Climatic Dependence of Terrestrial Species Assemblage Structure

Kevin R. Walker

Thesis submitted to the
Faculty of Graduate and Postdoctoral Studies
University of Ottawa
in partial fulfillment of the requirements for the
PhD degree in the
Ottawa-Carleton Institute of Biology

Department of Biology
Faculty of Science
University of Ottawa

Acknowledgements

Many people have been helpful and supportive during the development and completion of this thesis. I am sincerely grateful to my supervisor, Dr. David Currie, for giving me the opportunity to pursue my degree under his supervision. David’s insights and philosophy of science have provided me with a new perspective on and approach to doing and practicing science. Thank you to my committee members Dr. Lenore Fahrig and Dr. Jeremy Kerr for their challenging questions and intellectual support, and to my colleagues for their suggestions, recommendations, and conversations throughout my experience as PhD candidate: Adam Algar, Rachelle Desrochers, Katie Gibbs, Jay Fitzsimmons, Véronique Boucher Lalonde, Derik Lawlis, and Hector Vazquez. Thank you also to Dr. Rees Kassen and Dr. Antoine Morin who have provided invaluable comments, suggestions, and recommendations towards this thesis. Lastly, I am thankful to and grateful for my mother, Diana Walker and my father, Larry Walker. I could not have completed this thesis without all of their emotional and financial support. I dedicate this thesis to both of them.

Statement of Thesis Contributions

The following thesis is presented as a series of manuscripts that will be submitted for publication. Some of the chapters are related in subject matter, thus have some repetition among the text. I apologize in advance for such repetition.

Table of Contents

List of Tables

List of Figures

Abstract

An important goal of ecological studies is to identify and explain patterns or variation in species assemblages. Ecologists have discovered that global variation in the number of species in an assemblage relates strongly to climate, area, and topographic variability in terrestrial environments. Is the same true for other characteristics of species assemblages?

The focus of this thesis is to determine whether species assemblage structure, defined primarily as the body mass frequency distributions and species abundance distributions relate in convergent ways to a set of a few environmental variables across broad spatial scales.

First, I found that for mammals and trees most of their geographic variation across North and South America in assemblage structure is statistically related to temperature, precipitation, and habitat heterogeneity (e.g. different vegetation types) in convergent ways.

I then examined bird assemblages across islands and continents. Despite the evolutionary and ecological differences between island and continental assemblages, I found that much of the variation in bird assemblage structure depends on temperature, precipitation, land area, and island isolation in congruent patterns in continent and island bird assemblages.

Frank Preston modeled species richness based on the total number of individuals and the number of individuals of the rarest species. Building on Preston's model, Chapter 2 hypothesized that gradients of diversity correlate with gradients in the number of

individuals of the rarest species, which in turn are driven by gradients in temperature and precipitation. This hypothesis assumes that species abundance distributions relate to temperature and precipitation in similar ways anywhere in the world. I found that both the number of individuals of the rarest species (*m*) and the proportion of species represented by a single individual in samples of species assemblages *(Φ)* were strongly related to climate. Moreover, global variation in species richness was more strongly related to these measures of rarity than to climate. I propose that variation in the shape of the log-normal species abundance distribution is responsible for global gradients of species richness: rare species (reflected in *m* and *Φ*) persist better in benign climates.

Even though body mass frequency distributions of assemblages show convergent patterns in relation to a set of a few environmental variables, the question remains as to what processes are responsible for creating the geographical variation in the body-size distribution of species. Several mechanisms (e.g. heat conservation and resource availability hypotheses) have been proposed to explain this variation. Chapter 5 tested and found no empirical support for the predictions derived from each of these mechanisms; I showed that species of all sizes occur across the entire temperature gradient.

In conclusion, assemblage structure among various taxonomic groups across broad spatial scales relate in similar ways to a set of a few environmental variables, primarily mean annual temperature and mean annual precipitation. While the exact mechanisms are still unknown, I hypothesize several to explain the patterns of convergent assembly.

Résumé

Un but important de l'écologie est d'identifier et d'expliquer la variation de premier ordre dans les caractéristiques des assemblages d'espèces. Un des patrons ayant déjà été identifié par les écologistes, c'est que la variation mondiale de la richesse en espèces est liée à la variation du climat, de l'aire et de la topographie. Est-ce que d'autres caractéristiques des assemblages d'espèces peuvent être reliées à ces mêmes variables?

Le but de cette thèse est de déterminer si la structure des assemblages d'espèces, ici définie comme la distribution des fréquences de masse corporelle ainsi que la distribution d'abondances des espèces, est reliée de manière convergente à un petit ensemble de variables environnementales, et ce, partout dans le monde.

D'abord, j'ai déterminé que, pour les mammifères et les arbres, la majorité de la variation géographique dans la structure des assemblages d'espèces est reliée statistiquement à température, précipitation, et l’hétérogénéité du couvert végétal , et ce, de manière convergente pour l'Amérique du Nord et du Sud.

Je me suis ensuite penché sur l'assemblage des oiseaux sur les îles et les continents. Malgré les larges différences évolutives et écologiques qui distinguent les îles des continents, je démontre que la majorité de la variation dans la structure des assemblages d'oiseaux dépend de la température, la précipitation, la superficie et l’isolation de façon congruente sur les îles et les continents.

Frank Preston a modélisé la richesse en espèces d'une localité, basée sur le nombre total d'individus ainsi que le nombre d'individus de l’espèce la plus rare. En s'appuyant sur les modèles de Preston, Chapître 3 propose une nouvelle hypothèse voulant que les gradients de diversité dépendent des gradients du nombre d'individus de l’espèce la plus

rare. Celle-ci dépend des gradients de température et de précipitation. Cette hypothèse repose sur le postulat que la distribution d'abondances des espèces dépend de la température et la précipitation, et ce, de la même manière n'importe où au monde. J'ai mis en évidence que le nombre d'individus de l'espèce la plus rare (m), ainsi que la proportion d'espèces représentées par un individu unique (Φ) dans des échantillons locaux étaient fortement reliés au climat. D'ailleurs, la variation globale de la richesse en espèces était plus fortement reliée à ces indices de rareté qu'au climat. Je propose que la variation dans la forme de la distribution log-normale d'abondances d'individus soit responsable des gradients mondiaux de richesse en espèces. En d'autres mots, les espèces rares (indiquées par m et Φ) persistent mieux dans des climats bénins.

Malgré que la distribution des fréquences de masse corporelle des assemblages d'espèces soit liée de manière convergente à seulement quelques variables environnementales, la question demeure à savoir quels processus sont responsables des gradients géographiques de variation en masse corporelle des espèces. Plusieurs mécanismes ont été proposés pour expliquer cette variation. Dans Chapitre 5, j'ai testé les prédictions dérivées de chacun de ces mécanismes sans trouver de support empirique pour aucun. Je démontre aussi que des espèces de toutes tailles se retrouvent sur le gradient de température en entier.

En conclusion, la structure des assemblages d'espèces, pour différents groupes taxonomiques et à travers le monde, est liée de façon similaire à un petit nombre de variables environnementales. Bien que les mécanismes soient encore inconnus, j'en propose plusieurs pouvant expliquer ces patrons d'assemblages convergents.

Introduction

"*To do science is to search for repeated patterns, not simply to accumulate facts…to search for patterns of plant and animal life that can be put on a map"*—MacArthur 1972

Ecologists are fundamentally concerned with understanding and predicting the distribution and abundance of organisms. Additionally, an important goal of ecological studies is to identify and explain the statistical regularities in characteristics of species assemblages. However, much of ecology has focused on explaining unique properties of particular biotic assemblages, of individual species' distributions, or of particular inter-specific interactions. As stated in Ricklefs and Miller's *Ecology*, ecology is "…the study of the interactions of organisms with their physical and biological environment" (Miller & Ricklefs 2000). If ecology is about the interactions of organisms and if these interactions vary across space and time, then discovering and predicting broad scale regularities across space seems unlikely.

Moreover, it is often known and taught that species assemblages are structured or influenced by a large number of factors: idiosyncratic historical differences among regions, in rates of evolution and extinction (Latham & Ricklefs 1993; Ricklefs & Schluter 1993; Wiens & Donoghue 2004; Wiens *et al.* 2005; Weir & Schluter 2007; Krug *et al.* 2009), biotic interactions (Tilman 1985; Mulder *et al.* 2001; Michalet *et al.* 2006), disturbance (Huston 1979; Molino & Sabatier 2001; Svensson *et al.* 2012) and phylogenetic niche conservatism (Webb *et al.* 2002; Graham *et al.* 2004; Wiens & Donoghue 2004; Wiens *et al.* 2005; Wiens & Graham 2005; Lowenberg-Neto *et al.* 2011; Stevens 2011). These factors vary across space and time, between continents, and between islands and continents, which suggests that broad-scale variation in assemblage structure is unlikely to be predictable.

There has been much less effort by ecologists to identify ecological commonalities—a set of Newtonian style laws that account for the variation in the properties of species' distributions, abundance, productivity, and other related factors. One such commonality that has emerged over the past two decades is that most broad-scale variation in species richness is related to area, macroclimate, habitat heterogeneity, and isolation (Wright 1983; Currie 1991; Francis & Currie 2003; Hawkins *et al.* 2003; Kalmar & Currie 2006, 2007; Field *et al.* 2009; Tittensor *et al.* 2010). Species richness though is just one characteristic of assemblage structure.

Perhaps an equally powerful descriptor or characteristic of species assemblages than a list of species names is the body mass frequency distribution (BMFD) of an assemblage. Since nearly every aspect of an organism's physiology is body-size and mass[1] dependent (Peters 1983; Schmidt-Nielsen 1984), body mass is essential to many ecological and life-history characteristics such as population density, range size, and perhaps other characteristics (Peters 1983; Schmidt-Nielsen 1984; May 1988; Brown *et al.* 2004). This body mass-metabolism relationship has been used to scale from individuals to entire ecosystem processes (such as biomass production, net primary productivity) and stoichiometric patterns (Enquist & Niklas 2001; Enquist *et al.* 2003; Niklas *et al.* 2003a; Kerkhoff *et al.* 2005; Kerkhoff & Enquist 2006). Since body masses are also highly heritable or conserved among congeneric taxa across time and space (Smith *et al.* 2004; Lyons & Smith 2010), characteristics of species assemblages related to body mass (e.g. total resource use and those mentioned above) should also be predictable. Thus

---

[1] For the purpose of this thesis, the terms body mass and body size are interchangeable.

understanding the factors influencing body mass distributions over broad-spatial scales may be more important for the understanding of how assemblages are structured compared to using only the number of species.

In an attempt to explain why there are so many kinds of species, Hutchinson (1959) proposed that spatially co-occurring species should differ in body size by a specific size ratio (ratio of 1.3 – 2.0) due to competitive processes. However, because constant ratios of body masses should lead to roughly flat or uniform BMFDs on logarithmic scales, there is no reason to suggest that the BMFDs should vary systematically with climate. Later, Diamond (1975) proposed a series of community "assembly rules" suggesting that due to resource competition, species of similar body mass in similar trophic guilds cannot coexist. Holling (1992) further proposed that an irregular structure of the landscape and resource availability also determined size distribution and the number of species that occur in a region. All of these hypotheses (except Holling) suggest that the BMFD should be approximately uniform. Body mass distributions that deviate strongly from a uniform distribution suggest that biotic interactions are not responsible for their shapes indicating that other characteristics of the environment might be more important. Compared to species richness, the BMFD can provide more information about the evolutionary and ecological processes influencing assemblage structure.

Although it is often reported that shapes of the BMFD become more uniform with a decrease in scale and become more modal at continental scales, the shapes of BMFDs across similar scales are not consistent across continents (Brown & Nicoletto 1991; Marquet & Cofre 1999; Bakker & Kelt 2000; Kelt & Meyer 2009). Flat or uniform distributions often reflect competitive exclusion of similar sized species (Hutchinson 1959; Brown & Nicoletto 1991). Other studies have reported that characteristics of the environment also influence the shapes of the BMFD. For example, in open environments medium-size species (e.g. 500 g < mass < 8000 g) are often rare or absent while in arid environments large-sized species (e.g. mass > 8000 g) are rare (Legendre 1986; Croft 2001; Lyons & Smith 2010). It has also been reported that habitat specialization (e.g. arboreal species), as well as the lack of Pleistocene extinctions (e.g. *Proboscidea* of Africa), creates bi-modal distributions (Bakker & Kelt 2000; Kelt & Meyer 2009). In addition, bi-modal distributions can reflect past historical events such as the Great American Biotic Interchange between North and South America where North American mammals migrated to South American habitats with similar climates to their original North American ones (Marquet & Cofre 1999; Morales-Castilla *et al.* 2012). In summary, the geographical variation in the distribution of body sizes along with variation in the BMFD can provide important insight into the evolutionary and ecological factors influencing assemblage structure.

An important and yet unresolved question about regional assemblages and their characteristic structure is whether assemblages are structured by regional or local processes. Currently, it is unclear of the importance of both regional and local processes towards structuring species assemblages. (Mouquet *et al.* 2003; He *et al.* 2005; Houseman & Gross 2006; Rajaniemi *et al.* 2006; Harrison & Cornell 2008; Algar *et al.* 2011). From a predictive perspective, if assemblages are structured predominantly from local processes (e.g. competition or predation), then seemingly these processes would vary across space and be specific to individual assemblages. Consequently, it seems unlikely that characteristics of assemblages (e.g. BMFDs) would be predictable across space. Contrarily, if regional processes (e.g. abiotic variables) are responsible for assemblage structure, it seems likely that assemblage structure (e.g. BMFDs) should be predictable from a few set of environmental variables irrespective of the kinds of organisms studied (e.g. animal or vegetable) or the scale of the study (e.g. regional or local). I attempt to address this question in this thesis.

