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World-Wide Body Size Patterns in Freshwater Fish by Geography, Size Class, Trophic Level, and Taxonomy

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World-wide body size patterns in freshwater fish by geography, size class, trophic level, and taxonomy

A dissertation submitted in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

By

Shishir Adhikari

M.S., Tribhuvan University, 2006

2015

Wright State University

WRIGHT STATE UNIVERSITY
GRADUATE SCHOOL

August 19, 2015

I HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER MY SUPERVISION BY Shishir Adhikari ENTITLED World-wide body size patterns in freshwater fish by geography, size class, trophic level, and taxonomy BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Doctor of Philosophy.

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ABSTRACT

Adhikari Shishir Ph.D., Environmental science Ph.D. program, Wright State University, 2015. World-wide body size patterns in freshwater fish by geography, size class, trophic level, and taxonomy.

The unifying themes of my thesis are patterns in world-wide freshwater fish body sizes and their underlying mechanisms. First, I explored Bergmann's rule in unprecedented detail, which states that body size is negatively correlated to temperature. Categorizing species by body size into quantiles and by trophic levels, I regressed the classes against latitude, temperature, seasonality, minimum temperature and habitable space. I found that Bergmann's rule applies to freshwater fish in general but the strength varies by size class and trophic levels. I concluded that Bergmann's rule in fish is driven by the exclusion of small fish from cold climate due to limits in energy storage and behavioral thermoregulation. Second, I investigated the relationships between extreme body size and species richness. Stressful environments promote an ecological similarity among species, reducing body size ranges and species richness. Thus, there may be a strong relationship between extreme body size and species richness. However, I found that only the size of the smallest species were strongly related to species richness. The observed strong relationship may be due to physiological constraints on the smallest species in stressful environments. The lack of relationship between the size of the largest

species and species richness may be due to the high dispersal ability of the largest species homogenizing body size across space and their relative insensitivity to harsh environments. Third, I examined body size and trophic level conservatism and similarity across species within a genus. Body size and trophic level are evolutionary conserved traits; thus I expected high body size conservatism, but due to constraints imposed on extreme body sizes and trophic levels, body size conservatism may vary for all body size classes and trophic levels. I found conservatism of these traits to be substantially lower in freshwater fish than mammals. Divergence in body size among closely related species that are very small or large may allow those species to reduce constraints due to extreme size and to coexist with other species, leading to lower body size conservatism than in the medium size class. Relatively low body size conservatism and high similarity in body size among families and genera, suggest that freshwater fish body sizes are, in contrast to mammals, highly plastic and responsive to environmental variations. Trophic levels were more conserved than body size. Trophic adaptation connects species by their function and physiology. In addition, it also demonstrates the direct interaction between species and their community and ecosystem processes.

Table of Contents

Chapter 1	1
1 Background Information	1
1.1 Introduction	1
1.2 Data and data sources	5
Chapter 2	8
2 Global geography of body size in freshwater fishes: revisiting Bergmann's rule	8
2.1 Abstract	8
2.2 Introduction	9
2.3 Materials and Methods	14
2.3.1 Latitudinal analysis	14
2.3.2 Randomization tests	15
2.3.3 Environmental predictors	15
2.3.4 Trophic level analysis	16
2.4 Results	17
2.4.1 Body size latitudinal pattern	17
2.4.2 Body size decile analysis	18
2.4.3 Environmental predictors	22
2.5 Discussion	26
Chapter 3	34
3 The size of the smallest species in an assemblage is tightly linked to richness in worldwide fish distributions	34

3.1	Abstract	34
3.2	Introduction	35
3.3	Methods	39
3.3.1	Area correction	39
3.3.2	Randomization tests.....	39
3.4	Results	42
3.4.1	Simulation I	44
3.4.2	Simulation II.....	45
3.4.3	Simulation III.....	47
3.5	Discussion	47
Chapter 4		54
4	Body size and trophic level conservatism among freshwater fishes of the world	54
4.1	Abstract	54
4.2	Introduction	55
4.3	Methods.....	59
4.3.1	Statistical analyses.....	60
4.4	Results	63
4.4.1	Body size conservatism (congener regression)	63
4.4.2	Body size similarity across taxonomic hierarchy	66
4.5	Discussion	68
Chapter 5		73
5	Phylogenetic caveats	73
Conclusion		76
Appendix A.....		79
Bibliography		81

List of Figures

Figure 1.1: Freshwater ecoregions of the world.	7
Figure 2.1: Conceptual diagram of the magnitude of effect of body size change for small vs. large fish.....	12
Figure 2.2: Regression of median body size in freshwater fish ecoregional assemblages against absolute latitude.....	18
Figure 2.3: Global distribution of geometric mean body size (cm) by ecoregion	20
Figure 2.4: Latitudinal patterns of freshwater fish body size as a function of size decile within ecoregions of the world.	21
Figure 2.5: Slopes from regressions of body size against latitude, plotted as a function of decile within the frequency distribution of species within each ecoregion.	22
Figure 2.6: Variable importance from a Random Forest model	24
Figure 2.7: Slope coefficient of median body size against latitude for freshwater fishes representing four trophic groups.....	25
Figure 3.1: Conceptual diagram of possible effects of abiotic filters	38
Figure 3.2: Regression between extreme body sizes and species richness by ecoregion.	43
Figure 3.3: Results from the first simulation model keeping the empirical number of species per ecoregion but randomly selecting species from a global species pool.	44
Figure 3.4: Results from the second simulation using a latitudinal species pool.	46

Figure 3.5: Simulated R^2 and slopes obtained from the linear regression between species richness vs the smallest body size of species.	47
Figure 4.1: Body size conservatism at species level.	64
Figure 4.2: Estimation of body size conservatism for discrete logarithmic size categories for each trophic level and within genus.	65
Figure 4.3: Variance in body size vs. the number of species within genus.	66
Figure 4.4: Phylogenetic autocorrelation (Moran's I).	67

List of Tables

Table 2.1: Univariate least squares regression analyses of median body size as a function of various environmental variables.	23
Table 4.1: Results from nested mixed model ANOVA of overall variation in body size, variation in body sizes by trophic level, and overall variation in trophic level across the taxonomic hierarchy.	67

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Chapter 1

1 Background Information

1.1 Introduction

Understanding the pattern and processes that shape species assemblages is one of the fundamental challenges in ecology. In recent years, macroecological studies have increasingly addressed those challenges at large temporal, spatial, and taxonomic scale. Examining patterns emerging at large scales might help to understand the general ecological and evolutionary mechanisms governing organisms, populations, and ecosystems. Understanding those mechanisms and processes was a daunting task in absence of comprehensive databases and spatial coverage. However, now that biologists/ecologists have gathered large amounts of data covering a large spatial extents insight can be gained at large scales. In this study, I used species traits such as body size and trophic level to reveal large scale ecological patterns for freshwater fishes.

There are several traits such as body size, beak size, egg size, frost tolerance, and leaf area which are considered important dimension of a species' niche, which allow differentiation and therefore species coexist through reduce competition (Enquist et al., 2015). Body size may be one of the most important traits. Metabolic scaling theory, which explains many ecological patterns, identifies body size as a critical driver of

ecological and evolutionary patterns and processes (Gillooly et al., 2001; Brown et al., 2004). In fact, body size is related to almost every aspects of an organism such as morphology, physiology, ecology and speciation (Stanley, 1973; Cardillo et al., 2005; Olden et al., 2007). The study of body sizes may reveal the mechanisms and forces that structure biological diversity (Grime, 2006; Stegen et al., 2009) and may thus increase the generality and predictability of ecological models (Diaz et al., 2004).

Studies on body sizes have led to the formation of several large-scale biogeographic rules and mechanistic models. Biogeographic rules such as Foster's rule, Cope's rule, and Bergmann's rule are based on body size and its relationship to numerous biotic and abiotic factors (Bergmann, 1847; Cope, 1887; Foster, 1964). Foster's rule, also known as the island rule, states that species get smaller and bigger depending upon resource availability. Cope's rule explains the existence of many large-bodied species, because the selection generally favors large body sizes. Bergmann's rule suggests that body size is negatively correlated to temperature among groups of closely related animals.

There are different mechanistic models that describe the distribution of body size. Those models are not mutually exclusive and have faced much criticism. 1) Given that the body size distribution of species is right-skewed for many species, Brown et al., (1993) suggested that there is a lower and upper limit on body size due to physiological or energetic constraints. Species tend to be at optimum size to reduce those costs. However, Kozlowski and Weiner (1997) and Lovegrove and Haines (2004) criticized the idea of

single optimal size per taxon and suggested that every species has different optimal sizes due to the trade-offs between productivity and mortality. 2) Speciation and extinction processes can shape the body size distribution (Dial & Marzluff, 1988; Johst et al., 2002; Maurer et al., 1992). Due to short generation time and quick maturation, speciation events are faster in smaller species leading to high species richness. 3) Similarly, small species are numerous because many small individuals can fit in a given space. Number of individuals is positively related to species richness (Hutchinson & MacArthur, 1959; May, 1988). Although there are many models suggesting that body size patterns are consistent among taxonomic groups, mechanisms generating those models are still under scrutiny. The decisive study about the mechanism underlying body size distribution is yet to come. However, frequency body size distribution of species has led to a consensus that the smallest body size species are not numerous. Species richness peaks at intermediate body sizes.

As discussed above, body sizes have been linked to several biogeographic rules, mechanistic models and evolutionary processes. In this study, I explicitly examine Bergmann's rule for freshwater fish in chapter 2. Bergmann's rule is highly supported in homeotherms, but controversial in poikilotherms (Angilletta et al., 2004; Ashton & Feldman, 2003; James, 1970; Rensch, 1938). Especially, the mechanisms presumably underlying Bergmann's rule are controversial, given that some authors suggested poikilotherms also follow the rule (Blanchet et al., 2010; Fisher et al., 2010; Knouft, 2004; Lindsey, 1966; Ray, 1960; Van Voorhies, 1996). But, homeotherms and poikilotherms differ strongly in physiology and energetics of heat loss and heat gain. The original Bergmann's rule suggested that the lower surface area to volume ratio in large

species limits heat loss and enables energy conservation in cold climates. This may not be applicable to poikilotherms because poikilotherms do not keep their body temperature constant and thus do not necessarily need to expend more energy at lower temperatures. Therefore, I examined Bergmann's rule and its complexity in fish. I explored the relationship between body size and latitude for all species, endemic species and within trophic and body size classes.

In Chapter 3, I examined the relationship between body size and species richness. Recently, trait based theory suggests that abiotic filters (harsh environments) affect range and variance of species' traits (Enquist et al., 2015). Abiotic filters can create similarities in traits by excluding species reducing the range and variation in body size, and also species richness (Keddy, 1992; Weiher & Keddy, 2001; Kraft & Ackerly, 2010). Thus, I expect that the extreme sizes have a strong relationship to species richness due to the common factors controlling them. Assuming that there is an optimal size (Brown et al., 1993) and given that the smallest and largest species are furthest away from the optimal size, they might be more vulnerable to unfavorable environments and thus the first to be excluded by unfavorable environments. Thus, I hypothesized that extreme sizes have a strong relationship to species richness due to the common factors controlling them.

In chapter 4, I investigated the relationship between body size and taxonomy. As many phenotypic traits, body size and trophic levels are expected to be conserved among closely related species (Felsenstein, 1985; Freckleton et al., 2002). However, small changes in body size may provide species with opportunity to escape competition and predation and allow to coexist (Griffiths, 1986; Polo & Carrascal, 1999). Smith et al., (2004) found a strong conservatism in body size across the taxonomic hierarchy in

mammals. They found a strong congruence in body size for species within genera. Such congruence in body size among species could be the result of inheritance and/or constant ecological pressures. Body size is a conserved trait, but the body size conservatism could vary itself with body size as different body sizes experience different constraints and selection pressures. For example, smaller and larger species are highly constrained by their body sizes due to the lower and upper limits imposed on body size. Extreme sizes are constrained by physiology and energetic requirements. These constraints may act as a directional selection force and lead to relatively low body size conservatism. Among trophic levels, herbivores and top predators require more specialized and complicated physiological and size adaptations leading to higher body size conservatism than in omnivores and consumers.

In summary, the main focus of this study is body size of freshwater fish. I investigated the distribution of body size from several different perspectives: In chapter 2 and 3 across space, while in chapter 3 across taxonomy. In addition to the interesting findings of this study, the novelty of this study also lies in its use of an unprecedentedly comprehensive freshwater fish dataset.

1.2 Data and data sources

I adopted the biogeography of freshwater fish species developed for delineating Freshwater Ecoregions of the World (FEOW; Abell et al., 2008), and merged it with species trait data from FishBase (Froese and Pauly, 2011). Taxonomic conflicts were resolved using the online Catalogue of Fishes (Eschmeyer, 2015). My spatial units were FEOW's 449 ecoregional polygons selected to contain relatively homogenous fish assemblages and environmental conditions relative to neighboring ecoregions.

Ecoregions (Figure 1.1) cover almost all non-marine part of the Earth, exclusive of Antarctica, Greenland, and some small islands. Ecoregions vary widely in size, ranging from 23 km² to 4,539,429 km² with an average of 311,605 km². Ecoregions were delineated primarily based on two characteristics: First, ecoregions with tectonic activity and high species turn over are smaller in sizes. Second, ecoregions with glaciation history are larger in sizes (Abell et al., 2008).

I excluded diadromous species as well as ecoregions dominated by islands or lakes because these species and ecoregions are governed by different processes than purely freshwater, mainland faunas. Finally, I excluded Australian ecoregions because most of its freshwater fishes are recently derived from marine ancestors. The resulting database has 27,929 individual occurrences of 9613 species (85% of all freshwater fish species) in 344 ecoregions, of which 4609 species are considered endemic to only one ecoregion. For each species, I extracted the maximum total length from FishBase, which I log₁₀-transformed for analyses. This maximum total length correlates well with overall body size (Kosnik et al., 2006), and is the only size metric available for all species. Hereafter, I will refer to this maximum total length simply as 'body size'.

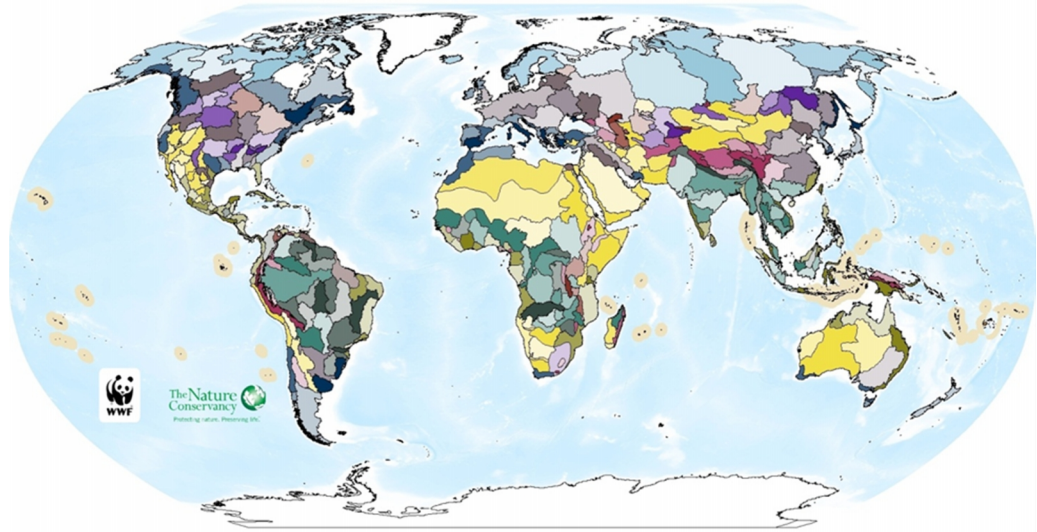


Figure 1.1: Freshwater ecoregions of the world.

Chapter 2

2 Global geography of body size in freshwater fishes: revisiting

Bergmann's rule

2.1 Abstract

Bergmann's rule states that animal body sizes increase with decreasing temperature. While the proposed mechanism was related to heat loss in homeotherms, the pattern has also been observed in poikilotherms and along latitudinal rather than temperature gradients. I analyzed body size patterns of freshwater fishes in ecoregional assemblages worldwide (9613 species) to determine 1) whether Bergmann's rule applies globally to freshwater fishes; 2) whether it applies equally to all size classes and trophic levels; and 3) which environmental variables best predict the pattern. I find that Bergmann's rule applies to freshwater fishes in general, but the strength of latitudinal patterns decreases across size classes, becoming negligible in the largest fishes. Similarly, the pattern exists in most trophic levels, but disappears among primary consumers. Temperature and seasonality are useful predictors of body size variation, but river discharge was more important for the largest fishes. I speculate that Bergmann's rule in fish is driven by exclusion of small fish in cold climates due to limits on energy storage and behavioral thermoregulation. Though my analysis provides broad support for

Bergmann's rule, the exceptions indicate that a more nuanced view of selective mechanisms is required to understand body size patterns in aquatic poikilotherms.

