 'pgls' in the package 'caper' (Orme et al. 2018) to determine if there was a phylogenetic signal in the relationship between species richness and latitude or between species richness and biotic factors, as the phylogenetic signal in the regression may differ from the phylogenetic signal in the individual traits (Symonds & Blomberg 2014). See Table A3 for the results of the tests of phylogenetic signal. With a Pagel's λ of 0 or not significant for both HSR and NSR, there was no phylogenetic signal detected. Therefore, phylogenetic comparative methods were not used for analyses with HSR and NSR and parasite surveys were treated as independent without corrections for host phylogeny. With significant phylogenetic signals in the CSR and TSR data, phylogenetic comparative methods were used to explore the relationships between species richness and latitude and between species richness and abiotic and biotic variables.

Spatial Autocorrelation

To test if the data were spatially autocorrelated, Moran's I was calculated using the function 'Moran.I' in the package 'ape' (Paradis et al. 2004). To test for spatial autocorrelation in the residuals of the models, Moran's I was calculated using the function 'testSpatialAutocorrelation' in the package 'DHARMa' (Hartig 2018) for both Latitudinal Model 175 and a new GLM with HSR as the response variable and both latitude and longitude as the predictor variables. While the data were positively spatially autocorrelated (observed = 0.1106872, expected = -0.005747126, sd = 0.02594316, P = 7.187603e-06), the residuals of the two models were not spatially autocorrelated (Latitudinal Model 175: observed = -0.0130610, expected = -0.0057471, sd = 0.0128980, P = 0.5707; new model: observed = 0.0091471, expected = -0.0057471, sd = 0.0130460, P = 0.2536). The residuals of the non-phylogenetic Latitudinal Models Nematodes, Cestodes, and Trematodes were also not spatially autocorrelated (Nematodes: observed = -0.00067698, expected = -0.00578030, sd = 0.01033400, P = 0.6214; Cestodes: observed = 0.00025883, expected = -0.00578030, sd = 0.01240200, P = 0.6263; Trematodes: observed = 0.00055997, expected = -0.00578030, sd = 0.01087600, P = 0.5599). PGLS models were not supported in this test so latitudinal GLMs for the 60-record CSR and TSR datasets were run and used to test for spatial autocorrelation in the residuals; no spatial autocorrelation was detected (CSR: observed = -0.038293, expected = -0.016949, sd = 0.030346, P = 0.4819; TSR: observed = -0.038154, expected = -0.016949, sd = 0.025656, P = 0.4085). As no spatial autocorrelation was detected in any of the residuals, corrections to the data were not necessary.

Pseudoreplication

To test if pseudoreplication significantly affected the models, as multiple, unique surveys were used per host species, species name was added as a variable in Model 175 (Table 2), with the species with the most surveys serving as the reference species. As there were no significant differences in HSR among species with one, few, and multiple surveys (P > 0.6 for all species comparisons), these models were interpreted without concern for pseudoreplication.

Differences in HSR by Dissection Type

To determine if surveys searching the alimentary tract or the whole body differed in the observed HSR, an analysis of variance was used to compare the mean HSR values of each dissection method (alimentary tract, alimentary tract with some other organs, whole body, and not specified). There was no significant difference between the means (F = 2.17, P = 0.0933).

APPENDIX 2.2

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