This thesis sought to determine whether characteristics of regional and local species assemblages show convergent patterns across broad spatial scales among different floras and faunas that have independently evolved. This thesis also tests whether variation in species assemblage structure depends more on region-specific processes (e.g. vicariance events), species-specific interactions, or depends more on characteristics of temperature and precipitation. Three objectives were thus established: 1). To determine whether assemblage structure of given taxonomic groups on different continents and among continents and islands relates to a set of a few environmental variables in consistent ways; 2). To hypothesize a new mechanism about gradients of species richness-that gradients of richness are causally determined by gradients of the number of individuals of the rarest species, which are determined by gradients in temperature and precipitation (this is based on the assumption that species abundance distributions relate in similar ways to temperature and precipitation across space); 3). To test whether using mean body mass accurately describes (as often assumed) the observed geographical variation of body masses and test the specific predictions from the leading hypotheses that attempt to explain the geographical variation of mammalian body sizes using various statistical methods.

This thesis is founded on the observation that the BMFD among taxa varies across space within continents, across continents, and at different scales (Brown & Nicoletto 1991; Blackburn & Gaston 1996; Marquet & Cofre 1999; Bakker & Kelt 2000; Smith *et al.* 2004; Allen *et al.* 2006; Rodriguez *et al.* 2006; Rodríguez *et al.* 2008; Kelt & Meyer 2009; Olson *et al.* 2009). This thesis, rather than describing how the shapes of the BMFD vary across space or scale, tests whether the characteristics of the shapes relate in predictable and consistent ways across broad-spatial scales among various taxonomic groups in relation to a few environmental variables such as temperature and precipitation.

To identify factors relevant to characteristics of species assemblages, this thesis relies on statistical macroecology-a big picture approach that seeks to identify predictable regularities in the structure and functioning of biological systems and to identify the processes that produce these patterns in nature. An underlying assumption is that statistical regularities or symmetries result from similar causal mechanisms. Most of the analyses depend on relating the variation in dependent variables across broad spatial scales to a few environmental variables and on the strength of such correlations to determine how well assemblage structure relates to selected characteristics of the environment.

The data used in this thesis occur across a broad-spatial space (e.g. across continents), but at different resolutions (e.g. the size of the individual units of observation, 100 x 100 km^2 vs. 0.1 ha). Chapters 1, 5 (both mammalian data), and Chapter 2 (avian data) test for significant relationships of a few environmental variables using coarse-grained range map data. A limitation in these chapters is that range maps tend to treat all species equally, and they do not include abundance data. On the other hand, tree data for Chapters 1, 3, and 4 use fine-grained data (e.g. number of individuals and number of species) at local sites that are limited in size (0.1 hectare). Data in these local sites could potentially bias the results particularly if the local site does not fully represent the regional assemblage. In addition, such fine-grained data could inaccurately represent species abundance distribution due to sampling error or sampling bias. However, even with such potential problems, such data have been used successfully to test and identify patterns across broad spatial extents (Gentry 1982; Clinebell *et al.* 1995; Enquist & Niklas 2001;

Niklas *et al.* 2003b; Currie *et al.* 2004; Burns 2007; Butt *et al.* 2008; Moles *et al.* 2009; Van Der Heijden & Phillips 2009; Kraft *et al.* 2011). Finally because macroecology relies on patterns and processes that occur over broad spatial scales, controlled or manipulative experiments typically cannot be performed, except with natural experiments, of which climate change is an example. However, once predictable statistical regularities have been identified, possible mechanisms can be addressed.

Chapter 1, using a few environmental variables, identifies broad scale commonalities in regional species assemblage structure, called *convergent assortment*, statistical patterns (not a mechanism) of predictable traits in sets of species assemblages (e.g. BMFD, species abundance distributions, functional traits and others). Kleidon and Mooney (2000) proposed that physics and chemistry constrain the number of different life histories or "species" that can occur under given environmental conditions, which raises the question of whether body masses (or other life history characteristics) of species also relate predictably to environmental conditions, even if species' names do not. This chapter tested whether assemblage structure, defined as BMFD and proportion of species in defined size classes of mammals and trees species relate to a set of a few environmental variables in consistent ways across the Americas. To describe the BMFDs, I used several descriptors (mean body mass, body mass skew, body mass variance, evenness of the BMFDs, and proportion of species in size classes) of the BMFD in 1196 200 x 200 km^2 grid cells for mammals across the Americas and used a similar procedure for 175 sites of 0.1 hectares for trees across the Americas. Even though the main biomes of the two continents are different: North America has cold dry regions while South America has warm wet ones and each continent has its own unique evolutionary and ecological history, this analysis tested the degree to which characteristics of biotic assemblages depend on climate related variables. I correlated characteristics of the BMFD from multiple regression analysis for mammals and trees to temperature, precipitation and habitat heterogeneity and then determined whether convergent patterns emerged by examining observed values as a function of predicted values.

Using a few environmental variables, Chapter 2 tested whether bird assemblage structure (e.g. BMFD) on islands and continents were similarly related to a few environmental variables and tested whether assemblage structure between islands and continents are actually ecologically different. From an evolutionary perspective, species assemblages on islands are usually portrayed as unique when compared to continental ones. First, for a given area, the number of species on islands is lower compared to that on continents, but as the area increases, the number of species increases faster on islands than on continents (Rosenzweig 1995). In contrast, the number of endemic species on islands is usually higher compared to that on continents (Kier *et al.* 2009). The geographic ranges of many island species are thought to show an initial increase (species becoming habitat generalist by escaping predation and parasitism), followed by a reduction (species becoming habitat specialist or subject to new predators or diseases: a process known as a 'taxon cycle' (Wilson 1961; Ricklefs & Cox 1972). Many of these evolutionary and ecological differences on islands typically result from the islands' isolation, their hard boundaries, their young age, and *in situ* speciation (MacArthur & Wilson 1963; MacArthur 1967; Losos & Schluter 2000; Whittaker *et al.* 2008).

Compared to their related continental species, small-bodied species evolve toward larger sizes while large-bodied species evolve toward smaller sizes (Foster 1964; Van Valen 1973; Case 1978; Adler & Levins 1994; Palkovacs 2003). These evolutionary changes in body size among closely related species between continents and islands are known as the "Island Rule". If evolutionary processes or ecological factors in fact structure island assemblages in different ways than those of continental assemblages, then it seems unlikely that characteristics of assemblages should relate to a set of a few environmental variables in similar ways. I used the relationship between assemblage structure of continents to temperature, precipitation, and area to predict assemblage structure on islands.

In Chapter 3, using Preston's canonical log-normal species abundance distribution, I tested the hypothesis that gradients of diversity are determined by gradients in the number of individuals of the rarest species, which in turn are driven by gradients in temperature and precipitation. For this chapter, my hypothesis relies on the assumption that convergence in assemblage structure is a common phenomenon. Specifically, it relies on the assumption that the geographical variation of the canonical log normal species abundance distributions relate to variation in temperature and precipitation in similar ways across space.

Broad scale ecological patterns are primarily dependent on a set of a few environmental variables, not on their different histories, geologies, or biotic interactions. It is well known that the broad spatial scale variation in the number of species depends upon temperature and precipitation (Currie, 1991; O'Brien, 1998; Francis & Currie, 2003; Hawkins *et al.*, 2003; Kalmar & Currie, 2007; Field *et al.*, 2009). Despite these strong correlations, proposed mechanism(s) driving biodiversity gradients remain few (except see (Allen *et al.* 2002). I attempted to unify the correlative approach with a mechanistic one and test whether gradients of biodiversity are caused by gradients of the number of individuals of the rarest species, which are themselves ultimately driven by gradients in temperature and precipitation.

Half a century ago, to explain why larger areas have more species, Preston (Preston 1962b, a) developed a mathematical model based on the canonical log normal distribution of species abundances. Preston's model predicted that species richness depends on individual density within the community as well as on the number of individuals of the rarest species. For the tests described in this chapter, I used Preston's model to test if the mechanism underlying geographic gradients of species richness might involve geographic variation in the number of individuals of the rarest species. I proposed that geographic gradients in richness arise from climate-dependent variation in the persistence of rare species. I tested three predictions of this hypothesis. It is already known that climate-richness correlations are very strong. First, I tested whether the proximal correlations (climate-rarity, rarity-richness) was stronger than the distal correlation (climate-richness). Second, if the tendency of rare species to persist is the driver of species richness gradients, then it should not matter how gradients of rarity arise. I tested whether the climate-rarity relationship observed on an elevational gradient is consistent with the climate-rarity relationship observed over latitudinal gradients. Third, I used structural equation modeling (path analysis) to test whether climate affects species richness via a measure of the persistence of rare species, rather than directly. Rarity here was considered as on one of the seven forms of rarity outlined by Rabinowitz *et al*. (1986) based on their range size, habitat breadth, and abundances.

Chapter 4 attempted to estimate the minimum sampling area needed to protect the rarest species based on abundance data, rather than based on species area relationships. In Chapter 4, I again used Preston's model to estimate the number of individuals of the rarest species (m) and the minimum sampling area for at least two individuals of the rarest species. Using the Alwyn Gentry tree data from Phillips & Miller (2004), I multiplied an appropriate scaling factor (in ha) to m, for 196 sites across the world. I then presented how this minimum for at least two individuals of the rarest species varies across continents and latitudes. Furthermore, because temperature and precipitation are related to many ecological patterns (see above references), I tested whether the minimum area correlated to temperature, precipitation, and the interaction between temperature and precipitation. Lastly, I estimated the cost in US dollars required to protect the rarest species among various countries and related this cost to the country's gross domestic product.

Because Chapters 1 and 2 used the BMFDs of different taxa to test whether convergent patterns exist in relation to a set of a few environmental variables, I wanted to conduct additional tests of the mechanisms that have been proposed towards explaining the geographical variation of body sizes. Chapter 5 outlines three such tests. Virtually all hypotheses about geographic variation in body size assume that body sizes vary with climate (or latitude) in a very simple manner: more large-bodied species and fewer smaller one in cold places. If this were the case, then mean body size should capture this variation well. First, I determined whether using mean body size of regional assemblages for describing the geographical variation of body size distributions are accurate as is commonly assumed by macroecologists (Blackburn & Hawkins 2004; Rodriguez *et al.* 2006; Rodríguez *et al.* 2008; Morales-Castilla *et al.* 2012). But if using mean or median body size of an assemblage does not accurately capture the geographical variation of body sizes, then such technique might incorrectly assign a pattern to a proposed mechanism (e.g. heat conservation hypothesis).

Second, I tested the pattern proposed by Bergmann that, on average, higher latitudes have fewer smaller species. Third, I tested the specific predictions from several competing hypotheses (heat conservation hypothesis, resource availability hypothesis, and the assumptions of the metabolic theory of ecology) that attempt to explain or describe the geographical variation in the distribution of mammalian body sizes, and offered an alternative hypothesis (the evaporative water loss hypothesis, EWLH) to explain the geographical variation in mammalian body sizes.

For these tests mentioned above, I calculated the number of species in ten body size categories in 1196 200 x 200 km^2 grid cells across the Americas, which resulted in a sample size of 11960. To test the competing hypotheses, I used the following independent variables reflecting each of the different hypotheses: mean annual temperature (K), mean annual precipitation (mm), resource seasonality (maximum monthly net primary productivity minus minimum monthly net primary productivity), and a categorical variable distinguishing among body size categories. I tested the predictions of each hypothesis using ANCOVAs.

Chapter 6 focused on the question of whether giant (elephant bird) and dwarf (dwarf elephant) body sizes deviate from expectations based on the relationship between maximum body size and land area. I used two data sets from Marquet and Taper (1998) and Millien and Gonzalez (2011) relating the maximum body size of mammals as a function land area across mountain tops of the S.W. U.S.A and Mediterranean land bridge islands to predict the body sizes of the extinct insular bird giants and dwarf mammals. If insular body size evolution is determined by specific clade interactions, (Raia & Meiri 2006, 2011) or by species specific competitive interactions, independent of area (Palombo 2009), it seems unlikely that body sizes should relate to island area in similar ways to that of extant contemporary mammals observed on continental mountaintops or land-bridge islands.

Since much of ecology has focused on the mechanisms to ‘understand’ natural patterns, the search for predictable patterns has often been eclipsed. Here, I show that a considerable degree of the composition of biotic assemblages across different continents and among different taxa is, in fact, predictable and show similar relationships to climatic variables (e.g. convergent assortment). Indeed, convergent assortment might form the basis for a new general pattern in macroecology.

1. Chapter 1: Convergent assortment of creatures great and small

Abstract

Aim: Many aspects of individual species' ecology depend strongly on climate and on body size. I hypothesize that, as a result, geographic variation in characteristics of species assemblages such as the body mass frequency distributions should relate predictably to climate, despite geographic variation in evolutionary histories.

Location: Western Hemisphere

Methods: I calculated several descriptors of the body mass frequency distributions of mammal species whose geographic ranges overlap 200 x 200 km^2 grid cells (n=1196) across the Americas. For each grid cell, I estimated mean annual temperature, total annual precipitation, and habitat heterogeneity. I then tested whether descriptors of the body mass distributions related strongly to climate, and indistinguishably so in North and South America. I conducted a similar procedure for 175 local (0.1 hectares) species assemblages of individual trees.

Results: First, very little (<3%) of the spatial variation in mammal or tree body sizes is related to mean body mass. Body size distributions are complex: peaked or skewed or punctuated with gaps in some regions, but not others. Second, for both mammal species and individual trees, geographic variation in body size frequency distributions is strongly related to temperature, precipitation, and habitat heterogeneity, $R^2 \approx 0.60$. Differences in body size distributions between continents account for an order of magnitude less variation than the congruent variation related to climate.

Main Conclusions: Mean body size is a weak descriptor of geographic variation in body size, despite abundant literature on the subject (cf. Bergmann's rule). In contrast, descriptors of body size distributions (evenness of the BMFDs, body mass variance, and proportion of species in size categories) relate strongly to climate across the Americas. Congruence of body sizes probably does not arise from resource partitioning. Rather, I suggest that climate and body mass may constrain the sets of physiologies that can survive in any given location. Any hypothesis about geographic variation of species' ranges must account, first and foremost, for the strong relationship of body size structure to climate.