2.2 Introduction

Body size is a fundamental dimension along which ecological processes and interactions are structured (Peters, 1983). Accordingly, geographic body size patterns within and among species have been extensively studied. Bergmann (1847) rule is one of the oldest and most prominent patterns; it states that body size increases with decreasing temperature because large organisms have lower surface area to volume ratios that reduce heat loss in cold climates. The rule was initially formulated for homeotherms and applied to closely related species (Rensch, 1938; James, 1970), but later was extended to poikilotherms and more distantly related species (Ray, 1960; Lindsey, 1966; Van Voorhies, 1996). Why Bergmann's rule would apply to poikilothermic species remains uncertain because thermal conformers expend less rather than more energy at lower temperatures. Moreover, studies of poikilotherms both support (Ray, 1960; Lindsey, 1966; Van Voorhies, 1996; Knouft, 2004; Blanchet et al., 2010; Fisher et al., 2010) and reject (Mousseau, 1997; Power & McKinley, 1997; Ashton & Feldman, 2003; Angilletta et al., 2004) Bergmann's rule; there is no clear consensus. In this chapter, I evaluate Bergmann's rule and potential underlying mechanisms using a worldwide database of freshwater fishes, providing a strong test of latitudinal variation in body size of poikilotherms.

Relatively few tests of Bergmann's rule are available for freshwater fish despite their high diversity, endemism, and ecological importance, and previous results have been inconsistent. Belk and Houston (2002), and Rypel (2014) showed poor support for

the rule at the intraspecific level, however many studies have supported the rule at the interspecific level (Ray, 1960; Knouft, 2004; Blanchet et al., 2010; Fisher et al., 2010). Most of the studies were limited to a few species and relatively small geographical extent (e.g., Belk and Houston, 2002; Blanck and Lamouroux, 2007). The few macroecological studies on body size conducted on freshwater fish (e.g., Knouft, 2004; Griffiths, 2012) were limited to a single continent (mainly North America), except for (Blanchet et al., 2010), which covered river basins world-wide. The premise of my study is that describing body size patterns across large geographic areas and accounting for the full species diversity within a taxon will allow more conclusive tests of the validity of Bergmann's rule as well as the evolutionary and ecological factors structuring body size in natural assemblages.

At a mechanistic level, the effects of temperature on body size in poikilotherms are linked to metabolic rate, just as for homeotherms. However, the general direction of thermal effects on metabolism are reversed for homeotherms, who increase their metabolic rate to buffer themselves against decreasing ambient temperature, in contrast to poikilotherms (Randall et al., 2002). Instead, two other temperature-dependent mechanisms may explain Bergmann's rule in poikilotherms. First, intraspecific comparisons of adult body size against temperature suggest that age at maturation is lower in warmer temperatures because of higher metabolic rates (Atkinson et al., 2003; Atkinson & Sibly, 1997), leading to smaller body sizes in warmer environments. Second, many poikilotherms show behavioral thermoregulation, wherein they preferentially use warm microhabitats during the cold season (Angilletta et al., 2002; Beitinger & Magnuson, 1979). Such behavioral responses to temperature may allow poikilotherms to

raise their body temperature, but at the cost of enhanced exposure to predators (Zaret & Suffern, 1976; Hurst, 2007). Smaller individuals are more vulnerable to predators, leading to selection pressure for larger body sizes in climates that necessitate such behavioral thermoregulation. However, beyond a certain size the effectiveness of this type of thermoregulation may be compromised due to the long heating times necessary to elevate the temperature of a large body mass when only short periods of heating by physical activity or sun may be attainable (Olalla-Tárraga et al., 2006).

For both of these poikilotherm-specific mechanisms, as well as the original heat-retention hypothesis, the potential benefits of further increase in body size depend strongly on the initial body size. For species that are already large, an additional increase in size may have only minor benefits, whereas small species may experience disproportionately large benefits from a comparable absolute increase in body size. This is because growth rates (as a proportion of mass gain per time; Peters, 1983), changes in surface area to volume ratio, and susceptibility to gape-limited predators all decrease non-linearly with body size, such that the same incremental increase in absolute size experiences sharply diminishing returns in benefits with size (Figure 2.1). As a result, there are sound theoretical reasons to expect a lower benefit of and thus a lower selection pressure on tuning body size to thermal regimes in large-bodied organisms than in small bodied ones, regardless of the specific nature of the benefits. Moreover, other size-specific selection pressures are likely to stabilize the size of the largest species (Brown et al., 1993), such as high risk of mortality prior to first reproduction (Roff, 1992), limitations in the availability of sufficient food and habitat (Damuth, 1981; Minns, 1995).

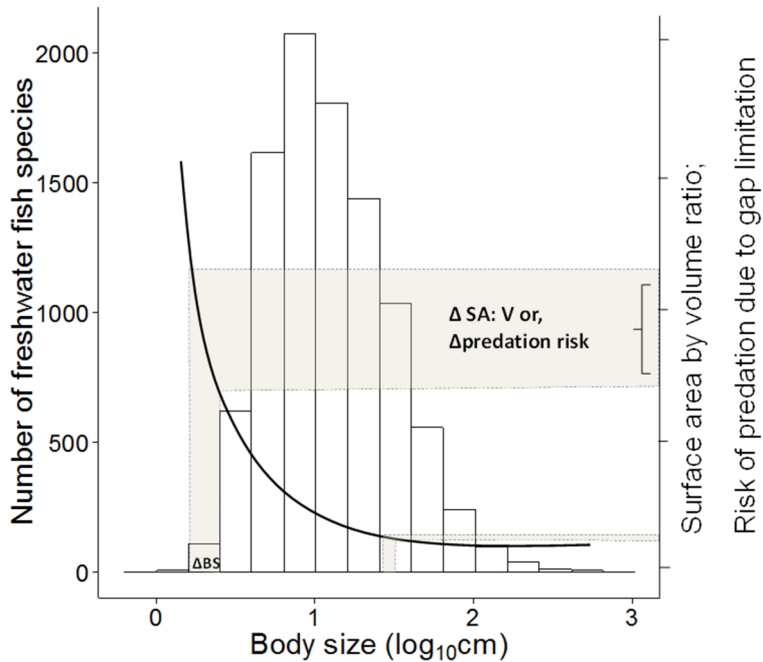


Figure 2.1: Conceptual diagram of the magnitude of effect of body size change for small vs. large fish. The histogram shows the observed frequency distribution of maximum body size for freshwater fish species worldwide. The exponential curve depicts size-related changes in factors that affect individual fitness, such as surface area (SA) to volume (V) ratio or susceptibility to gape-limited predators. For such size-dependent aspects of fitness, the shaded areas indicate how a fixed absolute increase in fish body size may confer a much larger selective benefit to small fish than to large fish.

Though temperature is the putative driver of body size patterns, wide fluctuations through time and space complicate its role in macroecological patterns. Simply using the yearly average temperature may not suffice to sufficiently characterize the forces responsible for body size distributions. The fluctuations and extremes of temperature could be just as important as the average in driving body size evolution (Gaines & Denny, 1993). For example, very low temperatures — even over short periods — could

lead to cessation of metabolic processes, enabling yearly minimum temperature to be the key selective force shaping body size (Atkinson, 1994). Similarly, climate seasonality often causes fluctuations in food availability, and the fat storage necessary to survive the harsher season can be a major constraint on fitness (Lindstedt & Boyce, 1985). Higher latitudes have longer harsh seasons with low food availability, requiring species to have longer fasting endurance by increasing energy storage (Blackburn et al., 1999; Cushman et al., 1993). Thus, both minimum temperature and seasonality may cause size-dependent winter mortality (Hurst, 2007) that selects against small species due to their higher mass-specific metabolism and lower energy storage capacity.

The sensitivity of body size patterns to latitudinal variation in temperature should also depend on the likelihood of gene flow between thermally-disparate populations. Dispersal and gene flow interfere with adaptation to local conditions across a species' geographic range (Kirkpatrick & Barton, 1997). Thus, the fact that larger species generally have strong dispersal abilities and large individual home ranges (Bernatchez & Dodson, 1987; Etienne & Olf, 2004; Marquet & Taper, 1998; Minns, 1995; Roff, 1988) could homogenize body sizes across their geographic range within a species, and thus weaken Bergmann's pattern relative to small-bodied species. Endemic species provide a particularly strong test of this idea because they are expected to be well adapted to local conditions, regardless of body size. Therefore, I compared the latitudinal patterns of body size among endemic species to those of wider-ranging species to illuminate the role of evolutionary history in creating latitudinal patterns of body size (Hewitt, 2000).

Trophic interactions are generally size-structured in aquatic food webs (Jennings, et al., 2001; Newman & Cohen, 1986; Petchey et al., 2004). Consequently, systematic

temperature-related shifts in body size of some species may cause selection pressure on other species mediated by trophic relationships, to also change in size. Among trophic guilds of freshwater fishes, primary consumers violate typical patterns of predator-prey size ratios, because they mostly consume small-sized foods regardless of fish body size. This decoupling may make algivores and detritivores less responsive to temperature and thus cause differences in latitudinal body size patterns among trophic guilds. Specifically, I expect body size pattern in primary consumers to show weaker dependence on temperature and latitude than in secondary consumers and top predators because their body sizes are relatively independent of prey size compared to carnivorous species embedded in size-structured interaction webs. To address this hypothesis, I examined the relationship between body size and latitude separately for each trophic group.

In this study, I investigate latitudinal patterns in body size for freshwater fish across the world at an ecoregional scale. My goals are to determine 1) whether Bergmann's rule applies globally to freshwater fishes; 2) whether the same pattern arises across all body size classes and trophic levels; and 3) which environmental variables best predict the observed patterns. The geographic and taxonomic extent and comprehensiveness of my data are among the outstanding features of my analysis.

2.3 Materials and Methods

2.3.1 Latitudinal analysis

To test the overall applicability of Bergmann's rule to freshwater fishes, I regressed median body size across species against the latitude of each ecoregion's centroid separately for the northern and southern hemispheres. I used the median body

size because the distribution of body sizes of species was right skewed even after transformation. I also created a map of geometric mean body size distribution for direct comparison to results from marine ecoregions (Fisher et al., 2010). The separation by northern and southern hemisphere enabled me to test whether both hemispheres show the same pattern.

To investigate whether the strength of Bergmann's rule depends on body size, I split assemblages in each ecoregion into eleven body size deciles ranging from the single smallest species (0th decile) to the largest species (100th decile). For each decile, I fitted the linear slope relating body size to latitude for all species and for endemic species only. Differences in slopes among deciles were interpreted as signifying variation in the applicability of Bergmann's rule.

2.3.2 Randomization tests

To ensure that apparent patterns were not caused by statistical or sampling artifacts, I created 10,000 random realizations of ecoregion assemblages. I simulated ecoregion assemblages by pulling an equal number of species as observed for each ecoregion at random from the complete world-wide species pool without replacement. Both median and decile analysis were repeated for each randomized set of assemblages to provide a null model for inferring the importance of ecological or evolutionary processes.

2.3.3 Environmental predictors

To investigate the mechanisms underlying interspecific spatial variation in body size, I calculated ecoregional averages for four environmental variables: annual mean temperature, minimum temperature, temperature seasonality (standard deviation of daily

temperature across the year), and river discharge. All temperature variables are obtained from the worldclim website (Hijmans et al., 2005) for 10 arc minute grid cells. Air temperature was used as a proxy for water temperature, as modal air and water temperatures are strongly correlated at a broad scale (Caissie, 2006). River discharge was derived from a water balance model executed on a 30 minute global grid (Wisser et al., 2010).

I used two approaches for determining which environmental drivers may best explain variation in body size. First, I tested the basic association of each variable with median fish size using ordinary least square regressions (OLS). The three temperature-related variables were correlated, which limits their suitability for simultaneous inclusion in a multiple linear regression model. Centroid latitude was also tested as a predictor of median body size. Second, I used Random Forests (Breiman, 2001) for comparing the relative importance of the variables when included in a model simultaneously. Random Forests are a robust machine learning technique for determining variable importance, and also have the ability to model interactions among predictor variables (Breiman, 2001). I used the Random Forests implementation “cforest” in the party package in R and its associated function “varimp” to determine variable importance, because this function is able to take the substantial intercorrelation among mine predictor variables into account (Hothorn et al., 2006; Strobl et al., 2008; R Core Team, 2013). I repeated these analyses for each body size decile and for total species and endemic species.

2.3.4 Trophic level analysis

To test for differential evidence of Bergmann’s rule among trophic levels, I divided species into four levels according to trophic position score: 2.00 – 2.19:

herbivore, 2.20 – 2.79: omnivore, 2.79 – 4.00: carnivore, and >4.00: high level predator. Trophic position, as listed in FishBase, reflects a species' diet composition and the trophic level of each food type (Froese and Pauly, 2011). Primary producers and detritus were assigned the trophic level 1. Trophic level is calculated by adding 1 to the mean trophic position of the food, following (Romanuk et al., 2011). I calculated the median body size within each trophic level for each ecoregion, excluding cases with <5 species because this limited diversity would increase the odds of confounding issues such as phylogenetic biases. I then regressed median body size on latitude for each trophic level to test the strength of Bergmann's rule.

2.4 Results

2.4.1 Body size latitudinal pattern

Fresh water fish assemblages around the world exhibit a strong latitudinal gradient in median body size; larger body sizes are associated with higher latitudes ($0.0063 \pm 0.0005 \log_{10}\text{cm degree}^{-1}$) (Figure 2.2). This slope lies completely outside of the distribution of slopes derived from 10,000 randomized fish assemblages (mean slope: 0.00003 with a range of -0.0008 to $0.0010 \log_{10}\text{cm degree}^{-1}$), indicating that the observed pattern is not a sampling artifact. The observed trend matches the pattern observed in marine fish species (slope: 0.0037 ± 0.0007 using Fisher et. al.'s (2010) data and my methods) (Figure 2.3). Similar to Blanchet et al., (2010), I am unable to detect a latitudinal trend in body size in the southern hemisphere, which may be due to low sample size and reduced latitudinal coverage. There are only 85 ecoregions ranging from 0 to 44.60 degree in the southern hemisphere, within which visual assessment suggests similar latitudinal effects as in the northern hemisphere (Figure 2.2).

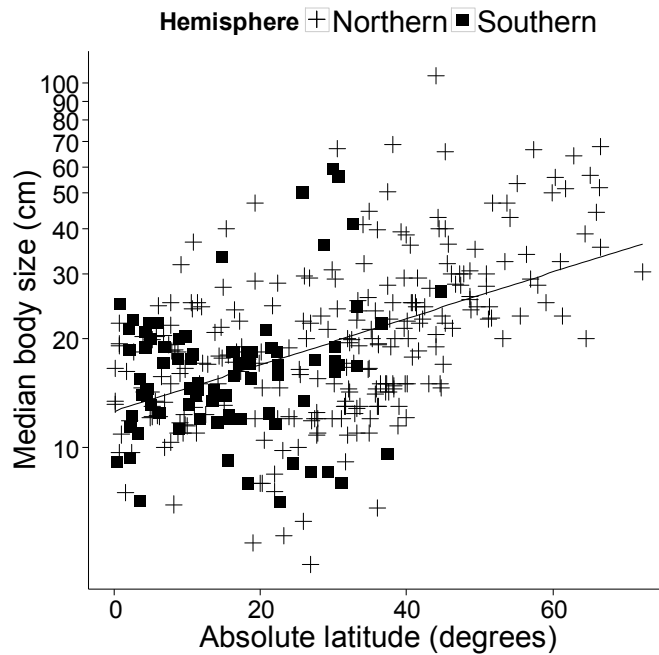
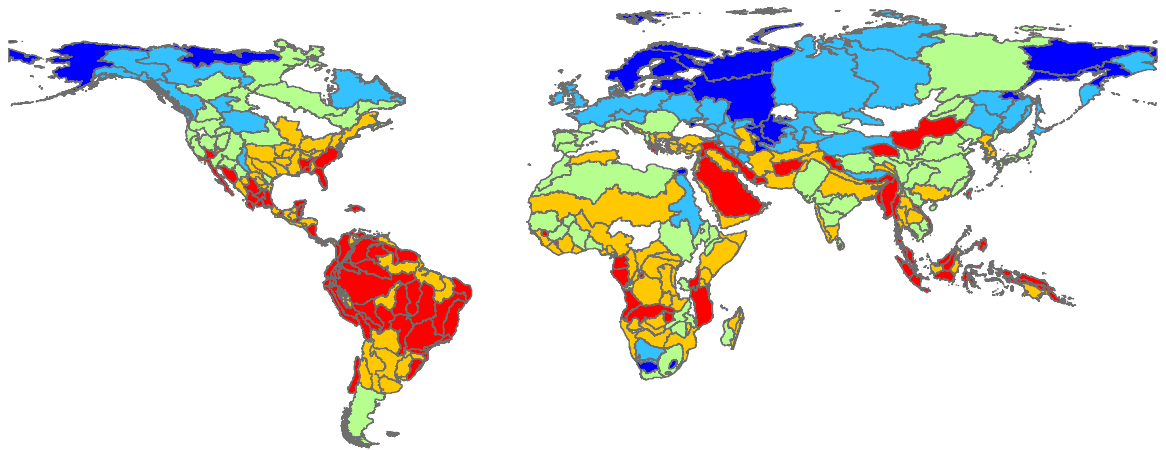


Figure 2.2: Regression of median body size in freshwater fish ecoregional assemblages against absolute latitude. Median body size of each assemblage was \log_{10} transformed for regression analysis, but here y axis has been back-transformed to original size. Ecoregional latitude was estimated using the centroid of each ecoregion. The regression line illustrates joint analysis of both hemispheres (plus symbols represent northern latitudes; solid squares represent southern latitudes).