Introduction

What factors are responsible for shaping the composition of species assemblages, local processes, or regional ones? Ideally, ecologists and biogeographers would like to be able to predict the composition of regional species assemblages. In part, the composition of species assemblages reflects a complex mixture of unique evolutionary and historical influences acting on individual species' distributions: geological history, climatic variations, dispersal and vicariance events, biotic interactions, chance, etc. (Qian & Ricklefs 2000; Whittaker & Field 2000; Buckley & Jetz 2007; Blount *et al.* 2008). Borrowing from S. J. Gould (1989), in a hypothetical replay of the tape of history, those historical vagaries could take species assemblages down a radically different path, and thus composition of assemblages would be unpredictable regionally and locally.

However, all these evolutionary and ecological processes are mediated by a common set of physical, chemical, and biological laws. While the tape of life plays, its participants are constrained by physics (gravity, density of surrounding media, mechanics), chemistry (stoichiometry), thermodynamics (reaction kinetics), etc. The rates of many of these processes depend strongly upon temperature and water availability (Brown *et al.*, 2004). They depend further upon organisms' body size (Peters 1983; Schmidt-Nielsen 1984).

Kleidon and Mooney (2000) proposed that physics and chemistry constrain *how many* different life histories (or species) can occur under given environmental conditions. I ask: might not the body mass frequency distributions of assemblages also relate predictably to environmental conditions, even if species' names do not? Species in similar physical environments often share traits, both in geographically isolated taxa (e.g., sunbirds in

Africa and hummingbirds in the Americas, marsupials in Australia and placental mammals elsewhere), and in independent lineages in the same environment (e.g., cetaceans and fish). This is termed convergent evolution. Simon Morris (2003) argued, "It really is not very important if the many details of an alternative history are different, because in broad outlook the study of evolutionary convergence demonstrates that the world, perhaps even any world, would have to look broadly similar".

Regional and perhaps even local, assemblage structure also seems likely to converge in physically similar environments. Nearly every aspect of organisms' physiology and ecology are dependent on body-size and/or climate, including metabolic rates, population density, growth rate, prey size, range size, etc. (Peters 1983; Schmidt-Nielsen 1984; Brown *et al.* 2004). Diamond (1975) proposed community "assembly rules", postulating that similarly sized species in a given guild cannot coexist or are forbidden, due to competition for similarly sized food items. Similarly, Holling (1992) proposed that the discontinuous structure of landscapes and resource availability dictates the number and body sizes of species that occur in an assemblage. Body size also dictates the density of trees, based on a simple power law (Enquist *et al.* 1998). It seems likely that other aspects of species' abilities to persist in particular environments similarly depend on body size and climate.

I hypothesize that, because temperature and water constrain multiple biological processes (e.g., Kleidon and Mooney 2000), regional and local species assemblages come to be composed of species with predictable body mass frequency distributions, in relation to climate. I refer to a statistical tendency for regional species assemblages to have predictable sets of traits (e.g. body mass frequency distribution, or other traits) in relation to environmental variables as "convergent assortment". Convergent assortment would result both from convergent evolution of traits, and from persistence of consistent subsets of species that disperse into a region. Convergent assortment predicts that: 1) characteristics of biotic assemblage structure (at the regional and local scale) such as body size distributions should correlate strongly with abiotic characteristics of the habitat, and 2) identical relationships should occur in independently evolved assemblages (e.g., on different continents). Convergent assortment is similar to the idea of environmental filtering affecting functional traits or phylogenies (Cornwell *et al.* 2006; Emerson & Gillespie 2008; Lebrija-Trejos *et al.* 2010; Algar *et al.* 2011). Convergent assortment, however primarily refers to statistical similarities while environmental filtering is depicted as a mechanism driving community structure.

Why is it important to know if BMFD relates predictably with climate across broad spatial scales among different taxa? First, nearly every aspect of an organism's physiology is body-size dependent (Peters 1983; Schmidt-Nielsen 1984). Body size relates to many ecological and life-history characteristics such as rates of metabolism, population density, range size, and perhaps other characteristics (Peters 1983; Schmidt-Nielsen 1984; May 1988; Brown *et al.* 2004). Body size also dictates the quality of resources required for maintenance, growth, and reproduction. Because of their high mass-specific metabolic rate, small-bodied species (< 100 grams) require high quality resources in order to assimilate quickly. Contrary, large-bodied species (>1000 grams) can utilize resources of poorer quality (Peters 1983; Brown & Nicoletto 1991).

Body sizes are also highly heritable and phylogenetically conserved among congeneric taxa across time and space. Moreover, the continental BMFD show remarkable similar patterns with respect to the BMFD worldwide despite the continents having unique taxa (Smith *et al.* 2004; Lyons & Smith 2010). As a result, characteristics of species assemblages related to body size (e.g. total resource use) should also be predictable. Thus understanding the factors influencing body size distributions over broad-spatial scales is important towards understanding the evolutionary and ecological processes effecting the geographical variation on body sizes. In summary, compared to species richness, the body mass frequency distribution can provide more information about the process influencing assemblage structure.

Regarding the shapes of the BMFD, it is often reported that the shapes become more uniform with a decrease in scale and are modal at continental scales. However, the shapes of the BMFD across similar scales are not consistent across continents (Brown & Nicoletto 1991; Marquet & Cofre 1999; Bakker & Kelt 2000; Kelt & Meyer 2009). Some studies have reported that characteristics of the environment or climate also influence the shapes of the BMFD. For example, in open environments, medium size species (e.g. 500 g < mass < 8000 g) are often rare or absent while in arid environments, large bodied species (e.g. mass > 8000 g) are rare (Legendre 1986; Croft 2001; Lyons & Smith 2010). As a result, the shapes of the BMFD could possibly provide information regarding the type of environments assemblages reside in.

Here, I examine whether regional variation the body mass frequency distributions relates predictably to ambient temperature and water availability. It is well known that body mass distributions in local species assemblages are typically modal and right-skewed (Brown & Nicoletto 1991; Bakker & Kelt 2000; Rodriguez *et al.* 2006; Rodríguez *et al.* 2008; Kelt & Meyer 2009), and that mean body size often decreases with temperature (an interspecific variant of Bergmann’s rule) (Blackburn *et al.* 1999; Blackburn & Hawkins 2004; Rodriguez *et al.* 2006; Rodríguez *et al.* 2008). As I show below, mean body size relates quite strongly to climate. However, mean body size captures very little of the overall geographic variation in body mass distributions. I examine whether climate successfully predicts much more than just mean body size, such as various other characteristics of the BMFDs.

Second, I tested whether body size distributions are congruent between North and South America, after controlling for climate. Because Pangaea began fragmenting during the Jurassic, 180 Myr BP (Scotese 2004), much of the evolutionary radiation of mammals and angiosperms and subsequent environmental jostling (tectonics, climate changes, paleo-anthropogenic influences, etc.) played out independently on the two continents. The faunas and floras of the two continents are quite distinct, with many species, and many families unique to each continent (see Table 1.1). Therefore, this analysis provides a natural experiment, testing whether regional species pool and local community assemblages in two different species pools converge as a function of climate related variables.

Material and Methods

I examined regional body size distributions in two ways. First, I examined body mass frequency distributions of mammals in the regional species pool that occur in different regions, without respect to relative abundance of individuals. Second, I examined the sizes of individual trees in local community assemblages, without respect to species. The tree plots were located across much of the Americas (Figure A.1).

Mammal species data

I first generated a grid with equal area cells, 200 x 200 km^2, covering North and South America. I used relatively large cells to minimize the potential effects of under-sampling in some South American regions. I superimposed the geographic ranges of the 1759 indigenous mammal species (Patterson *et al*. 2007). I excluded off-shore islands and coastal grid cells with <50% land. This resulted in 1754 mammalian species presence/absence in 1196 grid cells. Species richness represents the number of mammal species that occurred in each grid cell.

I included all mammal species in my analysis. Some earlier studies of mammal assemblages (Blackburn & Hawkins 2004; Rodriguez *et al.* 2006; Rodríguez *et al.* 2008) excluded volant species (bats) on the grounds that they use different resources, or different physical space, or have dissimilar metabolisms. However, applying similar reasoning, one might equally well exclude species that live in water, or underground, or that hibernate, or that are carnivorous, or that lack a placenta. My hypothesis provides no reason to exclude any particular group.

Species' body masses (g) were obtained primarily from Nowak (Nowak 1999b, a). I supplemented this source with Smith *et al*. (2003). When both male and female masses were given, the mean of the two was used.

Next, for each grid cell I generated a body mass frequency distribution (BMFD) of species that occur in each grid cell. To do this, I tallied the body masses of all species that occur in a given cell. I calculated the first three statistical moments (mean, variance, and skewness) of $\log_2$-transformed body masses. While the interpretation of mean body size and body size variance is intuitive, body mass skew is less so. As a first approximation, body mass skew describes the tail of the BMFD (Marquet & Cofre 1999). Body mass frequency distributions with a positive skew (right skew), have BMFDs typically characterized as having more small and medium sized species followed by a tail of few large species. For a negative skew (left skew), the BMFD typically has more medium and large bodied species followed by a left tail of few small-intermediate sized species.

The shapes of body mass frequency distributions are sometimes complex. To characterize complex shapes, I established 10 size bins that have approximately equal numbers of species in the hemispheric species pool (approximately 169 species per size category) but unequal ranges of body size (see Table A.1 for details). I chose this binning procedure because there are fewer large-bodied species than small-bodied species. Using the binned data, I calculated the evenness of the number of species observed among the size categories for each grid cell using the following equation: $G = e^{H} / S$ (Buzas & Gibson 1969) where e is the natural log base, H is the Shannon index for an individual grid cell, and S is the 10 size categories. This measure of evenness was used to estimate the shapes of the BMFDs. Evenness scales from zero to one, where zero represents a peaked distribution or a distribution with gaps and one represents a flat distribution or a distribution with no gaps. Most of the variation in the evenness relates to the number of empty size categories ($r^2 = 0.75$, Figure A.2). It is likely that species richness will affect the evenness measure since sites with fewer species have a higher likelihood of having no species among the ten size categories. As a result, I regressed evenness as a function of species richness and used the residuals from this relationship for the analysis.

I also carried out a principal component analysis (based on the covariance matrix) on the proportion of species in each grid cell that fall within each of the 10 size bins. Because I used the proportion of species, geographic variation in species richness does not influence the principal component analysis. Principal component 1 explained approximately 60% of the variation in changes of the proportion of species per bin, while components 2 and 3 increased the variation explained by an average of 8%. I therefore examined the geographical variation in principal component 1 (PC-1) in my analysis.

Principal component 1 was strongly negatively correlated with the proportion of species in size categories 2, 1, 3, 8, 9 while positively correlated in size category 10.

Environmental variables

Mean annual temperature (K), and mean annual precipitation (mm), were taken from WOLRDCLIM (Hijmans *et al.* 2005) at 30 arc-seconds (~1 km) resolution. These data are climate normals based on data from 1960-1990. Habitat heterogeneity was defined as the number of land cover types that occurred in a grid cell. Land cover classification data were obtained from: http://bioval.jrc.ec.europa.eu/products/glc2000/glc2000.php (~ 1 km resolution), which consists of 21 natural regional land cover types ranging from broadleaved evergreen forests to sparse herbaceous cover. All geographic system analyses were conducted using Arc/Info version 8.3 (ESRI 2003).

Data analyses

I tested the relationships between the descriptors of the BMFD and habitat variables using ordinary least-square regressions and simultaneous autoregressive models (see below). I used a single multiple regression model (described below) for each of the various descriptors of the BMFD (including the proportion of species in size classes and PC-1).

$$Y = c_0 + c_1T + c_2T^2 + c_3T\bullet P + c_4H \qquad (1)$$

where Y represents a descriptor of the BMFD (body mass mean, body mass skew, PC1, evenness of the BMFDs, and proportion of species in size classes), c_0, c_1,c_2 etc. are fitted regression coefficients and T is mean annual temperature (K), T^2 is mean annual temperature squared, $T\bullet P$ is the interaction between mean annual temperature (K) and mean annual precipitation (mm), and H is habitat heterogeneity. I chose these variables because they, or closely related variables, explain most of the geographical variation of species richness for many taxonomic groups (Currie 1991; Francis & Currie 2003; Hawkins *et al.* 2003; Field *et al.* 2009) and I am interested in testing of these environmental variables also relate with the geographical variation of BMFDs. I cube root transformed mean annual precipitation, and square root transformed habitat heterogeneity to normalize their distributions. I checked scatter plots for non-linearities between response and explanatory variables. Responses to temperature were non-linear; I therefore included a second-degree polynomial term. Residual plots were checked for homoscedasticity.

To test whether the shape of the BMFD and proportion of species in size classes relates to the environmental variables in the same manner between North America and South America, I calculated regressions that included a categorical dummy variable distinguishing between North and South America. For each regression of the form of equation 1, I fitted a parallel model:

$$Y = c_0 + c_{00}D + c_1T + c_{11}TD + c_2T^2 + c_{22}T^2D + c_3T \bullet P + c_{33}T \bullet PD + c_4H + c_4HD \tag{2}$$

Where *D* is a categorical variable (0, 1) representing North and South America. The terms containing the categorical dummy variables estimate the variance associated with variation in model parameters between the continents. I also related each dependent variable to continent alone to determine its effect on the body mass frequency distributions, independently of climate.

Since there are more small bodied species than large ones (May 1988), I wanted to confirm that changes in the frequency distribution of body sizes were not simply the result of geographical variation of species richness. I calculated mean body mass, body mass skew, and body mass variance using 1000 simulated data sets ranging in richness from 10 –

280 (increments of 10). This range represents the minimum and maximum richness values observed among the grid cells. For each simulated data set, I resampled without replacement from the species pool from each continent, without respect to climate. I tested whether the descriptors of the BMFD varied as a function of varying species richness. I found that they did not.

Finally, to allow a more flexible description of the shape of body mass frequency distributions, I related the proportion of species in each body size category (using the binning procedure mentioned earlier--bins with approximately equal number of species) to climate independently, and I tested to what extent these relationships were similar between continents. At each site, I expressed the number of species in each size category as a proportion of the total number of species at that site. Any relationship between total richness and climate is thus removed, since richness sums to 1 at every site. This yielded n=11960 size category × grid cell combinations. To these data, I fitted a model of the following form:

$$Y_{ij} = c_0 + c_{00}\theta_j + c_1T_i + c_{11} T_i \theta_j + c_2 T_i^2 + c_{22} T_i^2 \theta_j + c_3 T_i \bullet P_i + c_3 T_i \bullet P_i \theta_j + c_4H_i + c_{44}H_i \theta_j \qquad (3)$$

where Y_{ij} is the proportion of species in grid cell i that are in size category j; c_0, c_1, c_2, etc. are fitted regression coefficients; T_i, $T_i \bullet P_i$, and H_i are the same independent variables used above; and θ_j is a categorical variable (1 - 10) distinguishing among the different size categories. Equation 3 is an ANCOVA, essentially identical to equation 1, except that the categorical variable θ allows the slopes and intercepts to vary among the different size categories (see Table A.2 for slope coefficients for the different size categories). Lastly, because equation 3 involves pseudo-replication (each grid cell is counted 10 times and the data are not independent), I rarefied the data and used equation 3 on 10% of the data. I found that the results were nearly identical.

Because species ranges overlap multiple grid cells, some degree of spatial autocorrelation in body size distributions is inevitable. I first calculated Moran's *I* for each dependent variable, as well as the model residuals, using the SAM software ver. 4.0 (Rangel *et al.* 2006). All dependent variables were spatially auto-correlated to a degree (among the first 10 distance classes for all dependent variables, Moran's *I* maximum = 0.66, minimum = -0.83, average = -0.05). However, there was very little spatial autocorrelation in model residuals (Moran's *I* maximum = 0.21, minimum = -0.18, average = 0.01). To further account for spatial autocorrelation, I repeated analyses using a simultaneous autoregressive models (SAR, using the SAM software ver. 4.0 (Rangel *et al.* 2006)) for each of the dependent variables. The results were very similar to my original analysis (Table A.3 for results). I therefore only present the ordinary least squares results here.

Tree assemblages

The mammal data were coarse-grained: species presence/absence, irrespective of relative abundance, in 40,000 km^2 grid cells, based on range maps. In a second analysis, I used fine-grained data of body sizes of individuals, irrespective of species. For this, I used censuses of 34,421 individual trees (≥ 2.5 cm diameter at breast height, d.b.h.) in 175 plots (0.1 ha) across the Americas, gathered by Alwyn Gentry (Phillips & Miller 2004).

Similar to the mammal data, tree diameter at breast height (d.b.h.) was $\log_2$ transformed and the first three statistical moments of the distribution of d.b.h. values for the trees in each plot were calculated. I also created eight bins of equal width on the $\log_2$ scale, and I tallied the number of individuals in each bin. Using the binned, $\log_2$-transformed data, I calculated the evenness of the proportion of individuals observed among size categories for each transect using the procedure mentioned above. I also carried out a principal components analysis (similar to above) on the proportion of individuals (versus species in the mammal data) in $\log_2$ size bins. Differences among sites in the proportion of individuals observed in $\log_2$ size classes represent changes in the shape of the tree size frequency distribution (TSFD), but not in the total number of individuals. The first component (PC-1) explained around 70% of the variation in individuals among size classes. I therefore used only PC-1 in my analysis. Component 1 represented positive changes in the proportion of individuals in size categories, 1, 2, and 6 and negative changes in size categories 3, 4, and 5. I then tested whether the first principal component (PC-1) was related to the environmental variables.

Mean annual temperatures for the Gentry transects were obtained from WorldClim (Hijmans *et al.* 2005), while mean annual precipitation was obtained from Phillips & Miller (2004). In order to estimate habitat heterogeneity, I located each of Gentry's transects within the grid system described above, and I noted the number of land cover categories in the grid cell in which a transect fell. Thus, my measure of habitat heterogeneity represents regional heterogeneity, as opposed to heterogeneity on the transect itself. I include habitat heterogeneity in the model in order to keep the regression model similar to the one used for mammals.

Similar to the mammal data, I calculated Moran's *I* for each dependent variable, as well as the model residuals, using the SAM software (Rangel *et al.* 2006). All dependent variables had minor spatial autocorrelation (summary of the first 10 distance classes for all dependent variables, Moran's *I* maximum = 0.31, minimum = -0.60, average = -0.11).

There was very little spatial autocorrelation in model residuals (summary of the first 10 distance classes for all dependent variables, Moran's *I* maximum = 0.16, minimum = -0.20, average = 0.00). As for the mammal data, I repeated my analysis using a simultaneous autoregressive model (SAR, using the SAM software ver. 4.0 (Rangel *et al.* 2006)) for each of the dependent variables. Again, the results are qualitatively similar to the non-spatial analysis (Table A.3). All other analyses were conducted using S-Plus ver. 8.0 (Insightful, Inc., Seattle, Wash.).

Results

Mammals

Earlier studies have focused mainly on spatial variation in mean body size. However, mammalian species of most body sizes occur across all latitudes and longitudes (Figure 1.1a, b). Both the largest and smallest species occur nearly everywhere. Mean body size accounts for only 2% of this geographical variation in the $\log_2$ occurrences among grid cells (Figure 1.1e). Moreover, the shapes of the distributions are quite irregular. However, there are prominent gaps in the size distribution of mammals (e.g. small to medium sized species), particularly in western North America (Figure 1.1b).

The shapes of the BMFD vary geographically such that some regions have relatively flat distributions while other regions have strongly peaked distributions, or gaps among the size categories (Figure 1.2). When viewed in climatic space, the shapes (peaked or even) of the BMFD and the statistical moments of the body size distribution vary strongly as functions of both temperature and precipitation (Figure 1.3a-c). Warm, wet regions generally have uniform distributions with very few gaps, lower mean body mass, and a higher body mass skew. Subsequently, the BMFD in such regions are typically characterized as having many small-intermediate sizes followed by a few large-bodied species. The environmental variables explained 42% - 74% of the variation in the statistical moments and the principal components describing the body mass frequency distribution among sites in the Americas (Table 1.2). Note that while in most cases all independent variables were significant ($P < 0.05$), temperature was consistently the most important variable (Table A.4).

Despite the different geological and evolutionary histories of North and South America, characteristics of the BMFD relate to environmental variables in similar ways in the two continents, both as simple functions of temperature (see Figure A.3 a-d in Supporting Information) and as multiple regressions (Figure 1.4a-c, Figure A.4a-d). Statistical relationships that do not distinguish between continents account for, on average, 65% of the spatial variation among grid cells across the Americas. Allowing regression coefficients to differ between continents increased explained variation by, on average, 6% (Table 1.2). Thus, the effect of climate that is common to both continents is an order of magnitude greater than intercontinental differences. Continent and climate are somewhat collinear: South America is generally warmer than North America. However, the effect of continent alone with respect to each dependent variable was minor compared to the effect of climate (Table 1.2).

The proportion of mammal species in a given grid cell in the different body size categories as a function of climate, also shows remarkable convergences between North and South America (Figure 1.5). The environmental variables explained 77% of the geographical variation in the proportion of species observed in any given size category across the Americas. Note that this correlation accounts for geographic deviations from the hemisphere body size distribution (because my binning procedure divided the hemisphere species pool into approximately equal numbers of species within each of the ten size categories). Moreover, the correlation is independent of geographical variation in total species richness because the body size categories sum to one at every site. Distinguishing between continents (e.g. allowing the slopes and intercepts to vary between NA and SA) of the observed and predicted values in Figure 1.5 did not increase the explained variation. Perhaps surprisingly, regression coefficients relating proportional richness in a given size category to the environmental variables differ substantially among body-size categories (Table A.2), but relatively little between continents, as shown by the two linear regression lines in Figure 1.5, which are obscured by the one to one line. The difference between North and South America appears to be caused mainly by the slightly divergent pattern for the smallest species.

Trees

Similar to mammal assemblages, the occurrences of individual trees with respect to their sizes did not follow any latitudinal or longitudinal patterns (Figure 1.1c, d). The smallest trees though, were more common in equatorial regions, a pattern similar to Huston and Wolverton (2009). Moreover, the average tree size of a local assemblage explains very little of the geographical variation of individual tree sizes (Figure 1.1f, $r^2 = 0.03$). However, the statistical moments of the tree size frequency distribution (TSFD) do vary geographically and vary as a function of temperature and precipitation (Figure 1.3d-f). Warm wet regions generally have modal distributions, lower mean d.b.h., and higher positive skew, patterns associated with having more small-sized trees with few larger ones. Geographic variation in TSFD between NA and SA relates strongly to the environmental variables (Table 1.2), albeit slightly less so compared to mammals (29% - 62%). Similar to the mammal data, temperature was the most influential variable in the models (Table A.4). Despite North and South America having unique floras, their TSFDs relate to environmental variables similarly (Figure 1.4d-f, Figure A.5a-d, Figure A.6a-c). When the binary dummy variable was added to the model to identify the regression coefficients' differences between continents, the explained variation increased by an average of 8% (Table 1.2). Consequently, the TSFD of tree communities along with the proportion of individuals in size categories varies predictability and largely convergently as a function of climate related variables and less so with continent itself (Table 1.2).

Discussion

A large earlier literature has focused on geographic variation in mean body size, often under the heading of Bergmann's rule (see references above). My first important finding is that mean body mass is a poor descriptor of these distributions. Mean mass captures only 2% of the spatial variation in body masses while mean d.b.h. captures only 3% in the spatial variation of tree sizes. Body mass frequency distributions (BMFD) have quite variable shapes: peaked or flat, strongly, or weakly skewed, with holes or not. These shapes vary geographically.

Second, BMFDs and the proportion of species in defined size classes, as well as the size frequency distribution of trees in regional species assemblages (TSFD) relate strongly with climate. Moreover, they do so in remarkably similar ways in North and South America, even though the biotas on the two continents have very different evolutionary and ecological histories. Statistical convergence in characteristics of species assemblages suggests that similar processes structure species assemblages across broad spatial scales both temporally and spatially. I will return to these processes below.

Interestingly, earlier studies that omitted bats from BMFD (see above for reasons) failed to identify consistent patterns among continents (Blackburn & Hawkins 2004; Rodriguez *et al.* 2006; Rodríguez *et al.* 2008; Morales-Castilla *et al.* 2012). North American mammalian assemblages have relatively few bat species, but proportionately more similarly sized non-volant species, e.g., shrews. It has often been hypothesized that resource partitioning structures body size distributions in animal assemblages (Diamond 1975; Holling 1992). Yet, bats and shrews use neither the same resources nor the same physical space. It seems unlikely that local-scale processes, such as resource-based interactions would cause convergent patterns for mammals and trees between two continents. Moreover, I know of no model of resource-based interactions that would predict that the shapes of the distributions would relate strongly to climate (Figure 1.2, Figure 1.3b, e).

So then, what process or processes do cause the BMFD (or TSFD) to converge in relation to a few environmental variables on two continents? A number of hypotheses have been proposed to explain the geographical variation in the distribution of body sizes (Brown & Nicoletto 1991; Allen *et al.* 2006; Huston & Wolverton 2011). For example, Clauset and Erwin (2008) propose that there is a trade-off between the short-term selective advantage and long-term extinction risks for large-bodied species and taxon-specific lower physiological limits for the small-bodies species. Johst and Brandl (1997) discuss effects of a stochastic environment with frequent environmental fluctuations and infrequent 'catastrophes'. These studies though, attempt to explain why the BMFD have size specific peaked distributions and do not attempt to explain predictable geographical variation in body sizes. Other studies have proposed mechanisms to explain regional differences in mean (or median) body size (Blackburn *et al.* 1999; Blackburn & Hawkins 2004; Hawkins

& Felizola Diniz-Filho 2004; Rodriguez *et al.* 2006; Rodríguez *et al.* 2008). Yet, I show that variation in mean size is really a minor component of the story.

I propose that BMFDs and TSFDs are structured by body-size dependent responses of many different physiological processes to the physical milieus in which they occur. Most physiological processes, animal or vegetable, depend upon temperature (Berry & Bjorkman 1980; Gillooly *et al.* 2001; Brown *et al.* 2004) and available moisture (Lovegrove 2003; Tieleman *et al.* 2003; Reichstein *et al.* 2007). Kleidon and Mooney (2000) proposed that only specific sets of physiological traits or growth strategies could persist under given temperature and precipitation regimes (similar to that of Box 1981). These physiological traits depend on processes related to the allocation of carbon to plant compartments and phenology, which include photosynthesis, respiration, resource allocation, and reproduction. These traits relate strongly to body size (Enquist *et al.* 1998; Enquist & Niklas 2002; Falster *et al.* 2008; Hendriks & Mulder 2008). Kleidon & Mooney (2000) showed that more physiological combinations were viable in warm, wet climates than in cold or dry ones. Thus, they argued, geographic variation in species richness is a consequence of geographic variation in the number of viable physiological configurations, given climate. Kleidon and Mooney (2000) also found that small plants, particularly small trees, depend on precipitation for carbon production more so than large plants. Consequently, the abundance of small trees will be determined by water availability such that their abundance should be higher in warm wet regions. Increasing the abundance of small trees would decrease the average plant size and increase plant size skewness, which is consistent with the observed patterns (Figure 1.3d, f).

Incorporation of the body-size dependence of physiological rates into Kleidon & Mooney's (2000) model should lead to a predicted distribution of viable body sizes. To test this is beyond the scope of the present study. However, I hypothesize that body size distributions relate predictably to climate because the set of viable physiologies or growth strategies is not only climate-dependent (Kleidon and Mooney 2000), but also body-size dependent.

Even though Kleidon and Mooney (2000) focused on plants, similar processes could structure mammal assemblages in relation to the geographical variation of body sizes. Because many physiological traits, such as growth rate, metabolic rate, offspring production, mortality rate etc., relate with body size, it is reasonable to assume that different body sizes reflect different growth strategies (Blueweiss *et al.* 1978; Peters 1983; Schmidt-Nielsen 1984; Sibly & Brown 2007). It is also reasonable to assume that different lifestyle strategies (arboreal, fossorial, scansorial, etc.) reflect differences in growth strategies since each lifestyle uses different strata to obtain sufficient resources. If the different lifestyle strategies depend on body size and climate, then it is likely that the number of and type of species found within size categories will vary across space. For example, studies have found the number of species among the different lifestyle strategies (e.g. arboreal species) was not only higher among certain body size categories, but the number of species in each lifestyle strategy was also higher in tropical regions compared to temperate ones (Bakker & Kelt 2000; Sibly & Brown 2007; Kelt & Meyer 2009). These patterns suggest that, similar to trees, climatic constraints determine the number of successful growth strategies that can occur in mammal assemblages thereby causing geographical variation in the shapes of the BMFD. This hypothesis needs further testing.