2.4.2 Body size decile analysis

Bergmann's rule slopes show strong size dependency; latitudinal patterns of body size decrease with increasing fish size (Figure 2.4 and 2.5). In both, the all-species and endemic-species analyses, slopes remain fairly constant from the 10th to 90th percentile of body sizes (Figure 2.5A and 2.5B), but diverge sharply for the very smallest (0th decile) and very largest (100th decile) species in each ecoregion. The smallest species

show the strongest latitudinal patterns in size, while the largest species fail to follow Bergmann's rule



Geometric mean body length (cm)

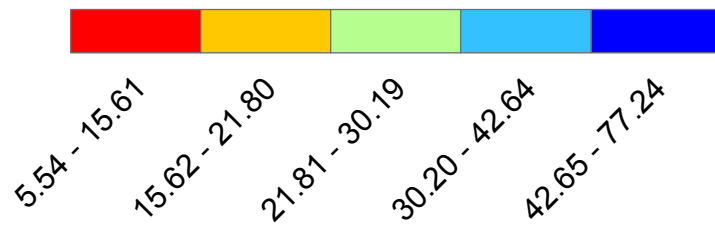


Figure 2.3: Global distribution of geometric mean body size (cm) by ecoregion containing 27,929 individual occurrences of 9,613 freshwater fish species. Ecoregions dominated by lakes and islands are excluded.

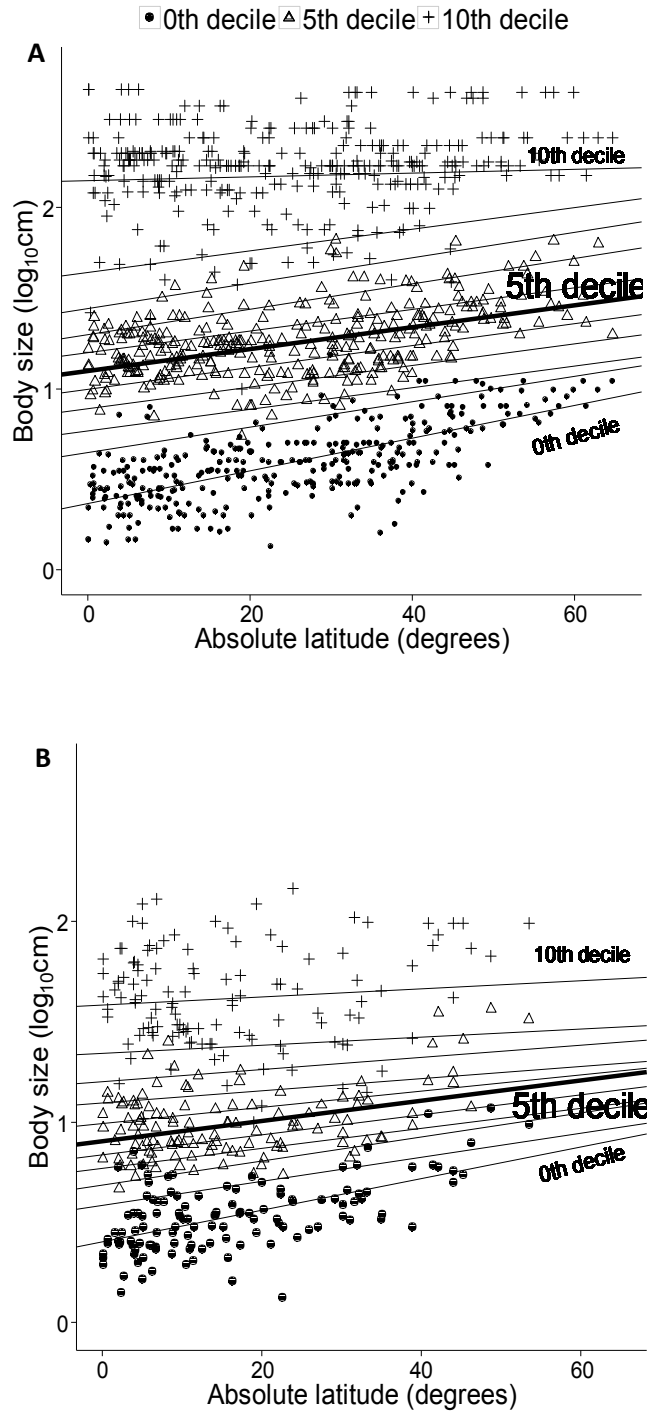
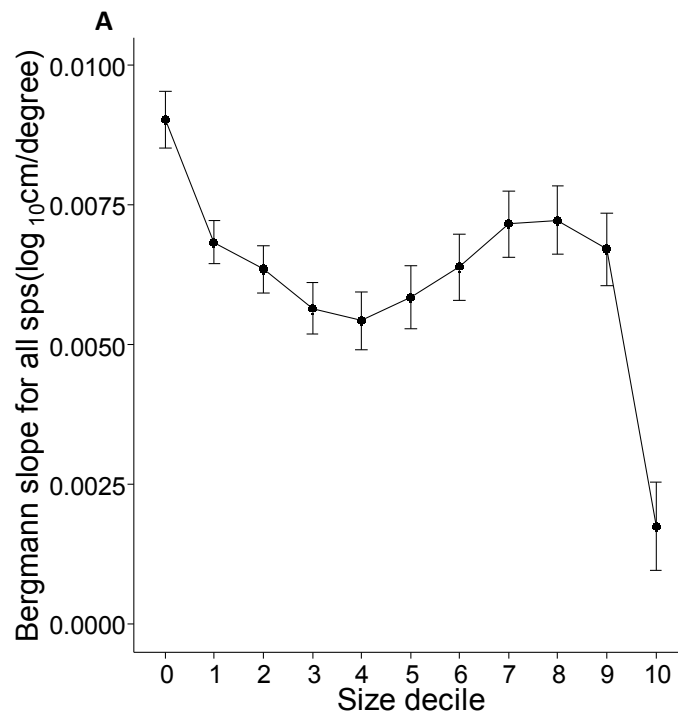


Figure 2.4: Latitudinal patterns of freshwater fish body size as a function of size decile within ecoregions of the world. Lines indicate regression of \log_{10} -transformed body size against latitude for 11 deciles in the size distribution observed in each ecoregion. Markers indicate observed fish size for the 0th (triangle), 5th (open circle), and 10th (cross) deciles for (A) all species, or (B) only endemic species.



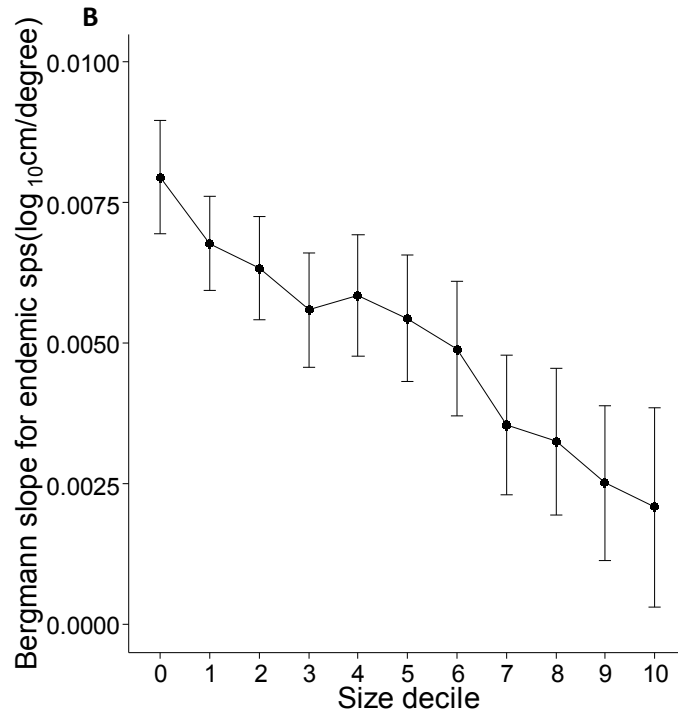


Figure 2.5: Slopes from regressions of body size against latitude, plotted as a function of decile within the frequency distribution of species within each ecoregion. Error bars show the standard error of slope estimates by decile for (A) all species and (B) only endemic species.

2.4.3 Environmental predictors

Analyzing explanatory variables individually, I find a significant relationship between median body size and three variables: annual mean temperature, minimum temperature, and seasonality (Table 2.1). In models including all species, latitude is the most important single predictor. However, for endemic species annual mean temperature and minimum temperature are more important than latitude (Table 2.1). River discharge shows no relationship to fish body size for either set of species.

Annual mean temperature has the highest variable importance in my Random Forest model for median body size (Figure 2.6). However, when body sizes were split up by deciles, the relative importance of mean temperature continuously decrease towards larger body sizes and became unimportant for the largest fish in both the endemic- and all-species models. Interestingly, river discharge emerges as an important variable in the all-species model for the largest body size decile. In contrast, at medium body sizes (3rd - 7th deciles), minimum temperature emerges as a relatively important variable for endemic species' body sizes. Unfortunately, the variable importance measure from my Random Forest models cannot be interpreted in an absolute sense but only as the relative influence of variables.

Table 2.1: Univariate least squares regression analyses of median body size as a function of various environmental variables.

Environmental variables	Slope (log10 cm/degree)	Standard error	Standardized slope	R²	Df
All species					
Absolute latitude	0.006***	0.0005	0.50	0.253	342
Annual mean temperature	-0.010***	0.001	-0.47	0.220	342
Seasonality	0.002***	0.0002	-0.42	0.242	342
Minimum temperature	-0.008***	0.009	0.49	0.184	343
River discharge	-4.301e-08	1.646e-07	-0.01	0.0002	337
Endemic species					
Absolute latitude	0.005***	0.001	0.40	0.160	120
Annual mean temperature	-0.010***	0.002	-0.43	0.180	120
Seasonality	0.002***	0.0006	0.29	0.008	120
Minimum temperature	-0.009***	0.001	-0.43	0.190	120
River discharge	-1.565e-12	1.293e-12	-0.12	0.014	100

Significance is indicated as: ***P<0.001, **P<0.01

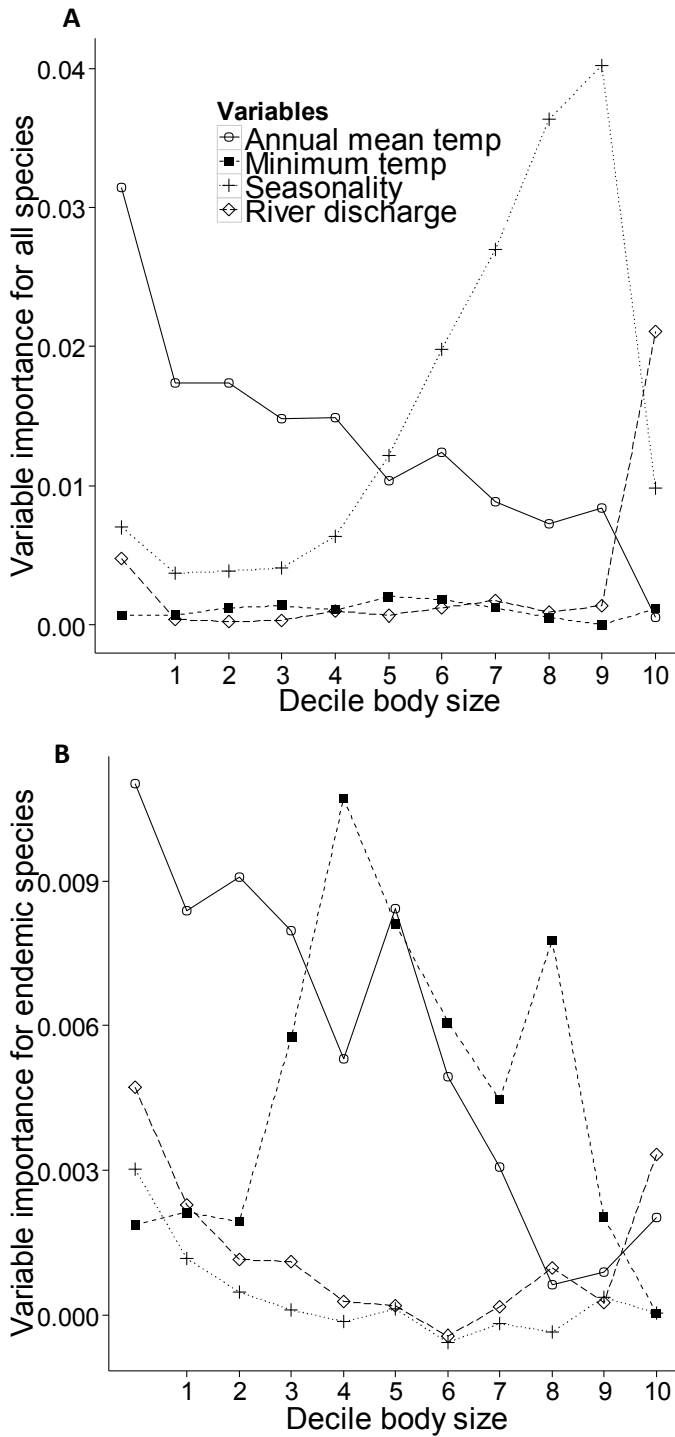


Figure 2.6: Variable importance from a Random Forest model using annual mean temperature, minimum temperature, seasonality, and river discharge as predictors of

freshwater fish body size by decile within ecoregional species pools around the world. Results are shown separately for A) all species and B) endemic species.

Analyzing each trophic group of fish separately shows significant differences in latitudinal patterns of body size (Figure 2.7). Primary consumers do not follow Bergmann's rule (slope: -0.0039 ± 0.0010). The body sizes of omnivores and high-level predators increase moderately with latitude (slope: 0.0036 ± 0.0006 and 0.0045 ± 0.0007 , respectively). Mid-level carnivores exhibit the strongest Bergmann pattern of all trophic groups (slope: 0.0060 ± 0.0005).

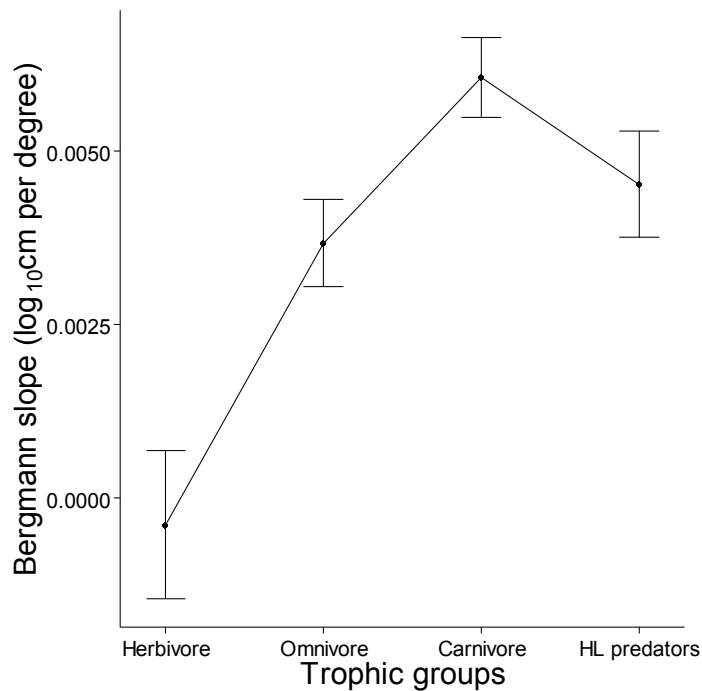


Figure 2.7: Slope coefficient of median body size against latitude for freshwater fishes representing four trophic groups. Bars indicate the standard error of the slope. Trophic groups represent categorizations based on trophic position in FishBase: herbivore 2.00 –

2.19 (n=189 ecoregions), omnivore as 2.20 – 2.79 (n=226), carnivore 2.79 – 4.00 (n=337), and high-level predators >4.00 (n=89).