Differences in body size frequency distributions between continents, which may reflect effects of history or details of biology, are statistically significant. However, they account for an order of magnitude less variation than the variation related to climate.

Moreover, these differences may simply reflect artifacts: contemporary environmental variables not included in the models (e.g., temperature minima or maxima rather than annual means), statistical artifacts (lack-of-fit of the polynomial models), sampling effects (how the sampling grid was placed over the continents), or errors in the species distribution data (e.g., better characterized distributions in North America vs. South America).

In contrast, the shape of body size distributions of biotic assemblages across different continents and among different taxa is remarkably predictable from climate. Bergmann’s rule (variation in mean body size) is, at best, a very minor component of the story about geographical variation of body sizes. Although I suggest a hypothesis that might explain my results, currently I can only speculate about the mechanism(s) generating convergent assortment. It will require future research to elucidate the exact mechanism(s) to explain convergent body distributions among different taxa.

Tables

Table 1.1 Number of mammalian families, genera, and species common and unique between North and South America. See materials and methods for data source.

	Families	Genera	Species
Shared	40	120	308
NA unique	7	94	542
SA unique	14	166	901

Table 1.2. The amount of explained variation (adjusted R^2) in models relating descriptors of the body mass frequency distribution and species evenness as a function of temperature, precipitation, and habitat heterogeneity ($n = 1196$ for mammals, $n = 175$ for trees). Dependent variables were first modeled as functions of the environmental variables without distinguishing between continents, as functions of both (allowing slopes and intercepts to differ between North and South America) and then as functions of continent alone. Most variables were nominally significant at $p < 0.05$ (see Table A.4 regression coefficients and standard error). For every dependent variable, at least one term containing a dummy variable distinguishing between North and South America was statistically significant (either slope or intercept). However, complete models that allow all slopes and intercepts to differ between continents (whether significant or not) explained only very small additional amounts of variation. For mammals, PC1 represents changes in the proportion of mammalian species per $\log_2$ size class. For trees, PC1 is the first axis of a principal component analysis of the proportion of individuals in $\log_2$ size classes.

Dependent variable: mammals

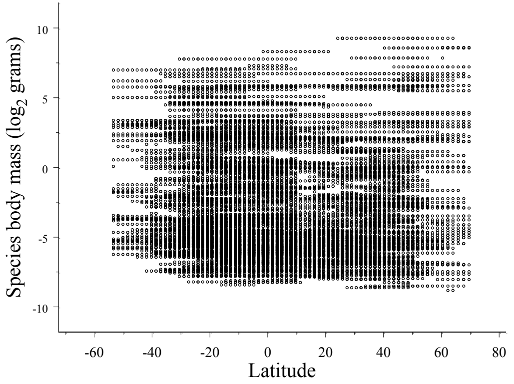
Independent variables	R^2 (climate)	R^2 (climate and continent)	r^2 (continent)
Mean body mass ($\log_2$)	0.71	0.75	0.15
Body mass variance ($\log_2$)	0.66	0.74	0.31
Body mass skew ($\log_2$)	0.42	0.52	0.05
Evenness	0.63	0.66	0.03
PC-1	0.74	0.79	0.08

Dependent variable: trees

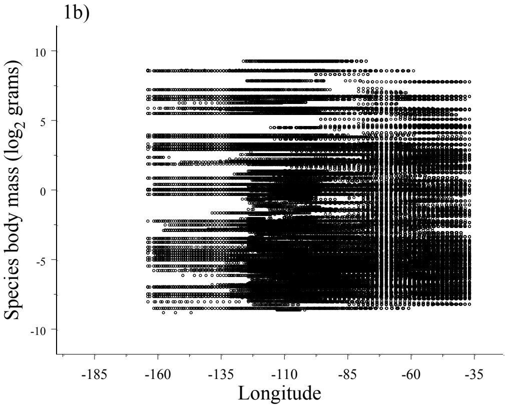
Mean d.b.h. (cube root $\log_2$)	0.62	0.70	0.22
d.b.h. variance (cube root $\log_2$)	0.29	0.36	0.04
d.b.h. skew ($\log_2$)	0.50	0.59	0.13
Evenness	0.49	0.52	0.16
PC-1	0.58	0.67	0.19

Figures

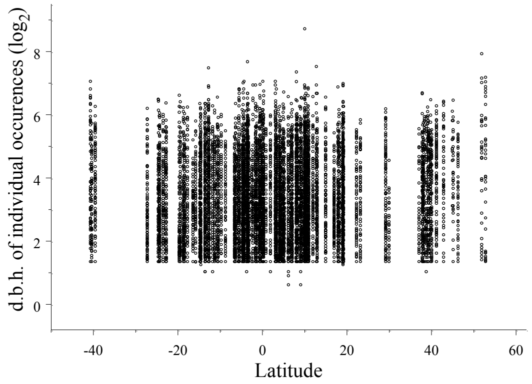
1a)



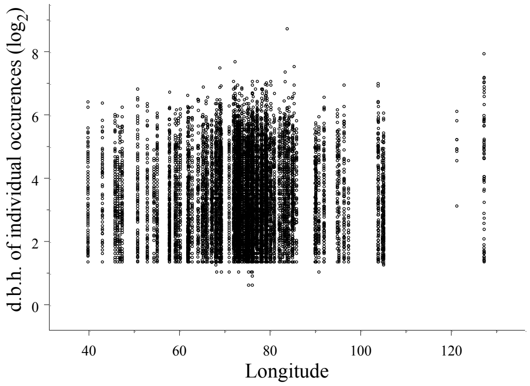
1b)



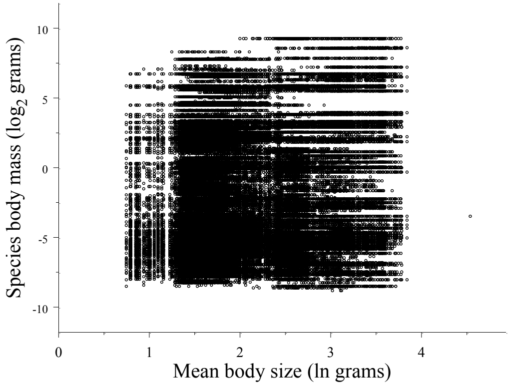
1c



1d



1e)



1f

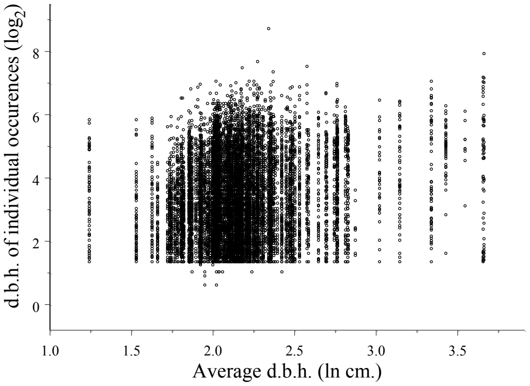


Figure 1.1. Log_2 regional occurrences of mammal species as functions of (a) latitude, (b) longitude, and (e) mean body size (ln grams). Also, occurrences of individual trees in local plots as functions of (c) latitude, (d) longitude and (f) mean d.b.h. (ln cm) for trees; N = 112,300 for mammals; N = 34,421 for trees.

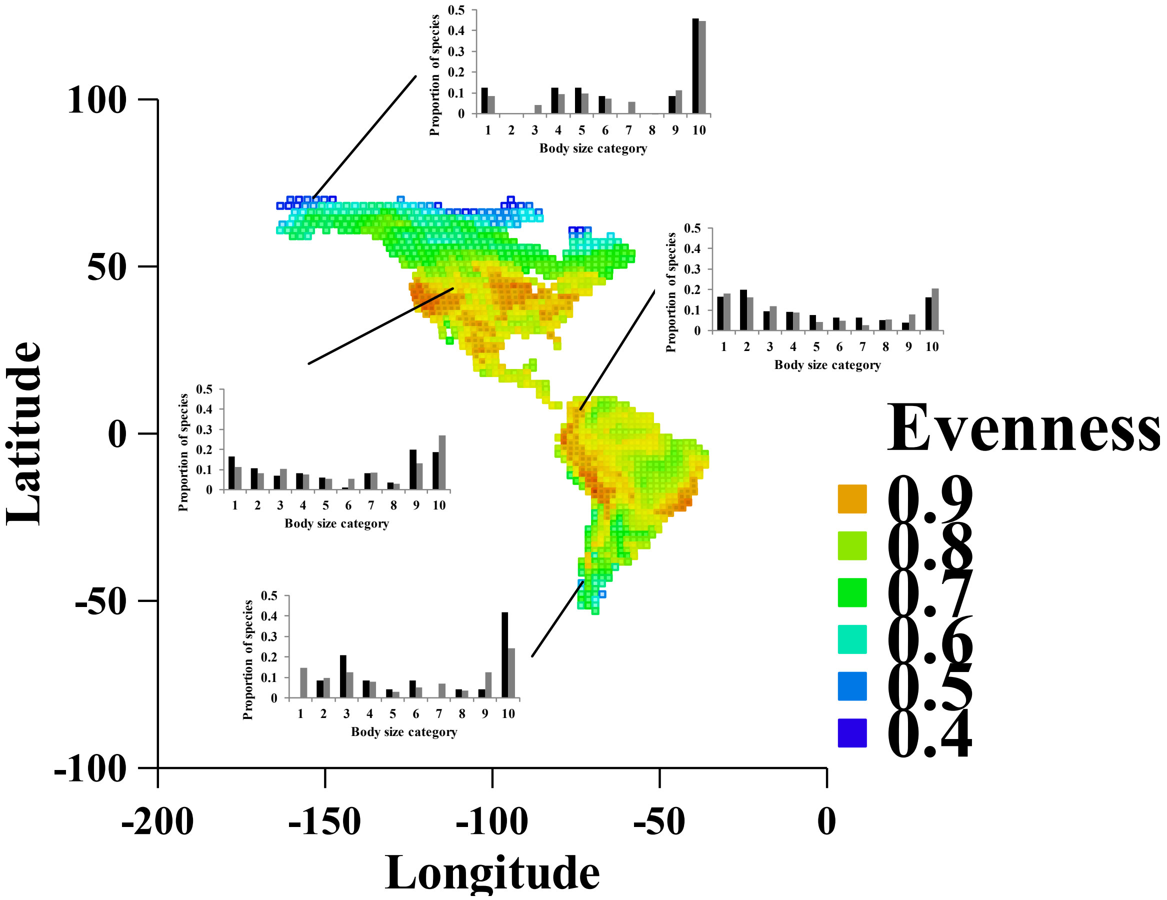


Figure 1.2. Evenness of the body mass frequency distribution of mammals across the Americas. Examples of the BMFD (proportion of species in 10 size categories) are provided for four localities; the y-axis is scaled to 0.50 for all inset figures (N = 1196). Black bars represent observed values, gray bars represent predicted values. Note that evenness is from the raw data, not the residuals from species richness.

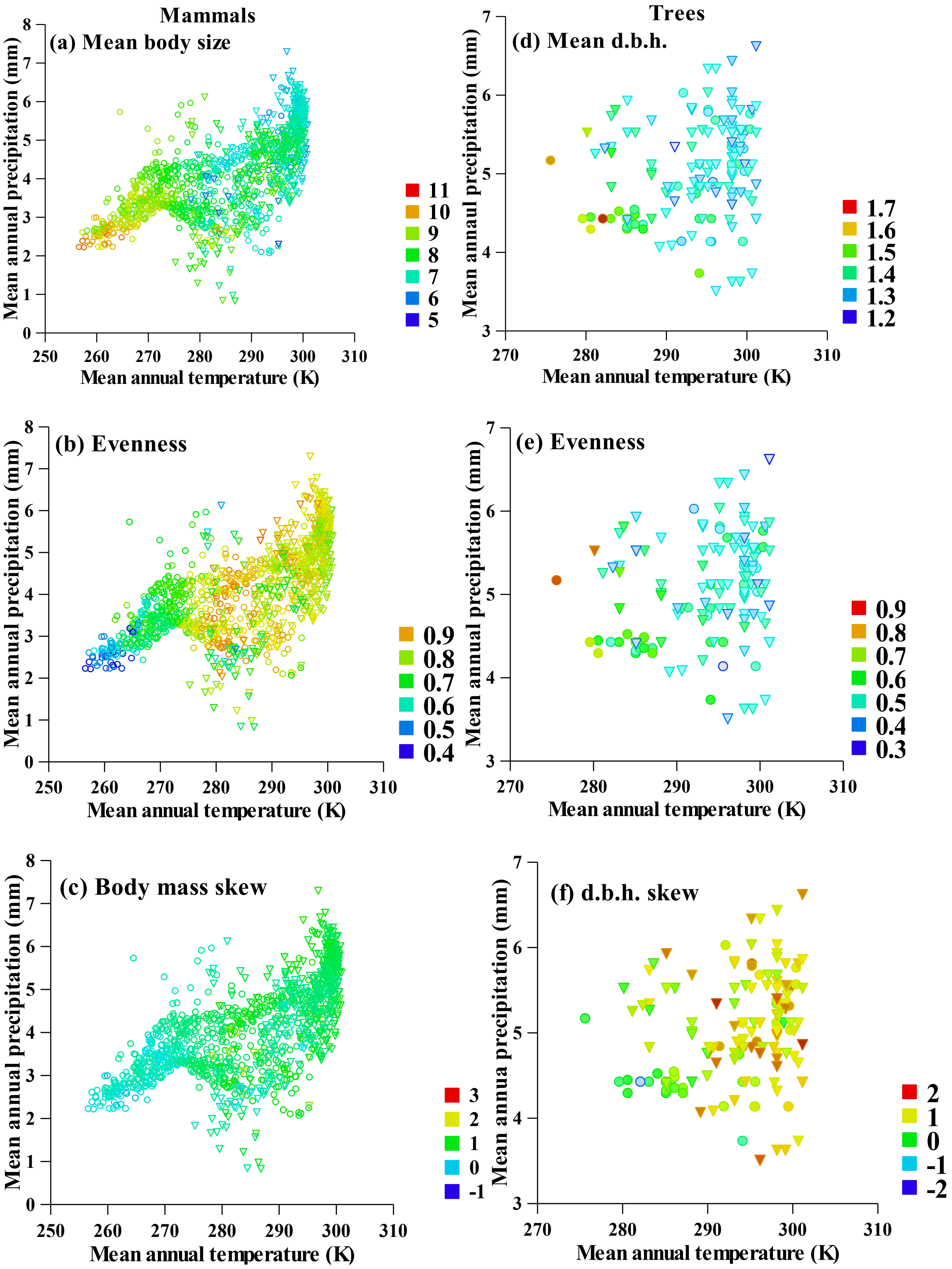


Figure 1.3. Descriptors of body size distributions in related to mean annual temperature (K) and mean annual precipitation (mm, cube-root transformation for mammals, $\log_{10}$ for

trees). For mammal species (n = 1196): (a) mean body size ($\log_2$); (b) evenness of the BMFD (raw data, not the residuals from species richness); (c) body mass skew ($\log_2$). For individual trees (n = 175): (d) $\log_2$ mean d.b.h (cube root, diameter at breast height); (e) d.b.h evenness; and (f) d.b.h skew. Circles represent North America; inverted triangles represent South America. The color axes represent the values for each dependent variable labeled.

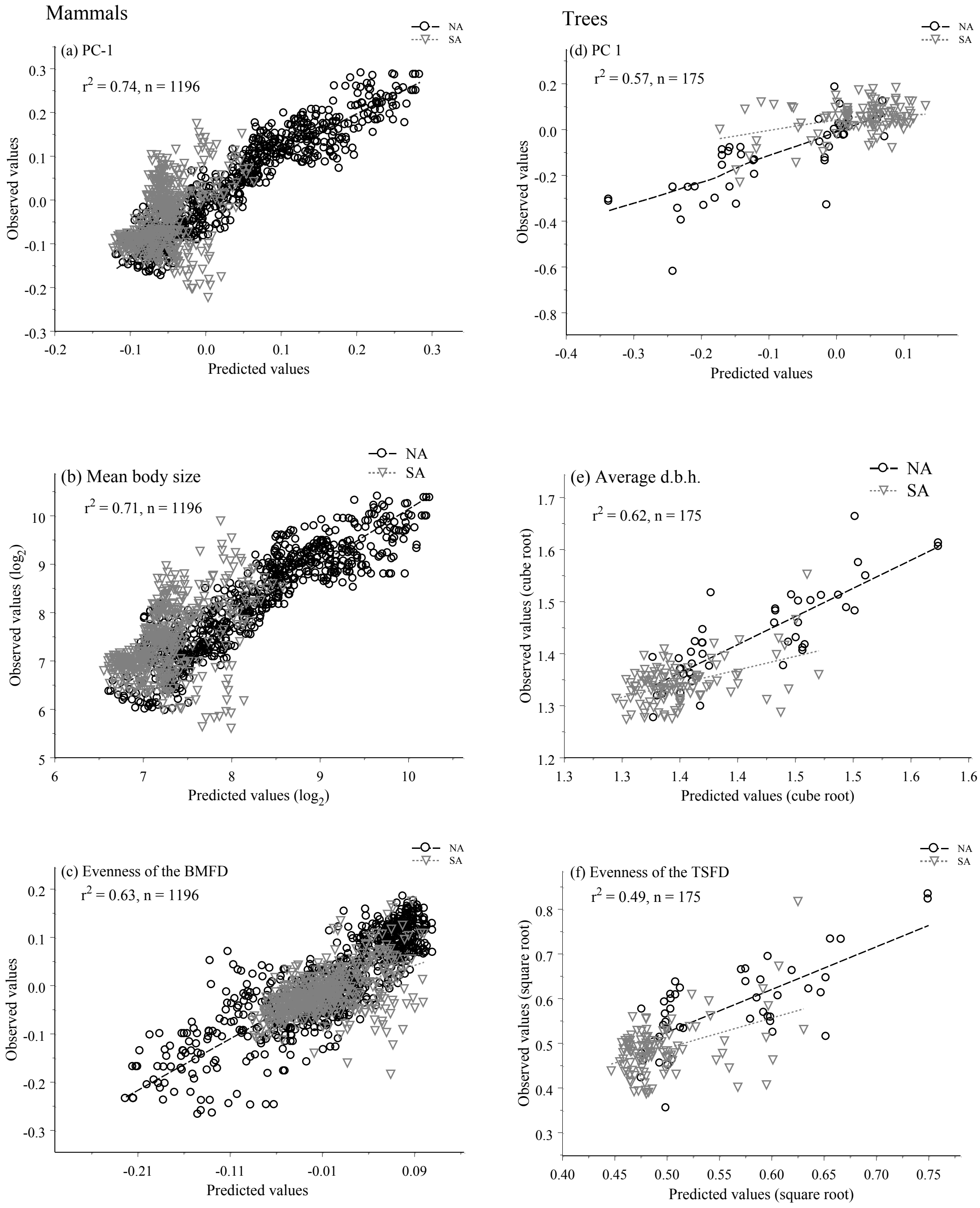


Figure 1.4. Observed values as a function of the predicted values for mammals and trees. For mammals (n = 1196): (a) PC-1; (b) mean body size ($\log_2$); and (c) evenness of body mass frequency distributions (BMFD). For trees (n = 175): (d) PC-1; (e) $\log_2$ average diameter at breast height (d.b.h., cube root transformation); and (f) evenness of the tree size

frequency distribution (TSFD). The predicted values were calculated from the multiple regression models as functions of climate and habitat heterogeneity, without continent. The black circles and solid lines represent North America while the gray inverted triangles and the hatched lines represent South America. Linear regression lines shown separately for each continent.

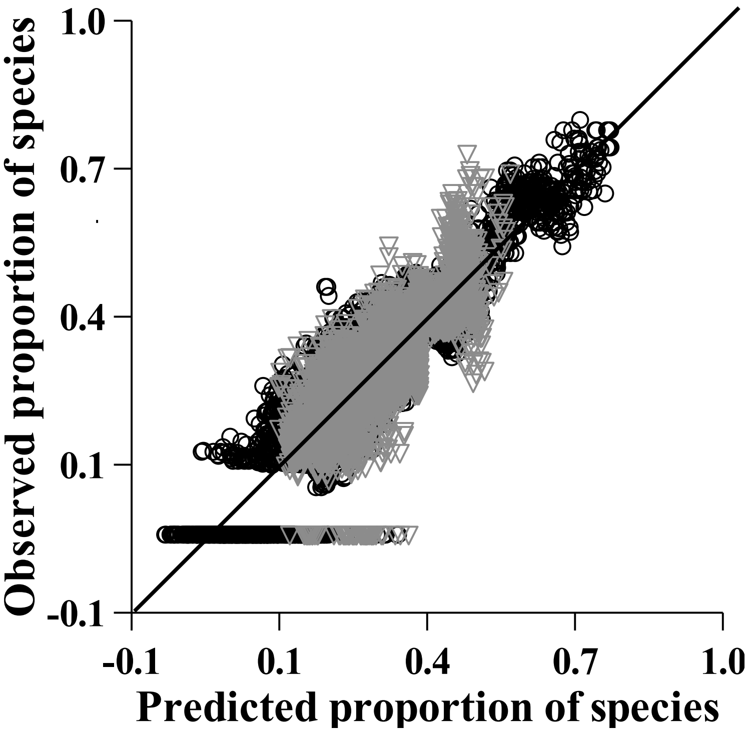


Figure 1.5. Observed number of proportional mammal species in 10 size categories as a function of the predicted values from equation 3. Proportion of species was transformed using an arc sine square root transformation. Linear regression lines shown separately for North America (black circles) and South America (gray inverted triangles), solid black line is the 1:1 line. (N = 11960); note the 1:1 over laps with the lines for NA and SA.

2. Chapter 2: Climate, isolation, and area: patterns and processes of bird body mass assemblage structure on islands and continents worldwide

Abstract

Life across our planet is undoubtedly diverse. Yet, there exist some common patterns that have motivated ecologists around the world to understand the processes giving rise to them. An important question often asked is whether the diversity and characteristics of species communities are structured by particular events such as geological histories and biotic interactions or are they determined more by factors such as contemporary environmental variables. Here I test whether bird assemblage structure, characterized by body mass frequency distribution on continents and islands across the world relates in predictable ways to temperature, precipitation, land area, and island isolation, despite the biogeographical and geological differences that exist between islands and continents. My results suggest that most of the variation in bird assemblage structure depends on temperature, precipitation, land area, and island isolation in similar patterns on continent and island bird assemblages. I did find however, that assemblage structure on islands was somewhat different from continents, and was characterized by higher average mass, lower mass variance, lower body mass maximum, and higher body mass minimum. I explain these differences based on the theory of island biogeography, in particular, how body mass affects extinction probabilities among isolated islands that vary in land area. Island characteristics other than climate, such as island isolation, could be important in structuring insular body mass frequency distributions, independent of trophic interactions or resource availability.

Introduction

Compared to continental assemblages, species assemblages on islands are usually portrayed as unique and very distinctive, especially when viewed from an evolutionary point of view. First, for a given area, the number of species on islands is lower than on continents, but this number increases faster as area increases (Rosenzweig 1995). Furthermore, the number of endemic species on islands is usually higher compared to those on continents (Kier *et al.* 2009). Many insular species are also thought to undergo a 'taxon cycle' where there is an expansion in range size (species becoming habitat generalist by escaping predation and parasitism), followed by a reduction (species becoming habitat specialist or subject to new predators or diseases) (Wilson 1961; Ricklefs & Cox 1972; Ricklefs & Bermingham 2002). Lower richness, higher endemism, and taxon cycles on islands typically result from their isolation, hard boundaries, young age, and *in situ* speciation (MacArthur & Wilson 1963; MacArthur 1967; Losos & Schluter 2000; Whittaker *et al.* 2008).

An important evolutionary difference between continental and insular species involves the evolutionary change of body sizes of insular species. Before being colonized by introduced species, many isolated islands lacked mammalian predators or large herbivores, which through evolutionary time, led to changes in the body sizes of insular species. Compared to their continental relatives, small-bodied species (> 1.0g < 1,000g) evolve towards larger sizes while large-bodied species(> 1,000 g) evolve towards smaller sizes; a pattern known as the island rule (Foster 1964; Van Valen 1973; Case 1978; Adler & Levins 1994; Palkovacs 2003).

Explanations for the “island rule” tend to include trophic interactions, lack of competition, lack of predation, available niche space, resource availability and many more casual factors (Foster 1964; Van Valen 1973; Case 1978; Lomolino 1985; Adler & Levins 1994; Palkovacs 2003). Evidence to support the island rule is more commonly observed among mammalian species (Case 1978; Lomolino 1985; Palkovacs 2003) and more recently among birds (Clegg & Owens 2002). However, the generality of the rule has been questioned (Meiri *et al.* 2006; Meiri *et al.* 2011). If the island rule (via trophic interactions or competition) is responsible for influencing body mass assemblage structure on islands, then as a first approximation, body mass structure on continents and islands will depend on regional specific processes and will therefore be unpredictable from another.

If body mass frequency distributions (BMFDs) between continents and islands are different, then this would be an important ecological difference between these assemblages. Nearly every aspect of an organisms’ physiology is body-size dependent (Peters 1983; Calder 1984; Schmidt-Nielsen 1984). Many ecological and life-history characteristics such as, rates of metabolism, growth rate, population density, dispersal distance, clutch size and range size relate to body size (Peters 1983; Schmidt-Nielsen 1984; Sutherland *et al.* 2000; Brown *et al.* 2004). Differences in body mass frequency distribution also affect community assembly based on resource competition of similar sizes species of a given guild as well as the discontinuous structure of the landscape (Diamond 1975; Holling 1992). Therefore, body size frequency distributions should be an important biological axis to understand the evolutionary and ecological processes shaping assemblage structure.

Regarding the relationship body size has with population size, it is commonly observed that the smallest (< 100 grams) and the largest species (> 1000 grams) have lower populations compared to the medium-size species (Brown & Maurer 1987; Marquet *et al.*

1995; Silva & Downing 1995). Subsequently, body size could possibly influence population structure among assemblages and put the smallest and largest species at greater extinction risk. The lower population densities observed for the smallest species is often explained by their high mass-specific metabolic demand coupled with their requirement of high quality resources (Peters 1983; Brown & Maurer 1987; Brown & Nicoletto 1991). Because high quality resources are often limited or rare for a given area, population densities of small-bodied species are typically lower compared to medium sized species. In contrast, large-bodied species can utilize a greater range of resources that can vary in resource quality (Bell 1971; Jarman 1971). However, because large-bodied species require much more resources compared to small species, their population densities are limited due to resource limitation.

Despite the evolutionary differences between island and continental assemblages, they are subject to many of the same ecological influences. MacArthur and Wilson (1963) emphasized the importance of the balance between colonization, extinction, and speciation to explain species richness and species turnover among islands. They modeled extinction risk as a function of island area and colonization potential as a function of island isolation (MacArthur & Wilson 1963; MacArthur 1967). To summarize briefly their theory, extinction rates have an inverse relationship with island area, but not with island isolation (except see (Wright 1985)). Immigration[2] rates have a positive relationship with island area (target effect) and an inverse relationship with island isolation (rescue effect, (MacArthur & Wilson 1963; Gilpin & Diamond 1976; Lomolino 1990; Stracey & Pimm 2009)). Landscape and metapopulation ecology emphasize these same processes acting on

---

[2] Note that in this chapter, immigration refers to the dispersal of species while colonization refers to species that have viable reproductive populations once they have dispersed to an area.

population dynamics on mainlands (Hanski & Gilpin 1991; Hanski 1998). Lastly, the ways that particular metabolic types or body sizes interact with the environment are presumably the same on islands as on continents (Kleidon & Mooney 2000). In other words, the different metabolic types or physiologies (e.g. defined by body size) depend strongly on temperature and precipitation (Chapter 1).