2.5 Discussion

My analysis of global patterns in the body size of freshwater fishes encompassed an unprecedented number of species, providing robust confirmation that Bergmann's rule generally applies to freshwater fishes. More importantly, distinguishing species by their relative body size and trophic group within each ecoregional assemblage revealed a more nuanced view that recognizes wide variation in the strength of Bergmann's rule among size classes and trophic groups. Latitudinal patterns of body size are strongest in the smallest species and among mid-level carnivores, while they are weak to non-existent at the largest body sizes and for primary consumers. These differences may help to explain some of the conflicting results reported in previous assessments of Bergmann's rule, which typically had restricted geographic and taxonomic coverage. Finally, my global-scale analysis of the environmental correlates of Bergmann's rule provides support for its interpretation as an adaptive response to cold temperatures. Moreover, my similar results from analyses of all species and endemics alone affirm the robustness of the patterns, and suggest that they reflect evolutionary processes rather than ecological assembly rules.

Before delving into the specific body size patterns that I observed, it may be instructive to review the general evolutionary forces and constraints governing body size in fishes. First, there must be a minimum body size below which fish cannot exist due to anatomical, physiological, or ecological factors. In adherence to Cope's rule (Cope, 1885) selection will generally direct body size evolution away from this minimum size (Alroy, 1998), as larger individuals of a species are dominant and more fit

(Peters & Wassenberg, 1983; Bonner, 2011). There is less basis for expecting an absolute upper limit on body size in freshwater fishes given that much larger marine fish exist. Therefore, the upper limits I observe are likely the result of energetic or other ecological constraints whereby the costs of reaching or maintaining an extremely large size exceed the benefits (Brown et al., 1993). Between these extremes, I may then expect that a majority of fish species have the potential to respond to selection for increases or decreases from their modal body size (Brown et al., 1993). For these intermediate species, it is important to recognize that the physiological and ecological benefits of a given increase in body size are expected to be highest at small sizes, and to decline rapidly with increasing initial size (Figure 2.1). As a consequence, I expect the strength of latitudinal patterns to be negatively related to body size: the smallest fish show the strongest positive relationship between latitude and body size, while the largest show almost none, with intermediately sized species falling somewhere in between. Both of these predictions are met by the world's freshwater fishes (Figure 2.1, Figure 2.5).

My estimates of Bergmann slopes for freshwater fish of median size are consistent with, but substantially expand upon, earlier studies (Ray, 1960; Lindsey, 1966; Knouft, 2004; Blanchet et al., 2010; Fisher et al., 2010). Relative to the latitudinal pattern of median body size indicated in this study, Fisher et al. (2010) showed a slightly shallower slope for marine fish from large marine ecoregions worldwide, and Knouft (2004) found a steeper slope for freshwater fish for North America in comparison to my slope. This slight difference in Bergmann slopes may be due the difference in the extent, scale and sample sizes of the study. Both my analyses and those of Fisher et al., (2010) are based on maximum body size of each species (extracted from Froese and

Pauly 2011), which precludes accounting for intraspecific variation and may not represent typical adult sizes in natural populations. Unfortunately, there is no alternative available for address large numbers of species at global geographic scales.

Although Bergmann envisioned the latitudinal body size pattern to be driven by temperature (Bergmann, 1847), this study and most others use latitude as a proxy for temperature (James, 1970; Blackburn & Gaston, 1999; Ashton et al., 2000). My subsequent analyses indicate that latitude perform slightly better than temperature variables at fitting patterns in freshwater fish body sizes (Table 1). In fact, the temperature-based selection pressure originally proposed by Bergmann is unlikely to apply as strongly to poikilotherms as to homeotherms (James, 1970). Thus, the predictive power of latitude may not solely lie in a direct functional connection to thermal ecology (Schemske et al., 2009), but rather in its additional association with other important factors such as competition and dispersal (Bernatchez & Dodson, 1987). However, I ultimately excluded latitude from the variable importance analysis, despite its initial slightly better performance, because of the lack of a simple, direct, mechanistic hypothesis for its influence on body size patterns, and, instead, the multiple related ways it could play a role, which are difficult to disentangle.

Though high correlation between latitude and temperature variables limits mechanistic inferences about environmental controls on body size patterns in my analyses, two key conclusions appear robust. First, temperature is an important predictor of latitudinal patterns of body size for most size deciles, particularly at the lower end of the size range. This pattern may reflect the underlying allometric size-scaling of individual metabolism or limits on behavioral thermoregulation (Brown et al., 2004).

Metabolic constraints on minimum body size arise because small organisms have higher basal metabolic demand per unit mass than larger organisms. As thermal conformers, body temperature of fish is similar to ambient temperature, and thus their metabolic rate decreases with water temperature (Cushman et al., 1993; Randall et al., 2002). Feeding and swimming start to decline around 7°C, and metabolic processes continue down to ~0°C (Fry & Hochachka, 1970). Extended periods of minimal feeding activity under cold temperatures may impose higher mortality on small fish due to the combination of higher mass-specific metabolic demands and lower energy storage capacity (Downhower, 1976; Oliver et al., 1979; Meyer & Griffith, 1997). Conversely, in the tropics, the year-round warmth and productivity of aquatic ecosystems could enable small-bodied species to survive despite their higher mass-specific metabolic rate. Second, fish often behaviorally thermoregulate by searching out the most desirable temperature available (Beitinger & Fitzpatrick, 1979). However, the resulting aggregations in a restricted habitat area may increase the likelihood of attracting predators. Small fish are particularly vulnerable to gape-limited predators, thus their increased exposure to predators when aggregated may outweigh the benefits of behavioral thermoregulation (Garvey et al., 1998). As a result, behavioral thermoregulation may be less viable as an adaptive response to cold climates for small fish than for larger species. Thus, both metabolic scaling patterns and limited options for behavioral thermoregulation may contribute to relatively steep scaling of body size with latitude in the smallest species in each ecoregion, and steady weakening of the latitudinal pattern with increasing size.

At the upper end of the size spectrum, the largest fish species showed little response to temperature but instead increased in size with river discharge. This shift is

not unexpected; temperature effects are expected to diminish with body size because large fish have a low surface area to volume ratio, low mass-specific metabolism, and low susceptibility to predation while behaviorally thermoregulating. Previous global-scale analyses have indicated that river discharge is a useful proxy for habitat availability for fishes, and is positively related to species richness (Oberdorff et al., 1995; Guégan et al., 1998). Freshwater ecosystem size is also positively related to food chain length (Vander Zanden & Shuter, 1999; Post et al., 2000), potentially because the size of predatory fishes increases with that of the ecosystem (Post, 2002). My finding that the size of the largest species in each ecoregion increases with river discharge at the global scale aligns nicely with increases in fish species richness and food chain length based on ecosystem size. Larger individuals require more food per capita, which requires drawing upon a larger home range. At a certain body size the carrying capacity of an ecosystem will fall below the minimum population size for long-term persistence (Thomas, 1990), such that the largest species can inhabit only the largest contiguous habitats (Minns, 1995; Marquet & Taper, 1998; Kramer & Chapman, 1999), for which river discharge serves as a proxy. Moreover, my null models demonstrate that the size pattern is not merely a sampling artifact of having more species in high-discharge ecoregions, but rather is a genuine pattern that is independent of species richness, latitude, and temperature.

At mid-decile body sizes the explanatory power of mean yearly temperature diminishes, and seasonality and minimum temperature emerge as more important variables. Seasonality and minimum temperature are strongly correlated, so together they likely reflect both the intensity and duration of cold conditions. These aspects of winter

endurance could impose high mortality on fish of any size (Oliver et al., 1979), and it is unclear why they would have more influence on mid-sized fish than smaller or larger species.

Similar to the variations in Bergmann's rule across body sizes, I found it to vary among trophic groups. As hypothesized a priori, all trophic groups except primary consumers showed typical Bergmann's rule patterns. The absence of consistent shifts in body size with latitude in herbivores and detritivores suggests that their body size has been shaped by different physiological or ecological limitations than apply to higher trophic groups. I believe that the most likely explanation for the difference is that primary consumer fishes do not adhere to the rules of size-structured trophic interactions that prevail in most aquatic food webs (Jennings et al., 2001; Petchey et al., 2004), and hence need not respond to Bergmann's rule shifts in the size of their prey. When such compensatory shifts are not required to maintain predator-prey size ratios, there is less reason to expect algivores and detritivores to respond to latitudinal patterns of temperature or other factors. In parallel, algivores and detritivores show low richness at high latitudes (Wootton & Oemke, 1992), perhaps reflecting the challenges of cold climates for species whose low-quality diet places a premium on digestive efficiency, which is generally temperature-dependent (Gaines & Lubchenco, 1982; Floeter et al., 2005). Size increases of fish are strongest in the transition from mid to high latitudes, but I had data for >10 species from only two ecoregions at latitude >46. Thus, limited representation of primary consumers at small body sizes or high latitudes may have prevented detection of size shifts with latitude even if they existed.

A key issue in large-scale biogeographic analyses is the relative roles of ecological assembly rules versus evolutionary processes in structuring species assemblages. The similarity in my findings from analyzing all species and endemic species alone is suggestive of a central role for evolutionary processes rather than simple ecological filtering from an initial species pool. Species endemic to each ecoregion provide a glimpse into the outcome of local adaptation processes because their maximum body size is presumably suited to the environmental conditions in that originating ecoregion. Endemic species are also likely to represent speciation-prone lineages with above-average capacity to suit their environment, though fish lineages are known to differ in their rates of body size evolution (Rabosky et al., 2013). I recognize that environmental conditions may vary widely within an ecoregion (e.g. elevation gradients) and that some ecoregional endemics are closely related rather than phylogenetically independent, but the 4609 of ecoregional endemics in my analysis must nonetheless provide some insight into the outcome of regional selection pressures. To complement the analysis of endemics, using all species gives a more complete picture of the body size range within each ecoregion as well as globally. Wide-ranging species included under the all-species approach are more likely to be under selection pressure for size plasticity than endemic species, hence it would be ideal to have ecoregion-specific measures of maximum body size. Such data are not available systematically across species and ecoregions, so I am unable to address adaptive shifts in body size within species. Taken together, the parallel patterns observed in endemics and all species indicates that latitudinal variation in body size of freshwater fishes likely reflects evolutionary

responses to ecoregional environmental conditions rather than merely ecological filtering from a shared pool of species.

In summary, I find that freshwater fishes of the world generally follow Bergmann's rule, but the strength of the pattern differs strongly among size classes and trophic groups. Relatively comprehensive coverage of species and geographies provided insights into the nuances of latitudinal patterns, giving reason for concern about generalizations based on a subset of species or putatively representative size estimates (e.g. median alone). The nature of the quantitative relationship between body size and latitude is more complex than previously recognized, but the observed patterns appear to reflect adaptive evolution rather than simply species sorting. The key environmental correlates also differ between the largest species (river discharge) and smallest species (temperature) in each ecoregion. Taken together, these findings help explain conflicting results from previous studies of poikilotherms, and underscore the potential for global analyses of other major taxa to test whether the same selection pressures shape body sizes of both homeotherms and poikilotherms.

Chapter 3

3 The size of the smallest species in an assemblage is tightly linked to richness in worldwide fish distributions

3.1 Abstract

I investigated body size and species richness patterns in freshwater fish distributions worldwide. The abiotic filtering hypothesis suggests that stressful environments promote ecological similarity among species. Consequently, the body size range is expected to be limited in high stress environments, which also tend to reduced species richness. Abiotic filters are expected to affect extreme sizes most strongly. Thus, I hypothesize that there is a relationship between species richness and extreme body sizes. I found that the size of the smallest species is strongly negatively related to species richness, while the size of the largest species only has a weak to non-existent relationship to species richness. Such a relationship could also be caused by a pure sampling effect: drawing a larger number of species at random from all fish species leads to a higher chance of drawing extreme sizes than drawing a small number of species. Using three null models that sequentially added ecological processes to the sampling effect I determined that the relationships between the extreme body sizes and species richness is not purely a sampling effect, but is also caused by filtering processes of species related to latitude and continent.

3.2 Introduction

Many ecological patterns, such as variation in species richness and body size, occur along latitudinal gradients. Body size is related to almost every aspect of organismal and physiological biology of species (Peters, 1983), and species richness has been a focal point of biogeography and conservation. Size based dispersal, extinction, and diversification processes imply that there should be an important relationship between body size and species richness (Stanley, 1973; Maurer et al., 1992). Elucidating this relationship has therefore great potential to move macroecology forward.

In contrast to earlier hypotheses claiming a negative relationship between body size and number of species at that size (May, 1988; Lawton, 1990), the more recent consensus is that most species have an intermediate body sizes while the smallest body sizes are not particularly speciose (Dial & Marzluff, 1988; Siemann et al., 1996). The unimodal distribution of body sizes within assemblages and taxon presented as a histogram of number of species in several logarithmic body size classes suggests that body size distribution is commonly right-skewed (Stanley, 1973; Dial & Marzluff, 1988; Blackburn et al., 1993). This right-skew indicates that the smallest body size classes are not the richest. There are more small species than large species. Small-bodied species may be numerous simply because a given level of resources can sustain more small individuals than large ones (Hutchinson, 1959; Ritchie, 2009) and more individuals means more species. Additionally, short generation time, quick maturation, fast speciation, and avoidance of extinction due to a high number of individuals can all lead to higher diversity among small species (Savage et al., 2004). The paucity of the smallest species has been attributed to a variety of causes such as the difficulty in optimizing

energy allocation to growth, reproduction, and storage for winter survival and the disadvantage of being away from the modal size as modal size species are better exploiters of, or competitors for, the available resources (Maurer et al., 1992; Brown et al., 1993; Koziowski & Weiner, 1997)

Extreme body sizes are likely to have a strong functional relationship to the ecology of assemblages (Dial & Marzluff, 1988). The concept of a modal body size implies that the average body size of an assemblage is optimized (Brown et al., 1993). Maximum and minimum sized species furthest away from a hypothesized optimal size and are therefore likely to be most influenced in size by environmental conditions, giving them the strongest functional relationship.

A leading hypothesis on constraints of body size extremes in species assemblages invokes limits imposed by harsh environments (abiotic filters). The abiotic filtering hypothesis states that more stressful environments lead to a higher degree of ecological similarity among species (Chase, 2007) limiting the range and variance of species trait distributions (here body size) (Keddy, 1992; Weiher & Keddy, 2001; Kraft & Ackerly, 2010), and decreasing species richness. For instance, the range of body sizes in an assemblage, which depends on the extreme sizes, may govern the richness of the assemblage due to availability of niche space (Woodward et al., 2005; Ritchie, 2009). I am not aware of any studies on the relation between species richness and extreme body size from assemblages of non-insular biogeography. Previous studies conducted on body size are mostly based on body size frequency distributions (May, 1988; Dial & Marzluff, 1988; Maurer et al., 1992; Brown et al., 1993; Blackburn & Gaston, 1994).

The smallest and largest species have different body size constraints (Blackburn et al., 1993). For example, the smallest species may be constrained by low temperature due to high mass specific metabolic rate, whereas the largest are more likely to be constrained by habitable space (details in chapter 2). Thus, a particular abiotic filter may constrain the smallest but not the largest body size. Consequently the distributional patterns of small and large species may differ along environmental gradients.

Given the abiotic filtering hypothesis and differential constraints of the smallest and largest species, I put forward four hypotheses on the relationship between extreme body sizes and species richness. First, body size distribution is preserved because all body sizes are affected equally when richness changes, meaning that all body sizes have the same probability of being added or lost. Consequently, the size of the smallest and largest species would be strongly related to species richness (Figure 3.1a). Second, body size distribution is not preserved because only extreme body sizes are affected, thus extreme body sizes have a high probability of being added or lost. Again, the size of the smallest and largest species would be strongly related to species richness (Figure 3.1b). Third, body size distribution is not preserved because only the smallest species are affected, thus the smallest species have a high probability of being added or lost. Therefore, the size of the smallest species would be strongly related to species richness (Figure 3.1c). Fourth, instead of the smallest species, only the largest species are affected. Therefore, the size of the largest species would be strongly related to species richness (Figure 3.1d).

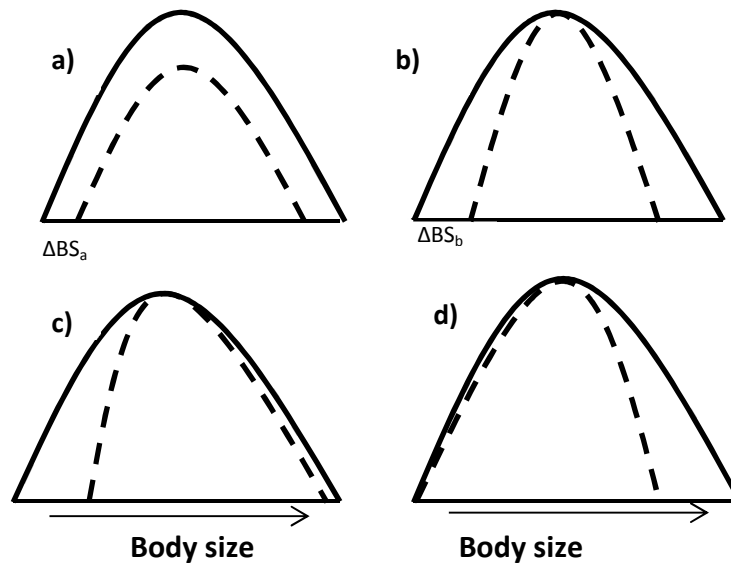


Figure 3.1: Conceptual diagram of possible effects of abiotic filters that could generate a relationship between species richness and the size of the smallest and largest species in an assemblage. The solid line shows the original frequency body size distribution (here I assume a normal distribution), and the dashed line shows a shift in body size distribution (especially range) due to abiotic filtering. The distribution of body size shifts a) equally from all directions b) equally from the two sides only c) from the left side only d) from right side only. ΔBS is the change in body size at extreme ends.

The concrete questions I address are a) what is the relationship between species richness and extreme body size? b) Is the relationship between species richness and extreme body size merely a sampling effect caused by variation in species richness (Figure 3.1a)? And c) can abiotic filters (related to latitude) account for the pattern? I used comprehensive data on freshwater fish world-wide at large geographic and

taxonomic extents and several advanced simulation models as null models to address these questions.

3.3 Methods

I used recent fish biogeography data from FEOW (Freshwater ecoregion of the world), and fish trait data from FishBase combined as mentioned in first chapter. Species richness was obtained by counting the number of species occurring in a given ecoregion.

3.3.1 Area correction

Species richness and area are positively correlated in a power law model (Arrhenius, 1921; Tjørve, 2003; Dengler, 2009). As my ecoregions vary in area, larger ecoregions have a higher probability of having more species (MacArthur & Wilson, 1967; Connor & McCoy, 1979). I used total discharge as a proxy for aquatic habitat area because measurements of absolute area of rivers are not available across the whole world. I corrected species richness for area (total river discharge) by log-transforming both variables, performing an ordinary linear regression, and extracting the residuals from this power law relationship. The residuals provide an area-corrected species richness metric. I regressed this corrected species richness against the smallest and the largest body size found in each ecoregion.

3.3.2 Randomization tests

The most straight forward way to investigate a pattern found between body size extremes and richness would be through direct experimentation. However, manipulations at this scale are not feasible, ethical or practical. Instead, I used simulation models to analyze the pattern. I created null models through randomization to isolate particular

processes that may have produced an observed pattern (Williams, 1947). Thus, my null models are not typical traditional “no effect” models but rather represent three hypothetical pattern forming processes for comparison against the empirical pattern.

In my first null model, I only considered a stochastic process that could lead to a connection between extreme body sizes and richness. Excluding all ecological processes, I used the empirical values for richness in the ecoregions and let extreme body sizes be determined by random draws from the entire pool of fish species without replacement. I created 10,000 random realizations of ecoregion assemblages and recorded the smallest and largest body sizes per ecoregion. Then I regressed the total number of species of each ecoregion against these values. From the regression, I obtained R^2 and slope which I compared against the empirical results.

The second null model differed from the first one by the inclusion of ecological reality allowing us to judge the incremental effect of this reality. As discussed above (Figure 3.1), abiotic filtering could be a major process leading to a relationship between species richness and extreme body sizes. I included abiotic filtering in this simulation by allowing its effects to enter the model via latitude. To achieve this, I created a specific species pool for each ecoregion by 10 degree global latitudinal band. Every species whose latitudinal range overlapped with an ecoregion’s latitudinal band was in the available species pool for random draws for that ecoregion. I again sampled species from this ecoregion specific pool without replacement until the original richness of the ecoregion was matched and recorded the smallest and largest body sizes for each ecoregion. By using a latitudinally restricted species pool for each ecoregion in this model, I am indirectly including abiotic filters that change with latitude, but I cannot

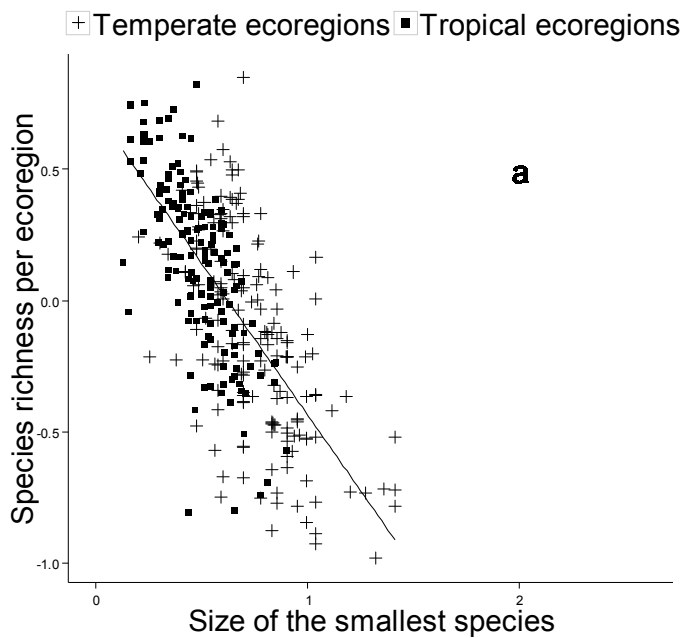
directly cover all ecological and evolutionary processes that could affect body size and species richness.

The third null model addresses the effect of continent on body size. Each continent has a different history and different geographic structure; thus, abiotic factors as well as historical factors related to continent may generate different patterns. To simulate this effect, I created a continent specific species pool for each ecoregion. I sampled species from this continent specific pool without replacement until the original richness of the ecoregion was obtained for each ecoregion. The rest of the methodology was identical simulation I and II.

Beyond explaining the relationship between species richness and extreme body sizes, my null models also disentangled the effect of species richness (sampling effect). Null models separate my first hypothesis (Figure 3.1a) from others (Figure 3.1b, c, d). The first hypothesis (Figure 3.1a) which suggested that there is an equal probability of affecting all body sizes such that species richness changes preserving original body size distribution. However, other hypothesis, especially second (Figure 3.1b), suggested otherwise. It suggested that the change in extreme body size brings the change in species richness. To find out the probable hypothesis, I compare the simulated slope and empirical slope from the relationship between body size and species richness. The steeper empirical slope than simulated indicates the scenario Figure 3.1a, and the shallower empirical slope than simulated indicates the scenario Figure 3.1b. This is because body size reducing equally from all sides have smaller changes in body size at extreme end (ΔBS_a) (Figure 3.1a) than body size reducing only from both ends (ΔBS_b) (Figure 3.1b) that is, $\Delta BS_b > \Delta BS_a$, given that the changes in species numbers are equal.

3.4 Results

I examined the relationship between the size of the smallest and largest species and species richness considering four hypotheses (Figure 3.1). I found a strong relationship ($R^2 = 0.49$; slope = -1.15 ± 0.06) between the size of the smallest species and species richness, and a weak relationship ($R^2 = 0.11$; slope = 0.49 ± 0.08) between the size of the largest species and species richness across ecoregions world-wide (Figure 3.2a, b). This result supports my third hypothesis (Figure 3.1c) suggesting strong relationship between the size of the smallest species and species richness



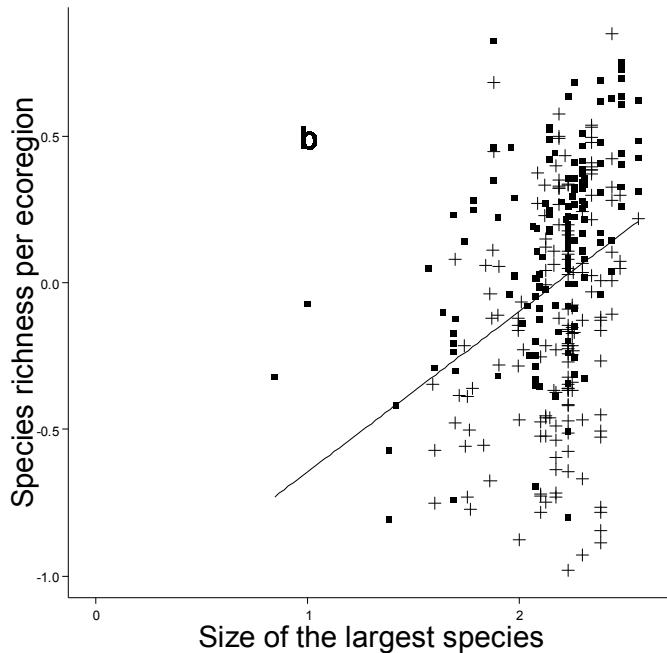


Figure 3.2: Regression between extreme body sizes and species richness by ecoregion. (a) Species richness against the size of the smallest species by ecoregion ($R^2 = 0.49$); (b) Species richness against the size of the largest species ($R^2 = 0.11$).

The result from the first simulation model indicates that the empirical relationship is not merely a sampling effect for either the smallest or largest species' size. In both cases, the observed R^2 was completely outside the distribution generated by the simulation model (Figure 3.3a, b). The relationship between the smallest species and species richness was stronger than expected, whereas the relationship between the largest species and species richness was weaker than expected had the relationship been due exclusively to a sampling effect. In addition, the average slopes from the simulation model were steeper than the observed slopes for the smallest and largest body sizes (Figure 3.3c, d) suggesting that the sampling effect is an imperfect match for the mechanism underlying the pattern.

3.4.1 Simulation I

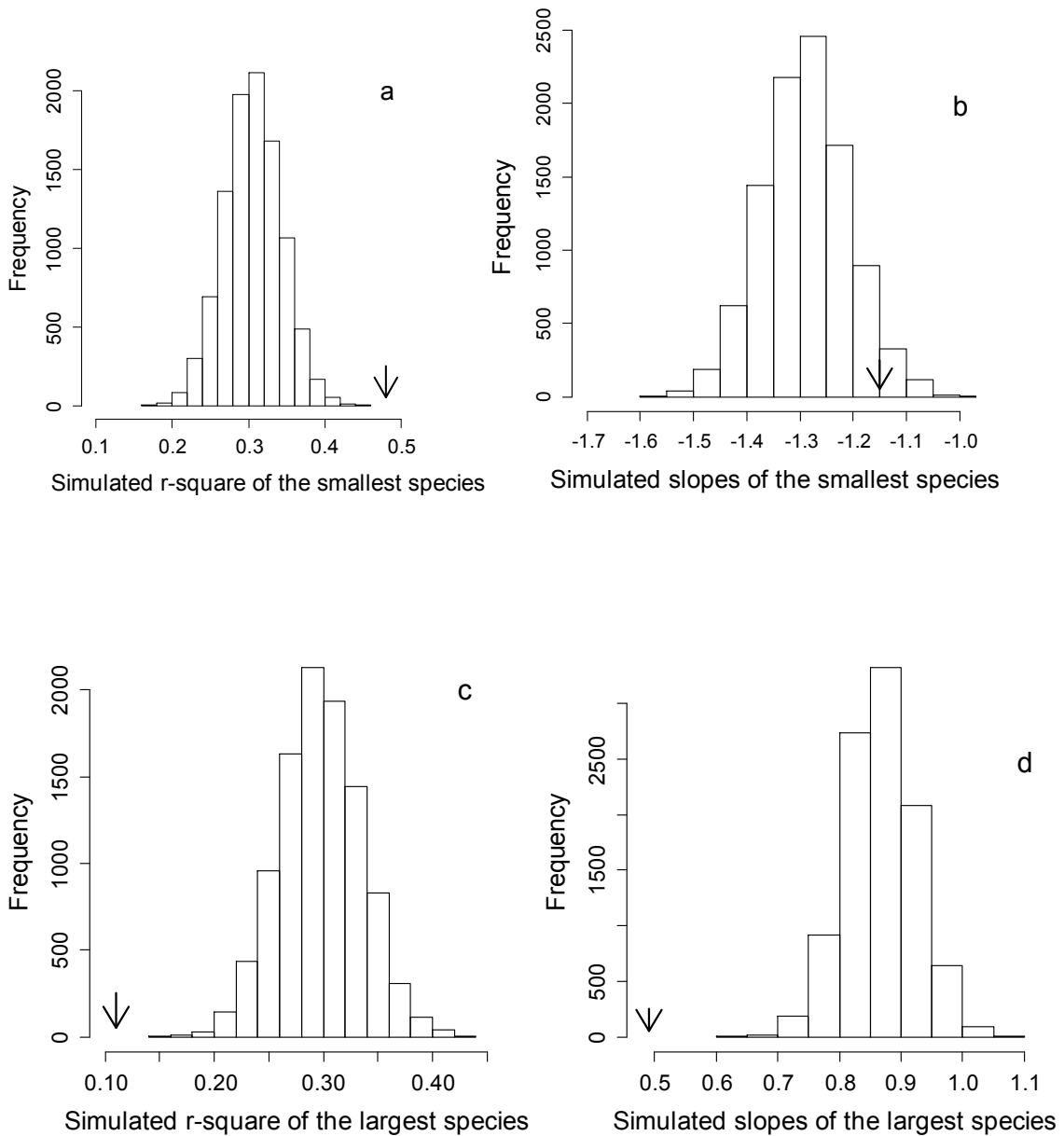
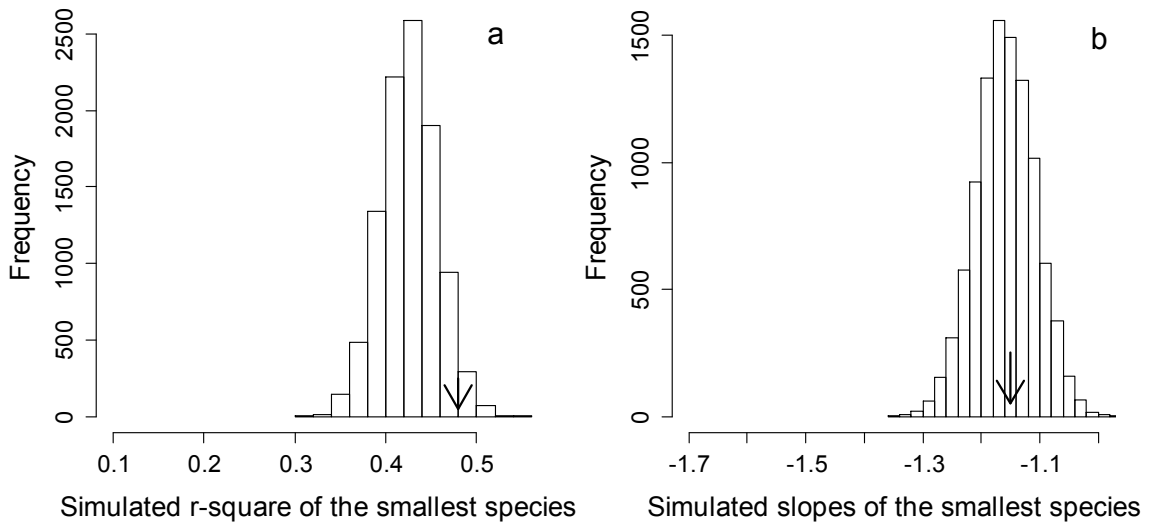


Figure 3.3: Results from the first simulation model keeping the empirical number of species per ecoregion but randomly selecting species from a global species pool. Frequency histograms show the distribution of (a) R^2 of the regression between the size of the smallest species and species richness, (b) slope of the regression between the size

of the smallest species and species richness, (c) R^2 of the regression between the size of the largest species and species richness, (d) slope of the regression between the size of the largest species and species richness. Arrows indicate values from empirical data.

When I controlled the pool of available species for random selection by latitude in the second simulation I found that the R^2 observed in the empirical data for the smallest size still fell outside 96% of the distribution of R^2 values from the simulation (Figure 3.4a). However, the slope found in empirical data closely fit the average simulated slope (Figure 3.4b). In contrast, the results for the largest body size were similar to the first randomization (Figure 3.4c, d).

3.4.2 Simulation II



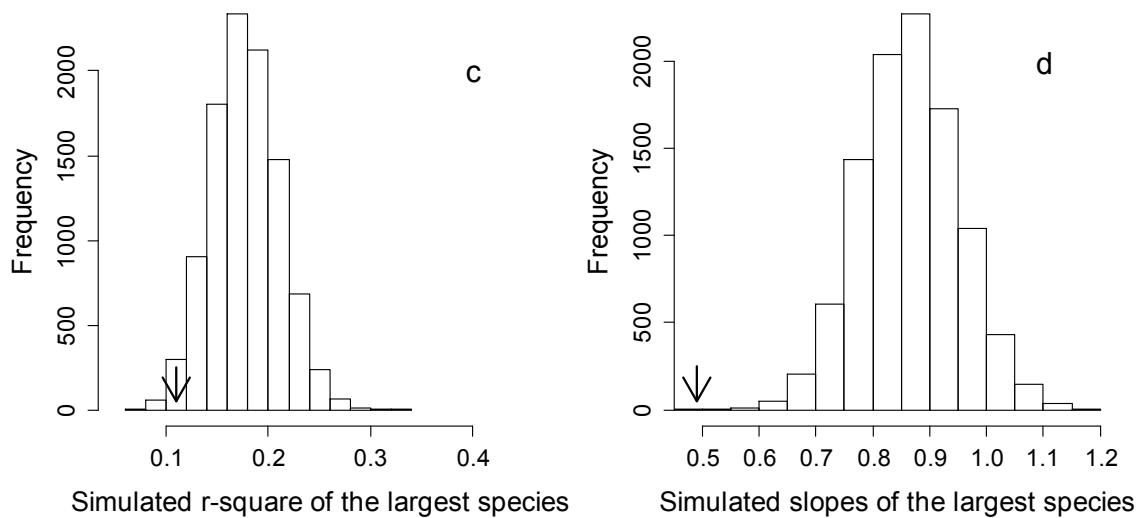


Figure 3.4: Results from the second simulation using a latitudinal species pool. Species are available for random selection in an ecoregion if parts of the species' latitudinal range overlapped the ecoregional latitude. Frequency histograms show the distribution of (a) R^2 , (b) slope of the regression between the size of the smallest species and species richness, (c) R^2 , and (d) slope of the regression between the size of the largest species and species richness. Arrows indicate values found in empirical data.