Most of the global variation in species richness of continental assemblages is related to climate, area, and topographic variability (Wright 1983; Currie 1991; Francis & Currie 2003; Hawkins *et al.* 2003; Field *et al.* 2009; Tittensor *et al.* 2010). Kalmar and Currie (2007) found that richness on islands follows the same patterns as those of continents after accounting for isolation. Might it be possible that the body mass frequency distribution is also related to climate, area, and isolation in similar ways on continents and islands? Alternatively, do characteristics of islands such as their isolation and area affect BMFD on islands differently to those on continents?

Materials and Methods

Here, I examine the global variation in the body mass frequency distribution of avian assemblages across sites worldwide. To do this, I assembled lists of breeding bird species from 238 continental areas and 385 oceanic islands from Kalmar and Currie (2007). Continental sites consist of contiguous non-overlapping land areas delimited by physiographic, geographic, or political boundaries and are not adjacent to one another. Island sites consist of single islands or atolls (see Table 2.1for site statistics). The continental and island sites may include a single homogenous habitat or a mixture of habitats. I used the method described in Kalmar and Currie (2007) for species counts and species occurrences. To reduce heteroscedasticity, I only included sites with 10 or more species in the analysis, giving a total of 238 continental sites and 319 islands sites. Adult mean body masses (g) were obtained from primary sources as well as field guides (see references in appendix). When body mass could not be obtained for individual species (approximately 10% for all 9769 species), I used the genus average body mass. When both male and female masses were given, the mean of the two was used.

To characterize the shapes of the BMFDs, I calculated the first three statistical moments (mean, variance, and skewness) of body mass on the $\log_2$-transformed data (transformation was done to normalize data). While body size mean and variance are often easily interpreted, body size skewness is less intuitive. Assemblages with a positive skew typically have many small and medium size species with a long tail of a few larger species. A negative skew typically indicates more large-bodied species with a long tail of a few small and medium sized species (Brown & Nicoletto 1991; Poulin & Morand 1997; Marquet & Cofre 1999; Bakker & Kelt 2000; Olson *et al.* 2009). Because body size extremes often relate to island area (Marquet & Taper 1998; Meiri *et al.* 2011; Millien & Gonzalez 2011), I also calculated the body size maximum and minimum for each locality.

For each locality, I also generated the BMFD of species. To do this, I established 10 body mass bins with an approximately equal number of species. I chose this method because there are fewer large-bodied species than small-bodied species. Using the binned data, I calculated the evenness of the proportion of species observed among size categories for each site using the following equation: $G = e^{H} / S$ where e is the natural log base, H is the Shannon index for an individual site, and S represents the ten size categories. This index measures the evenness of the species distribution among the ten size categories and scales from zero to one. Zero represents an uneven distribution or a distribution that has zero species in some size categories while one represents an even distribution or a distribution with few or no gaps. Differences among sites in the proportion of species in the size classes also represent changes in the shape of the BMFD. To characterize further the variation of the BMFD among sites, I used a principal component analysis on the proportion of species among the 10 size categories (based on covariance matrix). I used the first two components, which explained 62% of the variation. The first principle component (PC1) represents positive changes in the proportion of species in size categories 2 and 3 and negative changes in the proportion of species in size categories 4-7. Principle component 2 represents positive changes in the proportion of species in size categories 2, 4, and 5, and negative changes in size categories 3, 6, and 7.

Environmental variables

For the climate model, I used a slight modification of the model presented by Kalmar & Currie (2007) in that I did not include the interaction term between land area and mean annual precipitation. I chose not to include this interaction because I was interested to test if land area alone influences community structure. The regression model in this analysis also included an interaction term between mean annual temperature and precipitation. The small differences between my model and that of Kalmar & Currie (2007) do not alter my test in determining whether species assemblages are structured in similar ways on continents and islands in relation to the environmental variables. The final regression model includes the following independent variables:

$$Y \sim T + T^2 + P + T{*}P + A \qquad \text{eq. 1}$$

where Y represents the various body mass characteristics of assemblage structure, T represents mean annual temperature (K), T^2 represents mean annual temperature squared, P represents mean annual precipitation (mm), $T{*}P$ represents the interaction of temperature and precipitation, and A represents total land area (km^2). I did not include island isolation in equation 1 as Kalmar and Currie (2007) did) because I will use this equation to distinguish assemblage structure on islands from continents (see below).

The average annual temperature and average annual precipitation were estimated from weather station data (Leith Helmut 1960; Wernstedt 1960). For sites that did not have weather stations, temperature and precipitation were estimated from measurements at the nearest weather station(s) from climate maps (Decade 1977; Deichmann 1991). Island isolation was estimated by using the distance between the sampled island and the closest continent in kilometers. For statistical reasons, I added a constant of 0.5 to distance to continent to all sites before transformation. To normalize the independent variables, I used the following transformations: cube root transformation for mean annual precipitation, log transformation of total land area, quarter root transformation for distant to continent, although temperature data were not transformed.

Data analyses

I first wanted to determine the effect climate, area, and isolation had on each dependent variable while accounting for the other independent variables. To do this, I calculated the relationship each independent variable had with the BMFD descriptors by using numerous multiple regression models and used the residuals to determine the effect one factor (climate, area, or isolation) had towards explaining each dependent variable. For example, to determine the effect climate had on each dependent variable once area and isolation had been accounted for, I used eq. 2 and eq. 3

$$Y_1 = A + I \qquad \text{eq. 2}$$

where Y_1 represents the various descriptors of the BMFD mentioned above, A represents total land area (km^2), and I represents island isolation (km). Using the residuals from eq. 2, I then used eq. 3 to determine the effect of climate for each dependent variable:

$$\mathrm{Yr}_1 = T + T^2 + P * T + P \qquad \text{eq. 3}$$

Where Yr_1 represents the residuals for a given dependent variable (e.g. mean body mass, body mass variance, etc.) from eq. 2 and the climate variables are similar to those in eq. 1. I followed this procedure for all independent variable combinations for each dependent variable. This analysis was conducted with the island and continental data combined, and then conducted separately for the island and continental data.

Next, I wanted to predict the body mass structure of island assemblages from the continental assemblages. To do this, I used only the continental data and related each dependent variable to temperature, precipitation, their interaction, and area (eq. 1) to calculate the regression coefficient for each independent variable. Note that for this analysis, the island isolation term was not included in the model. I then used the regression model coefficients to predict each dependent variable for island assemblages. Lastly, I used linear regression models to compare the actual values as functions of the predicted values (island assemblage structure predicted from the continental pool) for each dependent variable. I checked regression analyses for non-linearities (using bi-variate scatter plots) in the relationships between dependent and independent variables. In addition, I examined residual plots for homoscedasticity. All statistics were performed using S-plus ver. 8.

Because spatial autocorrelation can violate the assumption of independence thereby inflating the degrees of freedom, I calculated Moran's I for each dependent variable, as well as the model residuals, using SAM software ver. 4.0 (Rangel *et al.* 2006). I observed essentially no spatial autocorrelation either in the raw dependent variables or in model residuals.

Results/Discussion

Global variation in avian assemblage structure, defined by BMFD relates strongly to climate and, to a smaller extent, to isolation and to area (Figure 2.1A). The total variation of the descriptors of the BMFDs explained by climate, area, and isolation ranged from 18% to 62% (Figure 2.1A). However, for body mass maximum and principal component 2 (PC2, positive changes in size categories 2, 4, and 5, and negative changes in size categories 3, 6, and 7), climate explained much less variation than that explained by area or isolation.

When I examined the relationship between the BMFDs and environmental variables separately for islands and continents, I found that climate was still the most important factor for nearly all of the BMFD descriptors (Figure 2.1B, C). For islands however, the effect of isolation was quite strong for body mass minimum while both area and isolation were important in explaining the variation in body mass maximum. In continental samples, climate was the most important factor in explaining most of the variation in the descriptors of BMFD with the exception of PC2 where land area was an important factor (Figure 2.1C).

The relationship between body mass assemblage structure and environmental variables on continents was similar to that observed on islands. I related the BMFD descriptors on continents as functions of temperature, precipitation, and area (eq. 1, excluding island isolation) to predict the BMFD descriptors on islands and found that, for most of the body mass variables, island and continental assemblages relate in broadly similar ways to the environmental variables (Figure 2.2, Figure 2.3A-H). Some notable differences were that island assemblages tended to have higher mean body mass, lower body mass variance, lower body mass skew (fewer large body birds in the right tail of the BMFD), lower body mass maximum, and a higher body mass minimum than on continental assemblages (Figure 2.2). Despite these differences, most of the variation in bird assemblage structure is to the environmental variables in broadly similar ways. However, the differences that do exist suggest that island characteristics, other than climate, are important for structuring the BMFD, in particular for the body size extremes (maximum and minimum).

However, when I included the isolation term (e.g. distance to continent) in the regression model (eq. 1) and compared the observed values of the various descriptors of the BMFD as a function of predicted values using both continents and island assemblages, I found the relationships were qualitatively very similar for all BMFD descriptors (Figure B.1A-G). These patterns were consistent with an effect of island isolation on the structure of island BMFDs. Moreover, when I control for island area and island isolation, I found that the BMFD on continents and islands related to climate in similar ways (Figure B.2A-D). When the effects of island isolation were taken into consideration, the results were consistent with the pattern that much of assemblage structure in the BMFD of birds respond in similar ways to a set of a few environmental variables on islands and continents across the broad geographical scales (Figure B.1A-G).

The island rule was developed to explain differences in body mass among closely related species on continents and islands; many of the hypotheses developed to explain such differences rely on species interactions such as predation, competition, and resource availability (Foster 1964; Van Valen 1973; Case 1978; Lomolino 1985; Adler & Levins

1994; Palkovacs 2003; Lomolino 2005). Since these are local processes, it seems unlikely that the observed patterns in entire island assemblages' results from these processes (although the results presented here do not exclude that possibility). I propose an alternative explanation of the observed patterns in reference to the theory of island biogeography (MacArthur & Wilson 1963; MacArthur 1967).

MacArthur and Wilson's island biogeography theory explains richness and species turnover on islands based on rates of colonization, extinction, and speciation. As mentioned, they proposed that extinction rates have an inverse relationship with island area, but not with island isolation (except see (Wright 1985)) and that immigration rates have a positive relationship with island area (target effect) and an inverse relationship with island isolation (rescue effect, (MacArthur & Wilson 1963; Gilpin & Diamond 1976; Lomolino 1990; Stracey & Pimm 2009)). I extend their theory to explain why islands do differ slightly in the BMFD than on continents and suggest that island characteristics other than climate may cause body size dependent extinction probabilities.

The core of MacArthur and Wilson's theory is the balance between immigration rates and extinction rates. Assume, for the moment, that immigration rate does not depend on body size (but immigration distance might (Sutherland *et al.* 2000)). Consider the probability of extinction for a given body size in relation to island area and island isolation. As mentioned earlier, many studies have observed that, in well-sampled local assemblages, the smallest (< 100 grams) and largest species (> 1000grams) have low population densities while the medium size species (ca. 100 - 1000 grams) reach the highest, although species of any size can have low density (Brown & Maurer 1987; Marquet *et al.* 1995; Silva & Downing 1995). Second, it is known that low population densities increase extinction probability (MacArthur 1967; Pimm *et al.* 1988). Finally, consider the positive relationship between population density and dispersal rate (Travis *et al.* 1999; Ims & Andreassen 2005; Matthysen 2005). Based on the population density size relationship, extinction probability should be lowest for medium sized species and highest for the smallest and largest species. In addition, if dispersal rate depends on population density, then by chance alone, the smallest and largest species will have a lower probability of dispersing to an isolate island, which of course will depend on island area and isolation as well. Even if such species did colonize an isolated island, it seems unlikely that the source continental pool (or nearby island pool) could rescue declining populations considering their low dispersal rate (Hanski & Gilpin 1991; Hanski 1998; Bjornstad *et al.* 1999; Hanski 2001; Ives *et al.* 2004; Abbott 2011). Moreover, if one assumes that the probability to establish on (not immigrate to) an isolated island successfully depends on body size, which relates back to extinction and dispersal probability, then the smallest and largest species should have fewer successful colonizations.

Consider that, if small and large bodied species immigrate to an isolated island, due to demographic or environmental stochastic processes, such species have a higher likelihood of going extinct (due to their lower population sizes and lower dispersal rates), while the medium sizes have a lower probability of extinction. However, this does not mean that the smallest and largest species cannot establish successfully on isolated islands; it simply means that they have a lower probability of doing so. These premises lead to several predictions. Because of the body size dependent extinction probability (see above), body mass minimum should show a positive relationship with island isolation and a negative relationship with island area. In contrast, body mass maximum should show a negative relationship with isolation and positive relationship with island area. Both of these predictions reflect changes in body mass extremes based on the probability of extinction for a given mass. With low population densities (Brown & Maurer 1987; Marquet *et al.* 1995; Silva & Downing 1995) and lower probability of dispersal (Travis *et al.* 1999; Ims & Andreassen 2005; Matthysen 2005), the largest and smallest species should occur on larger islands (predicted by (Marquet & Taper 1998)) as well as less isolated islands (predicted from this study). Because of their higher population densities and their higher dispersal probabilities, the incidences of the medium sized species should be independent of island area and island isolation, which would essentially allow medium sized species to colonize more islands.

The relationships between island isolation and island area and body size extremes were in agreement with the predictions (Figure 2.4A-D). The minimum body mass increased as isolation increases while it decreased (only slightly) as island area increases (Figure 2.4A, C). Moreover, body mass maximum decreased on more isolated islands and increased on larger islands; a similar pattern reported by Marquet and Taper (1998). These patterns were further demonstrated when the incidences of body mass are plotted as a function of island isolation, island area, and continental area (Figure 2.5A-C). In all cases, the smallest species and largest species (species with higher probabilities of extinction) occurred on less isolated large islands. Lastly, when species sizes were plotted versus their respective frequency of island occurrences, the intermediate (not the smallest) size species had the highest island frequency of island occurrences (Figure 2.5D). Interestingly, these incidence patterns resemble those described for mammal assemblages on the Sunda Shelf islands (Okie & Brown 2009) and which were also attributed to the medium-sized species having higher densities compared to the small and large bodied species.