Constraining the species pool by continent in the third simulation led to results similar to the second simulation. The observed R^2 was still outside the randomized 100% (Figure 3.5a) and the average randomized slope (-1.14 ± 0.06) was slightly closer to the empirical slope than in the second simulation (Figure 3.5b). The results of randomization for the largest body size were similar to the first and second randomization (Appendix A; Figure A1).

3.4.3 Simulation III

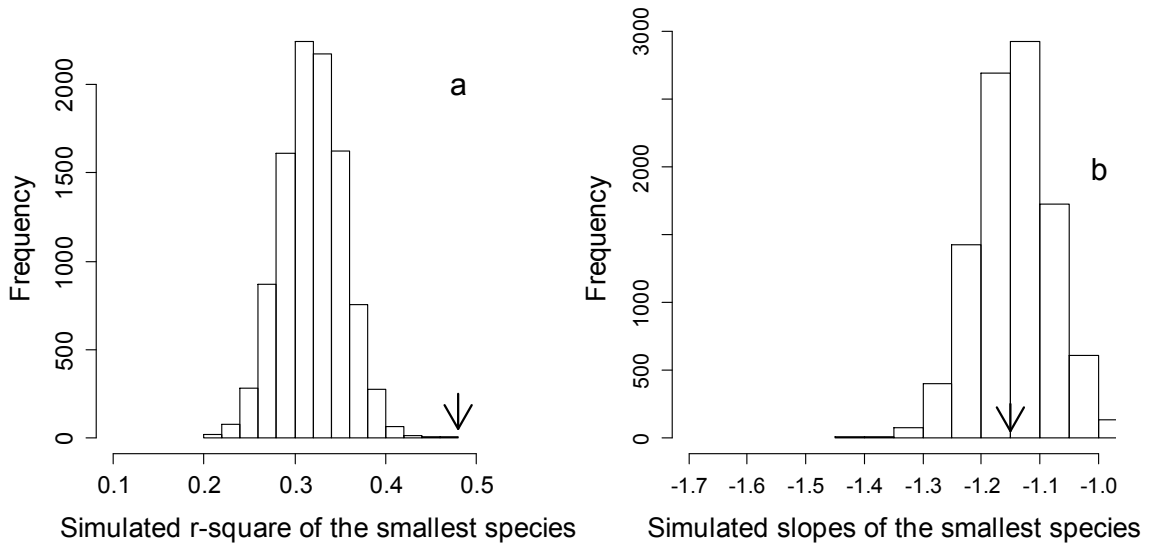


Figure 3.5: Simulated (a) R^2 and (b) slopes obtained from the linear regression between species richness vs the smallest body size of species. Body sizes pools for random selection were constrained by continent for each ecoregion while keeping richness per ecoregions to the empirical values.

3.5 Discussion

My analyses on the relationship between species richness and extreme body sizes in global freshwater fishes reveal a surprisingly strong negative relationship between the size of the smallest species and species richness, given the large extent and multiple sources of error and uncertainty in the database. The strength of the relationship I found could be considered conservative given the many sources of noise and even potential bias in my data, such as the smallest fish being more likely to be under-sampled in the tropics than in most temperate ecoregions (Paulo Petry, personal communication), weakening the pattern given that the tropics harbor the most species rich ecoregions. The strong negative

relationship between species richness and the smallest body size and weak positive relationship with the largest body size fit my third hypothesis (Figure 3.1c), in which variation in richness manifests itself mostly in the addition or loss of the smallest species. My null models suggest that the relationship is not merely a sampling effect (Figure 3.3, 3.4, and 3.5). Although I was not able to examine the direct effect of abiotic filters that are related to latitude, my results suggest that abiotic filters most strongly affect the smallest fish species (Figure 3.4) and thus could be responsible for the tight link between the size of the smallest species and species richness.

The relationship between species richness and extreme body sizes could be simply caused by a sampling effect, because higher richness leads to a higher probability of having extreme sizes randomly drawn from a species pool, but the results obtained from the first null model suggested otherwise (Huston, 1997; Tilman et al., 1997). I investigated this sampling effect using my first and second hypothesis and the first null model. My first hypothesis (Figure 3.1a) was that all body sizes are equally affected when species richness changes preserving the original distribution, while the second hypothesis (Figure 3.1b) was that only extreme body sizes are affected altering the original body size distribution, when richness changes. Thus, assuming a fixed change in richness, the change in body size at the extreme ends of Figure 3.1a should be smaller than in Figure 3.1b ($\Delta BS_a < \Delta BS_b$; see methods). Consequently, the slopes of a regression between species richness (as dependent variable) and extreme body size is expected to be steeper under the first hypothesis (Figure 3.1a) than the second (Figure 3.1b). If the average slope of the first null model, in which I randomized body size keeping species richness constant (sampling effect), mimics the first hypothesis then the average slope

should be close to the empirical. However, the empirical slope is shallower than the average null model slope rejecting the first hypothesis and supporting the second hypothesis suggesting that the obtained relationships between extreme body sizes and species richness are not purely a sampling effect.

My second and third null models add mechanisms to the sampling effect of the first model. They explore potential underlying mechanisms of the strong relationship between the smallest species and species richness, and the weak or non-existent relationship between the largest species and species richness. In the second and third null models, I incorporated coarse scale latitudinal and continental patterns related to abiotic filters and biogeographic history, and they showed a close association to the observed patterns (Figure 3.4b, 3.5b). Latitude has long been identified as a major factor generating many ecological patterns because of its correlation to various abiotic factors. Abiotic filtering such as environmental harshness, climatic instability, and climatic oscillations increases with latitude and affects both body size and species richness (Douglas, 1987; Leprieur et al., 2011). My results from the second simulation indicate that abiotic filters related to latitude may be generating a close relationship between species richness and the size of the smallest species across ecoregions. Harsher environments pose more severe constraints on the smallest species than the largest species due to their mass specific metabolic rate and energy reserve. Metabolic constraints on the smallest species arise because small organisms have a higher basal metabolic demand per unit mass than larger organisms (Downhower, 1976). In addition, large animals have a competitive advantage during hard times because they can resist longer periods of starvation due to higher capacity for energy storage (Werner &

Gilliam, 1984; Biro & Morton, 2004). Thus, the strong relationship between species richness and the smallest species may be due to the effect of harsher environments affecting the smallest species in the beginning ultimately changing species richness.

My third simulation suggests that continental effects such as historical contingencies, glacial history, and dispersal could also be responsible for the relationship between size of the smallest species and species richness in freshwater fishes. The importance of historical factors to species richness is consistent with dispersal abilities and their ability to colonize newly exposed areas (Griffiths, 2006). In the northern hemisphere, selective extinction of small range species caused by quaternary glaciations may explain present-day patterns of species distribution (Leprieur & Brosse, 2009; Olson et al., 2009). The contemporary species distribution is further attributed to dispersal constraints limiting or slowing the post-glacial recolonizations from the south (Matthews, 1998; Leprieur et al., 2011). For freshwater fish, the distance fish disperse is positively correlated to body size (Bernatchez & Dodson, 1987; Gaston & Lawton, 1988a, 1988b). Large fish are more efficient at recolonizing previously glaciated areas (Knouft, 2004; Griffiths, 2006, 2012). Thus, the fishes' differential ability to disperse and low species richness in previously glaciated areas may partly explain the strong relationship between the size of the smallest species and species richness.

Given that harsher environment and strong dispersal ability favors the largest species, the question arises why the same factors could not generate a strong relationship between species richness and the largest body size? Although the largest species are favored in harsher environments, they may not be governed by harsher environments. The large body size requires the acquisition of large amounts of food and much space for

resting and reproduction such that the largest species can inhabit only the largest contiguous habitats (Minns, 1995; Marquet & Taper, 1998; Kramer & Chapman, 1999). This means the largest species are limited by habitat availability independently of species richness (see Chapter 2 for more details). Thus, there is no strong relationship between species richness and the largest species. Similarly, the strong dispersal and migration ability in the largest species may homogenize the largest body size across space lessening the relationship between the largest species and species richness.

In addition to above mentioned factors, the weaker than expected pattern for the size of the largest species also indicates that with increase in species richness, the largest fish do not become much bigger. In aquatic food webs, where trophic interactions are generally size-structured (Newman & Cohen, 1986; Jennings et al., 2001; Petchey et al., 2004) and species richness is positively related to food chain length (Post et al., 2000; Post, 2002), I expect positive relationship between the largest body size and species richness but my results suggested otherwise. This indicates that species keep packing around the smaller size classes rather than continuously extending the food chain to higher trophic positions. This may be due to a positive relationship between energy demands and body size, and a negative relationship between available energy and trophic position in food webs, counteracting and constraining food chain length (Cohen et al., 2003; Maxwell & Jennings, 2006). This concurs with my above discussion of habitat availability for the largest species. Thus, the size of the largest species depends upon habitable space, food, and energy availability that is independent of species richness.

As discussed above, latitude related abiotic factors may have helped generate the strong relationship between the size of the smallest species and species richness.

However, in addition to the discussed latitude related mechanisms, the sampling effect may also have affected the relationship between smallest species and species richness. Although the first null model suggests that the obtained results are not a pure sampling effect, I cannot fully discount the sampling effect because there is a high probability of increase in the smallest size as species numbers decrease. Species numbers decrease and body size increases with increasing latitude. Thus, the sampling effect and latitude related factors working in the same direction may have strengthened the pattern between the smallest species and species richness. For the largest species, there is a high probability of decrease in body size with decrease in species number, but the largest body size does not change much with latitude. Thus, for the largest species, there is only the sampling effect and no latitudinal effect. If the relationship between the largest species and species richness were solely due to the sampling effect, I would expect a strong positive relationship; however, the almost non-existent relationship suggest that factors unrelated to latitude such as habitat availability, are governing the size of the largest species.

In conclusion, my study revealed a strong correlation between the size of the smallest species and species richness, and a weak to non-existent relationship between the size of the largest species and species richness at a large spatial scale, which lends support to my third hypothesis. My first null model suggested that my result could not be fully explained by a sampling effect. However, I cannot fully discount the sampling and latitudinal effect playing roles on further strengthening the relationship between the smallest species and species richness. The second and third null models showed that latitudinal and continental structures could substantially contribute to the underlying mechanisms, even though they are not mutually exclusive. I believe that metabolic

constraints on the smallest species and their dispersal limitations contributed to their strong relationship with species richness. In contrast, the largest species' strong dispersal ability, which could homogenize the largest body size across space and habitat limitation, which is not related to latitude, may be factors that weaken the relationship between the size of the largest species and species richness. My study opened up a new dimension in the study of body size and its association with other biological parameters, which need to be tested across a range of organisms and scales.

Chapter 4

4 Body size and trophic level conservatism among freshwater fishes of the world

4.1 Abstract

Given that body size is linked to various aspects of biology including fitness, it is expected to be highly conserved. However, divergence in body sizes among closely related species could also be selected for if it provides opportunity for the species to overcome constraints and allows species to coexist. To examine the conservatism and similarity in body size and trophic level of freshwater fish, I employed a variety of statistical techniques including congener regression, random nested ANOVA and approximation of phylogenetic autocorrelation to determine 1) how conserved body size and trophic level of freshwater fish are within a genus; 2) whether body size conservatism change across body size classes and trophic levels; and 3) how variable body size is across the taxonomic hierarchy. I found that both body size and trophic level of freshwater fish are conserved, but trophic level is more conserved than body size. Small and large size classes have less conserved body sizes than the middle size class, and herbivores and high level predators have more highly conserved body sizes than omnivores and consumers. The variability in body size at order level was higher than at

family and genus level, which were nearly identical. In addition, body size conservatism in freshwater fish was substantially lower than in mammals. Divergence in body size for small and large body size class species may allow those species to reduce body size constraints and coexist with other species. Trophic adaptations are more complicated than changes in body size leading to low divergence and high conservatism in trophic level. In conclusion, low conservatism and high similarity among body sizes within family and genus, suggests that freshwater fishes' body size is highly plastic and responsive to environmental variations, while trophic level is highly conserved.

4.2 Introduction

Evolution of body size has intrigued evolutionary biologist for a long time because body size is inextricably linked to numerous aspects of organismal biology (Schmidt-Nielsen, 1984; Peters, 1986). Body size has an allometric relationship to life history, metabolic rate, growth rate, population cycle, and generation time (Kleiber, 1947; Fenchel, 1974; Damuth, 1981; Calder, 1984). Body size is also one of the most studied traits of organisms, especially in terrestrial organisms, leading to the development of several eco-geographic rules such as Bergmann's and Cope's (Bergmann, 1847; Cope, 1887). However, these rules fail to fully link evolution and ecology of body size, and often ignore the evolutionary processes governing body size (Bininda-Emonds et al., 2001). Here, I study the evolutionary aspects of body size. In particular, body size and trophic level conservatism and similarity in relation to taxonomic distance.

Although considerable research has been done to understand body size, there are paucity of studies that uses large databases and comprehensive taxonomic coverage. Few authors have studied body size across order, family and genus on subset of taxa in

mammals (Maurer et al., 1992; Smith et al., 2004). In particular, body size similarity in freshwater fish across taxa has remained unexplored. Despite genetic data and phylogenies for many taxa becoming available I had to base my research on taxonomy because available phylogenies for freshwater fish comprise only 1.5 % of freshwater species.

Given that body size is linked to various aspects of biology including fitness (Brown et al., 1993), it is expected to be highly conserved leading to closely related species having similar body sizes (Felsenstein, 1985; Freckleton et al., 2002). For example, in mammals, Smith et al. (2004) found strong body size conservatism within a levels of a taxonomic hierarchy. They estimated body size conservatism among species within genus and found a high level of congruence in body size within genus. Such congruence in body size among congener species implies stabilizing selective pressure in body size, which could be phylogenetic or ecological in nature (Smith et al., 2004). However, there are exceptions where congeners diverge in body sizes. Divergence in body size provides opportunity for the species to overcome current constrains and allow species to coexist with other species including congeners. The slight divergence in body sizes open up the niches for species allowing access to novel habitat and unused resources (Griffiths, 1986; Polo & Carrascal, 1999), because body size is considered one of the major axis of niche space (Hutchinson & MacArthur, 1959; Wilson, 1975). The difference in body size promotes niche differentiation and reduce competition among species by setting up a competitive gradient across size (Brown & Wilson, 1956; Hutchinson & MacArthur, 1959; Brooks & Dodson, 1965; Schoener, 1967; Hall et al., 1970).

Further, there are evolutionary trade-offs associated with body size. It is argued that there is an optimal body size at which species maximize their fitness (Brown et al., 1993). However, the optimal size most likely depends on environmental conditions and can fluctuate (Kozłowski & Konarzewski, 2005). But, it is clear that species at extreme end of body size distribution have high body size trade-offs in life-history and ecological characteristics, because they are the furthest from the optimal size and vulnerable to unfavorable environments (Dial & Marzluff, 1988; Hanken & Wake, 1993). In addition, the smallest body sizes are constrained by the thermodynamics of energy exchange due to their high metabolic rate, so there is a limit in body size below which species cannot exist (Stanley, 1973). Similarly, there might be an upper limit for the largest body size due to thermoregulation, heat loss and gain, food and habitable space requirements (Brown et al., 1993; Olalla-Tárraga et al., 2006). This may suggest that the extreme body size species are constantly evolving toward modal body sizes. This constant selection pressure toward a modal size may result in less body size conservatism among congeners in small and large fish species than in medium size ones.

The processes that govern body size diversification are complex and it is difficult to point towards a single factor that can explain the size variation within taxa (Maurer, 2003). However, the contribution of a specific factor is sometimes responsible for certain properties of size variation that can be identified by comparing size variation in species that have a similar suite of characteristics (Colbert et al., 2001). In this study, I am examining the effect of diet on body size conservatism in freshwater fish. The effect of diet has a significant impact on fish survival and growth (Sebens, 1987). The prevalence of gape limitation in freshwater fish predators has created size-structure

trophic interactions (Newman & Cohen, 1986; Jennings et al., 2001; Petchey et al., 2004). In particular, high level predators are limited by their gape size, which is related to their body size. Gape size increases with body size, but as discussed above, other limitations on body size may constrain large species. Similarly, freshwater fish herbivores are limited by the distribution of food quality (Gaines & Lubchenco, 1982). The paucity of herbivores in the temperate zone may be related to food quality (Gaines & Lubchenco, 1982; Floeter et al., 2005). It has also been suggested that having a large body size is advantageous for herbivores because large sizes favor a longer gut, which helps in food digestion (Kramer & Bryant, 1995). Thus, it is worthwhile to examine body size within trophic levels because diet constraints may have driven size evolution in freshwater fishes. In particular, for above mentioned reasons, body sizes of high level predators and herbivores could be highly conserved. However, that may not be equally true for other trophic levels. For example, omnivores are more opportunistic and feed on both plants and animals and their body size may be neither important for digesting food nor capturing food.

The similarities in many traits are due to shared evolutionary history, which is also called phylogenetic signal of traits. These traits are conserved. However, the strength of the signal varies by the nature of the traits. For example, body size is more conserved than behavioral traits because behavioral traits are highly responsive to the environment. The allometric scaling of body size with physiological parameters may lead to high conservatism. Thus, I expect body size similarity to decrease from genus to, family to order. That is, at genus level as species are closely related I expect more body size

similarity than at family and order level. Similarly, at family level there should be more body size similarity than at order level.

In this chapter, using the comprehensive taxonomic coverage of freshwater fish, I first examined the degree of body size and trophic level conservatism for freshwater fish. I hypothesize that both traits are conserved to some degree, but trophic level is more conserved given the species group related to diet. Further, I categorized fish by body size and trophic level and examined body size conservatism within categories. I hypothesize that body sizes in small and large size classes are less conserved than in medium-sized fish due to constraints related to body size. Smaller species are generally constrained by metabolism, while larger sizes are constrained by energetic cost, agility cost, and heat stress (Blanckenhorn, 2000). Thus, the selection pressure may work against the size of smallest and largest species. Similarly, among trophic groups I hypothesize that herbivores and top predators exhibit a higher body size conservatism than omnivores and consumers, because body size is an important trait for them: Herbivores are limited by the efficiency of digesting low quality food and top level predators are limited by their gape size, both related to body size. I also estimated the phylogenetic signal in body sizes, substituting taxonomy for phylogeny. I hypothesize that body size is evolutionarily conserved and expect to see similarities in body size across order, families, and genera at increasing order.

4.3 Methods

I used the same dataset that I used for chapter II and III. The taxonomic classifications were provided by FEOW (Freshwater ecoregions of the world). This

analysis used unique sets of species. I omitted monotypic genera, thus the total number of species used were 8392.

Since a comprehensive species level phylogeny is unavailable, I approximated phylogenetic relationships for freshwater fishes by using taxonomic classifications to determine the potential similarity and autocorrelation in body size. Such an approximation assumes that the evolutionary distances among congeneric species are equal, and evolutionary ages of genera, families and orders are unrelated to body size variability. The violation of both assumptions may lead to an underestimation of body size conservatism because species within a taxon that diverged earlier are more likely to have also diverged more in body size than more recently diverged species. A final assumption is that the size of a taxon is not related to its evolutionary age. Smith et al., (2004) suggested that these assumptions are robust. I applied the methodology they used for analyzing mammal body size conservatism and correlation across taxa to my fish dataset. I used four taxonomic levels: order, family, genus, and species. Super family and super genus were not available in the dataset.

4.3.1 Statistical analyses

4.3.1.1 Body size conservatism (congener regression)

Conservatism (equivalent to the calculation of heritability in Smith et al., 2004) is estimated using correlation analysis of offspring and parental phenotypes, the correlation of full or half siblings. Here, I used a regression analysis to determine the degree of conservatism among pairs of species at the genus level (e.g. Jablonski, 1987; Smith et al., 2004; Hunt et al., 2005) that is analogue to ‘full sibs’ in quantitative genetics

(Falconer, 1989). The slope of the regression analysis between two species was considered as the conservatism measure (Wray and Visscher, 2008). Value of one indicates the highest body size conservatism, i.e. under complete genetic control (Ayala, 1982).

For this analysis, I generated all pairs of species within the same genus for genera containing two or more species. Then, I plotted the body sizes of pairs on the x- and y-axes of a graph, and analyzed the plots using least squares regression. I also repeated the whole process by restricting the number of species pairs per genus to the species richness of the genus. In this way, all genera were equally weighted and species rich genera were prevented from unduly influencing the analysis. I categorized body sizes into three discrete logarithmic body size classes (0.00 – 0.85, 0.85 – 1.30, >1.30), which can be interpreted as smaller, mid, and larger sizes. These size classes were selected to achieve approximately equal sample sizes. Further, to test the robustness of the study and stability of size class, I increase the size class using a sliding window of 0.1 for all classes until the smallest size reaches to 1.15 (e.g. 0.00 – 1.15, 1.15 – 1.60, >1.60). Similarly, I decrease the size class using the same sliding window for all classes until the smallest size reaches 0.55 (e.g. 0.00 – 0.55, 0.55 – 1.00, >1.00).

To estimate the trophic level conservatism, I classified the trophic structure into four trophic levels. The classifications were done similar to chapter 2: 2.00 – 2.19: herbivore, 2.20 – 2.79: omnivore, 2.79 – 4.00: carnivore, and >4.00: high level predator (Froese and Pauly, 2011). For each trophic level, the species body size pairs were generated and trophic level conservatism was calculated as described above.

To further ensure that obtained results are robust, I examined the influence of species richness within genus assuming that the most speciose genus can unduly influence the result. The most speciose genus contained 267 species and there were six more genera containing more than 100 species. Higher number of species may lead to a larger body size range by random chance (Huston, 1997; Tilman et al., 1997) Thus, the variation in species body size also increases, which decreases the body size conservatism among species within genus. To examine the effect of species richness within genus on variability in body sizes, I plotted the variance in body size as a function of species richness within genus.

4.3.1.2 Body size similarity across taxonomic hierarchy

To determine the distribution of body size variability across the taxonomic hierarchy and find out whether any particular level harbors exceptional variability or evenness in body size, I used a random nested mixed model ANOVA following Pagel and Harvey (1988) and Read and Harvey (1989). The variance components estimated from these analyses represent the degree to which variation in body size among freshwater fish can be explained by deep evolutionary history (order) as opposed to recent history (e.g. genus). In a mixed model ANOVA, I used log transformed body size as a dependent variable and taxonomic classification order, family, and genus as nested independent variable. I further performed nested ANOVAs for each trophic level to determine the trophic level specific similarity in body size across the taxonomic hierarchy. I also used trophic level, which is a continuous variable, as an independent variable and taxonomic classification as dependent variable and performed a nested ANOVA. All the ANOVAs were fit in the ‘lme4’ package in R (Bates et al., 2013).

Phylogenetic autocorrelation is usually determined based on a phylogenetic tree. It measures the correlation between pairs of taxa situated at a given phylogenetic distance, for a given phenotypic trait. Phylogenetic autocorrelation is useful on detecting variations in patterns and processes underlying phenotypic variation. Here, I approximated phylogenetic autocorrelation following Gittleman and Kot (1990), substituting taxonomy for phylogeny. Normally, phylogenetic autocorrelation is calculated using a phylogenetic distance matrix. Here, I created a binary distance matrix for each taxonomic level. For example, to calculate autocorrelation at the species level within genus, I assigned a distance of 0 to congeneric species and 1 to species in different genera. I repeated this procedure for all taxonomic levels and calculated Moran's I (Moran, 1950). Values of Moran's I range from -1 to +1. Positive values indicate more similarity within genus, while negative values indicated more dissimilarity in the trait than would be expected by random chance. Zero indicates that the traits are randomly distributed.

4.4 Results

4.4.1 Body size conservatism (congener regression)

To test for body size conservatism in freshwater fish, the body size of pairs of species from the same genus were regressed against each other. Overall, body size conservatism of freshwater fish was 0.54 ± 0.002 (Figure 4.1) measured by the slope from regression between all possible pairs of species within genus. This indicates that the body size of freshwater fishes are conserved but substantially less so than mammals (~ 0.95) (Smith et al., 2004). The results obtained were robust because body size conservatism did not differ when I restricted the number of species pairs per genus to the number of species within the genus.

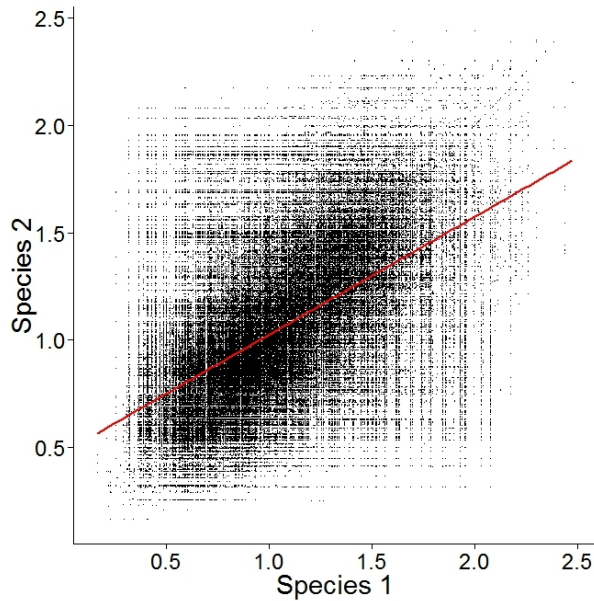


Figure 4.1: Body size conservatism at species level. All possible pairs of body sizes within genus are plotted as species 1 and 2. The body size conservatism is given by the slope.

Further, when regression analyses were conducted using three body size classes, I found that body size conservatism differs with body size class. Although, it is not strikingly different among the body size classes, smaller body sizes have less body size conservatism (0.21 ± 0.005) than mid-sizes (0.30 ± 0.004) and larger body size (0.24 ± 0.006) (Figure 4.2a). The tests using a sliding window of 0.10 in body size classes did not change the results and are thus not shown. There were slight changes in slopes, but the smaller size class always remained less conserved. Further, the examination of the influence of species number on the variation in body sizes showed that there is no significant pattern in the variation of body size and the number of species within genus (Figure 4.3).

Analysing body size conservatism for each trophic level, I found that herbivores (0.74 ± 0.007) and high level predators (0.78 ± 0.03) have a higher body size conservatism than omnivores (0.65 ± 0.002) and carnivores (0.51 ± 0.002) (Figure 4.2b). Due to the low sample size of high level predators (312 pairs) the results should be interpreted cautiously.

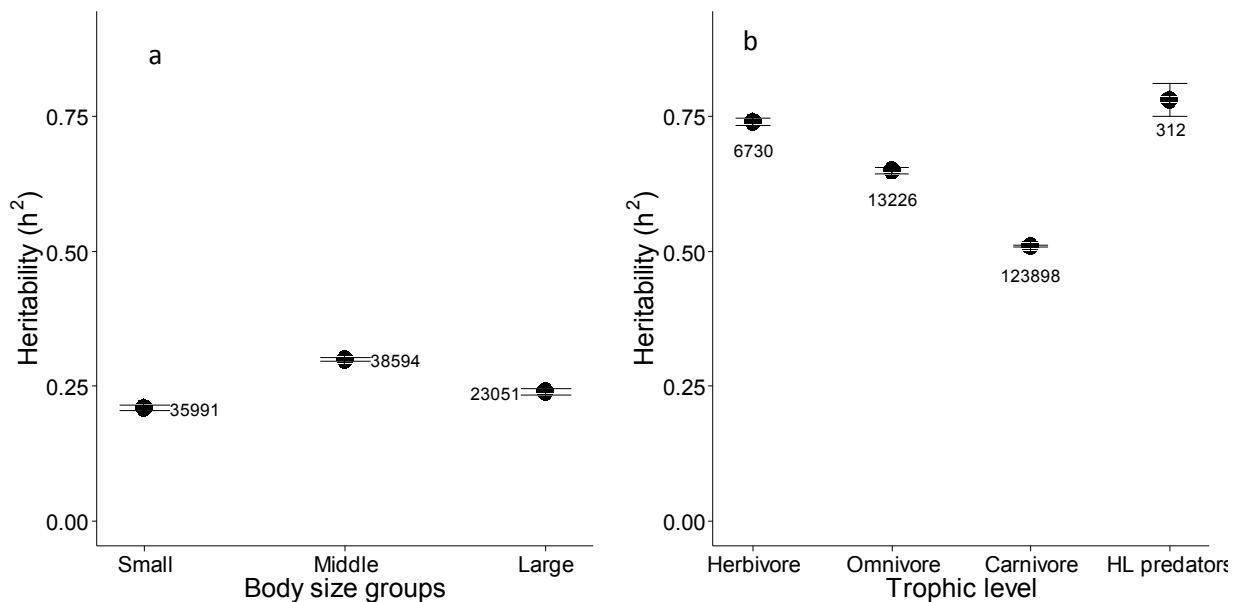


Figure 4.2: Estimation of body size conservatism for a) discrete logarithmic size categories b) each trophic level within genus. Body size conservatism was estimated by performing regression between pairs of species within a genus. a) Body size was categorized into smaller (0.00-0.85), middle (0.85 – 1.30) and larger size categories (>1.30). b) Trophic classifications were done using trophic groups given by Fishbase: herbivore 2.00 – 2.19, omnivore as 2.20 – 2.79, carnivore 2.79 – 4.00, and high-level predators >4.00. The numbers in both figures represent the number of body size pairs used in the regression.

Analysis of trophic level as dependent variable instead of body size showed that trophic level is a highly conserved trait (0.86 ± 0.001). In freshwater fish, trophic level is more conserved than body size.

4.4.2 *Body size similarity across taxonomic hierarchy*

Moran's I suggests that at least at the genus level freshwater fishes have a higher phylogenetic correlation ($I = 0.76$, $p < 0.05$) than expected by chance. Phylogenetic correlation decreases for family ($I = 0.40$, $p < 0.05$) and order ($I = 0.19$, $p < 0.05$) but even they were higher than expected (Figure 4.4). The nested ANOVA also supported the high variability in body size at order level (33.00%) and a lower variability at family (26.42%) and genus (26.28%) levels (Table 4.2). Interestingly, the family and genus levels showed a similar amount of variability in body sizes.

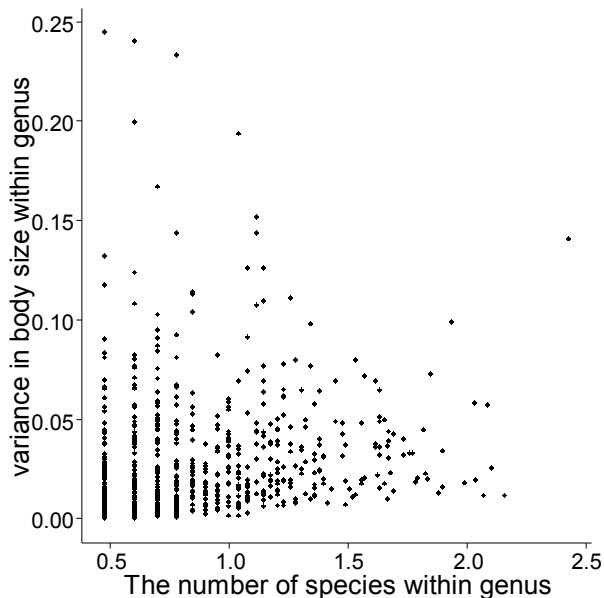


Figure 4.3: Variance in body size vs. the number of species within genus. The x axis has been \log_{10} transformed.

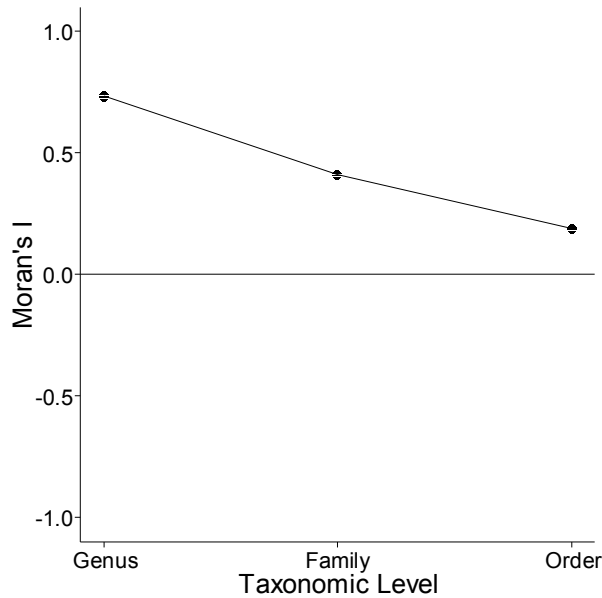


Figure 4.4: Phylogenetic autocorrelation (Moran's I) using Gittleman and Kot's (1990) approach. Genus indicates species within genus, family indicates genus within family, and order indicates family within order. High and low similarity in body size is indicated by values close to +1 and -1 respectively.

Table 4.1: Results from nested mixed model ANOVAs of overall variation in body size, variation in body sizes by trophic level, and overall variation in trophic level across the taxonomic hierarchy.

Variance source	Variance component	Percentage of total variance	Sample size (n)
Overall variation in body size:			
Order	0.0847	33.48	26
Family	0.0671	26.42	117

Genus	0.0665	26.28	716
Error	0.0350	13.82	
Total	0.253	100	
Overall variation in trophic level:			
Order	0.009	3.67	26
Family	0.127	51.83	117
Genus	0.082	33.47	716
Error	0.027	11.03	
Total	0.245	100	

4.5 Discussion

My analysis reveals that freshwater fishes have low body size conservatism (~0.54) in comparison to mammals (~0.95) (Smith et al., 2004). Trophic levels are more conserved than body size in freshwater fish. Further analyses on body size classes suggest that the body sizes in mid-body size fish are more conserved than in smaller and larger body size classes. Similarly, body size conservatism also differs among trophic levels. Among trophic classes, herbivores and top level predators show higher body size conservatism than omnivores and consumers. Similarity analyses across taxonomic hierarchy reveal that there is high variability in body size at the order level. However, the variability at family and genus levels is almost same. Low body size conservatism and high variability at the species level in freshwater fishes may be due to the opportunistic

indeterminate growth of freshwater fishes (Sebens, 1987; Charnov & Berrigan, 1991). Results obtained across freshwater fish taxa are recapitulated across different numbers of species pairs and different size classes too consistently to be a sampling artifact. Further, the lack of a relationship between the number of species and variance in body size within genus also confirms the robustness of the study.

Trophic levels are more conserved than body size. Trophic level conservatism is hypothesized to be higher than that of body size because trophic levels connect species more by their functions and physiology. For example, species eating similar food should have similar physiology to digest that food. Physiology also helps against toxins produced while eating and digesting the food. In addition, trophic levels also demonstrate the direct between species and their community and ecosystem processes. For example, energy flow is one of the major components of an ecosystem in a food web.

Conservatism is the proportion of phenotypic variance due to genetic factors. Low body size conservatism in freshwater fish in comparison to mammals suggests that freshwater fish body sizes are relatively plastic; they change in response to environmental factors. It is possible that morphological traits are significantly less conserved for poikilotherms than are for homeotherms due to the strong correlation between life history and body size for many homeotherms (Mousseau & Roff, 1987).

The body size in freshwater fish when classified by body size is even less conserved than across all species. However, as expected, the smaller and larger body size classes are less conserved than the middle sizes. This may be due to the selection pressure against those body sizes because those species already have high constraints related to

body size being farthest from the modal sizes, as modal size species are better competitors, and exploiters of resources (Maurer et al., 1992; Brown et al., 1993; Koziowski & Weiner, 1997). Thus, divergence in body sizes will allow those species to reduce the body size constraints and coexist with other species. There is a physiological minimum body size, from which species tend to evolve away (Stanley, 1973). Thus for small species, there may be many opportunities and selection for increase in size, resulting in a low body size conservatism in small body size class. However, a similar reason may not be applicable to large body sizes. Nonetheless, thermoregulation, heat loss and gain, food and habitable space requirements may have constrained large body sizes and led to selection toward a modal size (Etienne & Olff, 2004; Olalla-Tárraga et al., 2006).

The variable body size conservatism among trophic levels indicates that herbivores and top level consumers are more conserved than omnivores and consumers. In a body size structured food web, it is expected that the top level predators show high body size conservatism because predators are constrained by gape size, which is directly related to body size. However, herbivores showing high body size conservatism suggest that their body sizes are governed by different physiological or ecological limitations. They may be constrained by food quality and their digestive efficiency. Body size is related to length of gut, which in turn is related to digestive efficiency in herbivores making body size a highly conserved trait (Gaines & Lubchenco, 1982; Floeter et al., 2005).

The similarity in freshwater fish body sizes across taxonomic hierarchy obtained by two different methods, the nested random mixed model ANOVA and Moran's I,

showed a higher level of variability at order level followed by family and genus levels. However, there is not much difference in the variability at family and genus levels, which implies that the diversification in body size in freshwater fish may be attributable to relatively recent events. The evolution and current distribution of fish widely reflect paleogeographic and paleoclimatic complexity (Hocutt, 1986; Bermingham & Martin, 1998). It is possible that during series of glaciation periods in the past, freshwater fish were isolated and forced to shelter in refugia, which increased competition among species and thus promoted high diversification rates in body size among isolated survivors and thus body size at species level may have evolved to almost the same variability as at genus level (Knowles, 2001; Near & Benard, 2004).

Freshwater habitats are considered fish archipelagos, meaning they are isolated by physical barriers isolating species in different basins (Rosenzweig, 1995). This limits the gene flow among species, which promotes local speciation (Rosenzweig, 1995). Speciation leads to high body size conservatism (Calder, 1984). When species speciate, they tend to retain similar sizes as congeners due to the allometric scaling of body sizes (Calder, 1984). However, my results showed a low body size conservatism and relatively high variability in body size at the species level. This may be due to two different mechanisms 1) Body size of freshwater fish is highly responsive to environmental variation. It is possible that congeners have similar body sizes during speciation but later those species independently evolve in response to environmental favorable body sizes (Ricklefs & Latham, 1992). 2) The potential for indeterminate growth in freshwater fish, depending upon resources availability, can obscure body size conservatism and similarity among closely related species (Sebens, 1987; Charnov & Berrigan, 1991). Further,

freshwater fish body sizes highly vary depending upon the food availability during their first year (Sogard, 1997; Johnson & Grorud-Colvert, 2014).

Species rich taxa may have a large range and variability in body size, because high species richness leads to a high probability of having a large range of body sizes simply by a sampling effect or a random model of evolutionary change (Gould, 1988). I found no such association between variability in body size and number of species within a genus, which indicates that the obtained results were not due to a sampling effect. The relationship may further imply that 1) when lineages diversified, descendants did not expand their range of body size; 2) Many of the descendants with large range were outliers and therefore may have a high probability of extinction.

In conclusion, body size and trophic level are both conserved traits. However, body size is less conserved in freshwater fish than in mammals. This might indicate that body size conservatism varies from taxa to taxa, and largely depends upon the constraint related to traits, life-history, and development. The body size conservatism in fish is higher at the small and large end of the body size distribution, which may be due to constraints associated with body sizes. Similarly, herbivores limited by physiological and ecological mechanisms, and high level predators limited by gape size, showed higher body size conservatism than omnivores and consumers. Finally, low body size conservatism and high variability in body size at the species level both point toward the conclusion that freshwater fish body sizes are highly responsive to environmental conditions, with the caveat that indeterminate growth in fish may have also contributed to these results.

Chapter 5

5 Phylogenetic caveats

As in any study based on empirical data, but particularly studies based on large databases that were not specifically designed to answer the questions I posed, reservations remain about the quality of the data and their suitability to the study. Although I used published data, there were multiple sources of error and uncertainty in the database. Data from North America, Europe, and Australia were highly reliable. However, data from Asia, Africa and South America may have been less complete. Given the errors and uncertainty, the patterns I showed in my results are strong and robust. Thus, it is highly unlikely that improved quality of data will alter the results substantially.

The primary caveat of this study, especially for chapter 2 and chapter 3, is a lack of information on phylogeography and phylogeny. Here my discussion of the phylogeography and phylogenetic issues mostly focus on chapter 2, however the argument is equally relevant to chapter 3. I was unable to use a phylogenetically-explicit approach to analyze the geography of body size because even the best available phylogenies (e.g. Near et al., 2013) offer only order-level resolution of relationships among the 9613 species in my analyses. Only 1.5% of 9613 species are covered in this phylogeny. In freshwater fishes, there is extensive size variation within most families, and even many genera, necessitating highly-resolved phylogenies in order to properly use

phylogenetic comparative methods. Nevertheless, I recognize the potential for phylogeographic influence on body size patterns, and for phylogenetic autocorrelation to bias regression analyses of trait patterns. For instance, in the second chapter, fish assemblages found at high latitude in the southern hemisphere fail to support Bergmann's rule (Figure 2.2), perhaps because they are both depauperate and strongly biased in which clades are present. Fish lineages differ in propensity for body size evolution (Rabosky et al., 2013), amplifying the broader issue of phylogenetic non-independence when comparing traits among groups of species (Felsenstein, 1985; Revell, 2013). However, several aspects of my analyses minimize the risk of systematic bias due to either artifacts of historical phylogeography or phylogenetic autocorrelation. Regarding phylogeography, for chapter 2 where I categorize body size into 11 different deciles and for chapter 3 where I use only the size of the smallest and largest species (equivalent to 0th and 100th deciles from chapter 2), each of my regressions was based on 319 distinct ecoregions, generally encompassing 4-6 continents, making it unlikely that phylogeographic idiosyncrasies would be replicated. On average, each size decile encompassed data from 10.45 orders, 14.82 families, and 33.73 genera of fish at high latitudes (>44°), 10.64 orders, 29.00 families, and 87.36 genera at middle latitudes (22-44°), and 12.73 orders, 46.64 families, and 123.27 genera at low latitudes (0-22°; Table A1; Appendix A). The large number of lineages represented in my results from each size decile and latitudinal band leaves little scope for phylogeographic idiosyncrasies to be problematic. Finally, it is worth noting that if widespread lineages with conservative body sizes did influence my results, their effect would have been to reduce apparent latitudinal

gradients in body size. Therefore, my inability to correct for phylogeny may make my results slightly conservative.

The related but separate problem of phylogenetic autocorrelation biasing regression analyses is also minimized by my research approach. The body sizes for each ecoregion were extracted as quantiles from ecoregional size distributions, and thus can be thought of as representations of size patterns rather than the size of particular species. I look forward to the day when complete phylogenies allow comparative statistical analyses for the world's freshwater fishes, but the arguments above suggest that the patterns revealed by my analyses are likely to be robust even when explicitly accounting for evolutionary relationships.

Conclusion

My analyses of global freshwater fish body size world-wide at ecoregional scale, encompassing unprecedented numbers of species revealed some interesting and novel findings. Analyzing Bergmann's rule, my study confirmed that in general Bergmann's rule applies to freshwater fish. However, when species were classified by trophic level or body size a more nuanced view of size shifts with latitude emerged. The differences among body size deciles and trophic groups may help to explain some of the conflicting results reported in previous assessments of Bergmann's rule at smaller scales. The global analysis of the environmental correlates of Bergmann's rule pattern were not very robust due to intercorrelation among the factors; however temperature plays a prominent role at lower size deciles. In contrast, for the largest species, for which temperature has a negligible effect, availability of habitable space plays a limiting role.

In chapter two I found that the size of the smallest species in an ecoregion is strongly correlated to species richness, while the same relationship between the size of the largest species and species richness is very weak. My null models suggest that the result cannot be completely explained by a sampling effect. While the sampling effect plays a role in these relationships, it cannot fully account for them. Although the latitude and continental based null models were close to the empirical model for the smallest species, the causal connection between latitude, species richness and body size pointing

in the same direction may have further strengthened the relationship between the smallest species and species richness. However, this is not true for the largest species which exhibit no relationship between size of the largest species and latitude. The weak pattern between the largest species and species richness may be due to factors unrelated to latitude such as habitat availability.

Body size and trophic level are conserved traits, but in comparison with mammals body size of freshwater fish has low body size conservatism. Comparatively, higher trophic level conservatism than body size conservatism may be due to the more complicated physiological requirements of capturing and processing of certain types of food. The constraints employed on body size, especially at the smallest and the largest size, resulted on lower body size conservatism in small and large body size classes than in the medium size class. The smallest and the largest species are constrained by their physiology and energetic requirements. Among trophic levels, herbivores and high level predators showed high body size conservatism indicating the importance of body size on their feeding process. Herbivores are limited by the low food quality of their food and consequently the high space requirements of the digestive tract, and high level predators are limited by the gape size necessary to capture their prey. Finally, the variability analysis across the taxonomic hierarchy and overall body size conservatism reflect the indeterminate growth in freshwater fish. Further, it also indicates that freshwater fishes are highly responsive to environmental variation.

Interestingly, Bergmann's rule, species richness, and body size conservatism were different for different size classes. Moreover, Bergmann's rule and species richness were driven by the smallest species. At higher latitudes, the rareness of small species may be

due to their physiological limits, which affects the overall body size distribution and species richness. Thus, the size of the smallest species in an assemblage appears to be linked to and responsible for several macroecological patterns, which are themselves linked by metabolism and environmental constraints. Therefore, the smallest size could make for a more useful characteristic of an assemblage than the mean or median body size. In contrast, the lack of patterns in large species suggests that the largest species are governed by other constraints, such as habitat availability, which are not closely related to other macroecological patterns. In addition, the dispersal ability of the largest species may homogenize their distribution further obscuring macroecological patterns. My novel results may open up a new research area in extreme body sizes and would benefit from validation in other taxa.

Appendix A

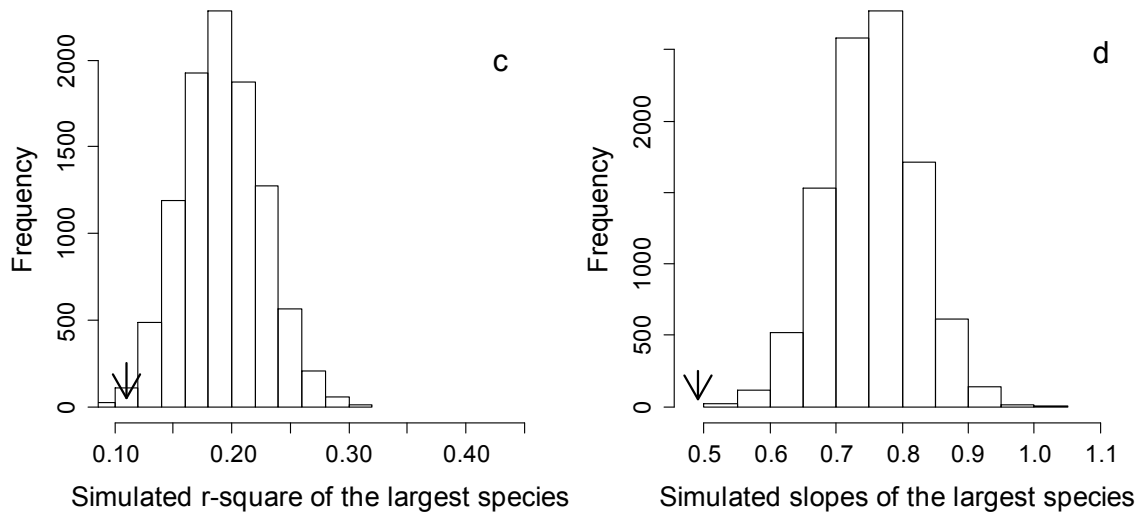


Figure A1: Simulated (c) R^2 and (d) slopes obtained from the linear regression between species richness vs the largest body size of species. Body sizes for each ecoregion were extracted from respective randomized continental pools keeping species number same as original.

Table A1: Count and averages of taxa in my analyses by 22 degree latitudinal band. When deciles fell between two taxa, both were counted.

Lat	0-22						22-44						>44					
Decile	G	F	O	G/Eco	F/Eco	O/Eco	G	F	O	G/Eco	F/Eco	O/Eco	G	F	O	G/Eco	F/Eco	O/Eco
0	82	31	10	0.61	0.23	0.07	51	20	7	0.44	0.17	0.06	30	14	11	0.50	0.23	0.18
1	123	40	13	0.91	0.30	0.10	91	28	11	0.79	0.24	0.10	38	17	11	0.63	0.28	0.18
2	150	51	13	1.11	0.38	0.10	98	31	11	0.85	0.27	0.10	40	17	13	0.67	0.28	0.22
3	139	46	10	1.03	0.34	0.07	102	33	11	0.89	0.29	0.10	37	14	11	0.62	0.23	0.18
4	146	49	11	1.08	0.36	0.08	116	37	10	1.01	0.32	0.09	40	20	13	0.67	0.33	0.22
5	152	53	14	1.13	0.39	0.10	99	36	13	0.86	0.31	0.11	44	21	15	0.73	0.35	0.25
6	155	57	16	1.15	0.42	0.12	102	29	12	0.89	0.25	0.10	40	17	12	0.67	0.28	0.20
7	135	51	14	1.00	0.38	0.10	103	32	10	0.90	0.28	0.09	33	11	9	0.55	0.18	0.15
8	125	51	14	0.93	0.38	0.10	84	28	12	0.73	0.24	0.10	30	11	5	0.50	0.18	0.08
9	104	49	13	0.77	0.36	0.10	76	26	11	0.66	0.23	0.10	25	12	7	0.42	0.20	0.12
10	45	35	12	0.33	0.26	0.09	39	19	9	0.34	0.17	0.08	14	9	8	0.23	0.15	0.13
Mean	123.27	46.64	12.73	0.91	0.35	0.09	87.36	29	10.64	0.76	0.25	0.09	33.73	14.82	10.45	0.56	0.24	0.17
N	144						123						52					

G = Genus; F = Family; O = Order; G/Eco = Count of genera divided by number of ecoregions; N = Number of ecoregions per latitudinal band

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