The effect of island isolation and island area on the body mass structure can be described as follows. As island isolation increases, the minimum body mass increases and body mass maximum decreases. In addition, with the increase in the minimum mass and a decrease in the maximum mass will also decrease both the body mass variance and body mass skew. The opposite pattern occurs across larger areas. For example, larger areas can support more types of body sizes, the smallest and largest causing continental assemblages to have a higher body mass variance. MacArthur and Wilson (1963) developed the theory of island biogeography to explain species richness and species turnover among islands that vary in area and isolation. It appears their theory (albeit slightly modified to include the effect body size has on extinction and dispersal probabilities) explains why the body mass structure of islands is slightly different from continental ones.

Although I have introduced a process that explains how island isolation affects extreme sizes, this body size dependent extinction probability could also explain why isolated islands have fewer species. However, it could also be argued that having fewer species will reduce the probability of having extreme sizes based on chance alone. A correlative study such as this one cannot resolve the direction of the causality. Moreover, a major limitation with the data used in this analysis is that there were no measures of abundance. It seems necessary to include abundance measures in relation to body size among island systems to further elucidate the processes structuring bird assemblage structure.

Summary

There is an ongoing debate regarding the type and importance of processes that structure species assemblages. Much of ecology assumes that species assemblages are structured primarily by evolutionary processes unique to individual species and localities. On the other hand, if processes that structure species assemblages depend on a set of a few environmental variables in convergent ways across space, then broad-scale commonalities should exist in ecological patterns. As mentioned, one such commonality involves the global relationship between species richness and area, macroclimate, habitat heterogeneity, and geographical isolation (Wright 1983; Currie 1991; Francis & Currie 2003; Hawkins *et al.* 2003; Kalmar & Currie 2006, 2007; Field *et al.* 2009; Tittensor *et al.* 2010). My results suggest that global variation in bird assemblage structure relates to climate and land area quite similarly to that of continental bird assemblages. I did find however, that island characteristics, other than climate, such as island isolation and island area were also important in structuring the BMFDs of bird assemblages. However, once climate, land area, and island isolation are taken into account, bird assemblage structure across islands and continents yield similar patterns (Figure B.1A-H).

Table

Table 2.1. Summary of site characteristics between islands and continents. The mean body mass, body mass variance, and body mass skew statistics refer to bird body masses. Mass was measured in grams.

Statistic	Samples	Richness	Area (km^2)	Temp. (K)	Precip. (mm)	Mean ($\log_2$)	Variance ($\log_2$)	Skew ($\log_2$)	Evenness BMFD
Islands	319								
Min.		10	0.7	254.6	25.0	4.9	3.2	-0.89	0.57
Max.		554	820033.0	301.2	5470.0	9.1	9.3	1.09	0.98
Mean		73.4							
Median		49	1079.0	297.5	1356.0	6.5	5.2	0.19	0.87
Continents	238								
Min.		22	89.0	258.8	42.0	5.0	3.3	-0.41	0.54
Max.		1396	1001000.0	302.6	4000.0	8.4	9.6	1.46	1.00
Mean		267.9							
Median		200	54791.0	291.3	707.5	6.4	6.2	0.52	0.92

Figures

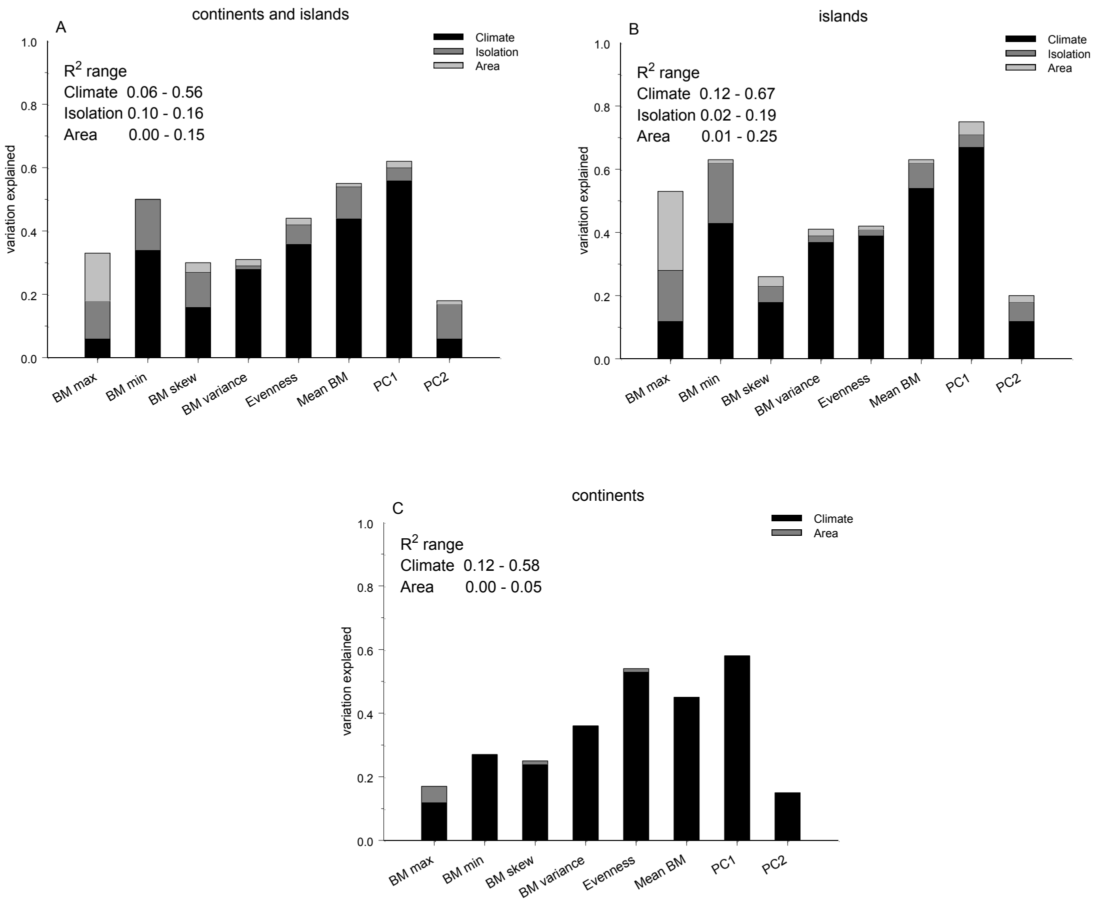


Figure 2.1. Variation of the descriptors of the body mass size distribution of bird species explained by climate, isolation, and area respectively using equations 2 and 3. (A) continents and islands combined, N = 557. (B) islands, N = 319. (C) continents, N = 238. Note that for continental data, island isolation was a constant and did not vary among sites.

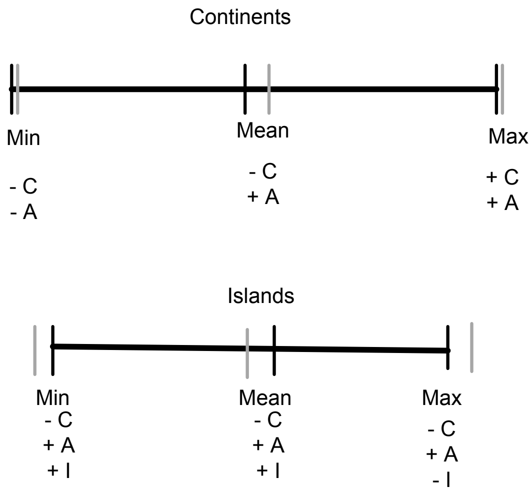


Figure 2.2. An illustration describing the differences between continental and island assemblages for mean body mass, maximum body mass, and minimum body mass in relation to the observed values (black) and predicted values (gray). The effect (+ or -) of climate (C), area (A) and island isolation (I) on the observed values. Note that the predicted values for island assemblages were estimated using the relationship continental assemblages had with independent variables.

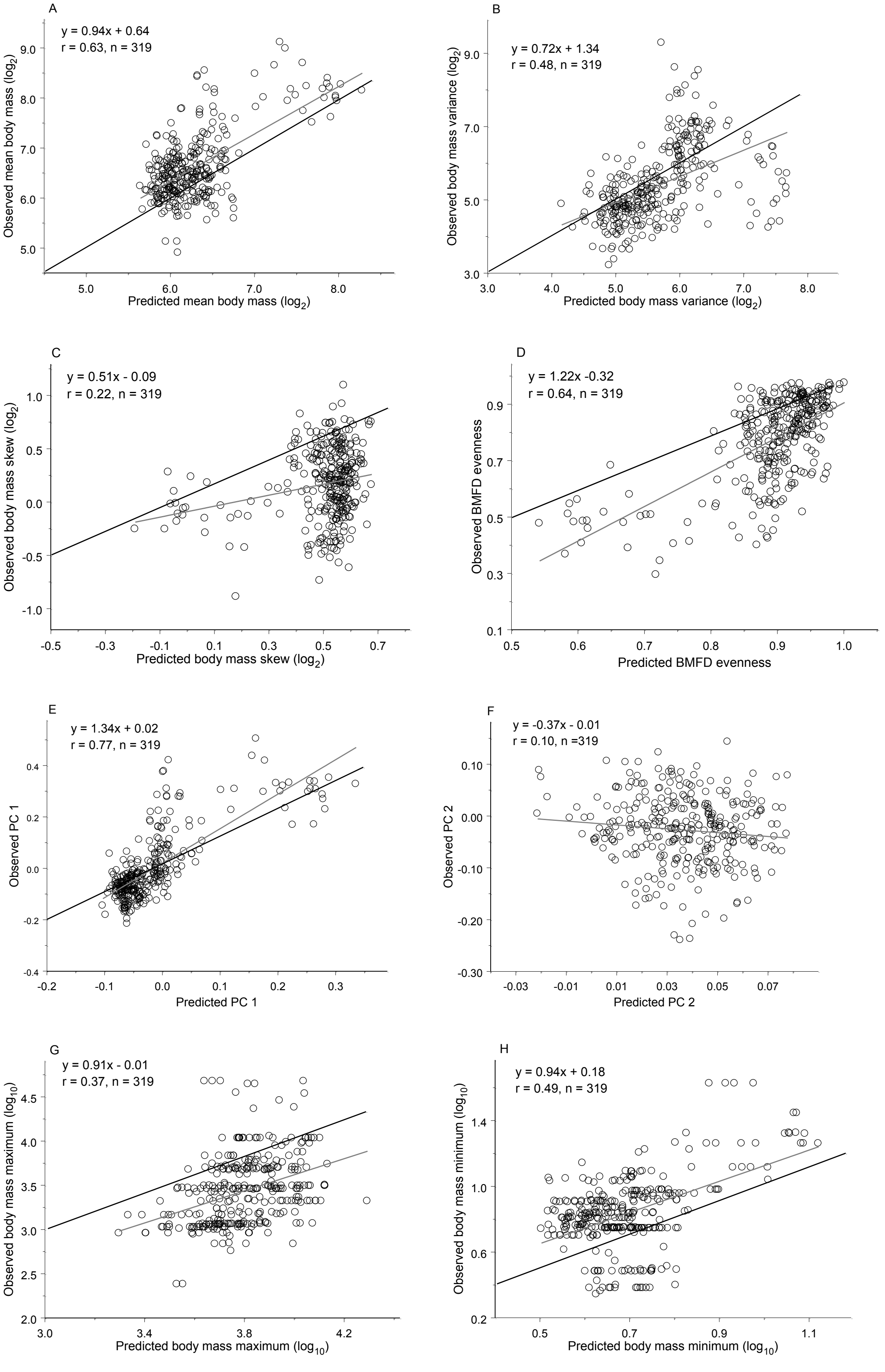

A
y = 0.94x + 0.64
r = 0.63, n = 319
Observed mean body mass ($\log_2$)
Predicted mean body mass ($\log_2$)
5.0
6.0
7.0
8.0
9.0
B
y = 0.72x + 1.34
r = 0.48, n = 319
Observed body mass variance ($\log_2$)
Predicted body mass variance ($\log_2$)
3.0
4.0
5.0
6.0
7.0
8.0
9.0
C
y = 0.51x - 0.09
r = 0.22, n = 319
Observed body mass skew ($\log_2$)
Predicted body mass skew ($\log_2$)
-1.0
-0.5
0.0
0.5
1.0
-0.5
-0.3
-0.1
0.1
0.3
0.5
0.7
D
y = 1.22x -0.32
r = 0.64, n = 319
Observed BMFD evenness
Predicted BMFD evenness
0.1
0.3
0.5
0.7
0.9
0.5
0.6
0.7
0.8
0.9
1.0
E
y = 1.34x + 0.02
r = 0.77, n = 319
Observed PC 1
Predicted PC 1
-0.4
-0.2
0.0
0.2
0.4
-0.2
-0.1
0.0
0.1
0.2
0.3
F
y = -0.37x - 0.01
r = 0.10, n =319
Observed PC 2
Predicted PC 2
-0.30
-0.20
-0.10
0.00
0.10
-0.03
-0.01
0.01
0.03
0.05
0.07
G
y = 0.91x - 0.01
r = 0.37, n = 319
Observed body mass maximum ($\log_{10}$)
Predicted body mass maximum ($\log_{10}$)
2.0
2.5
3.0
3.5
4.0
4.5
3.0
3.4
3.8
4.2
H
y = 0.94x + 0.18
r = 0.49, n = 319
Observed body mass minimum ($\log_{10}$)
Predicted body mass minimum ($\log_{10}$)
0.2
0.6
1.0
1.4
0.5
0.7
0.9
1.1

Figure 2.3. Observed values as a function of predicted values (from eq. 1) for island assemblages. (A) mean body size ($\log_2$). (B) body size variance ($\log_2$). (C) body mass skew ($\log_2$). (D) evenness of the body mass frequency distribution. (E) principal component 1. (F) principal component 2. (G) maximum body mass ($\log_{10}$). (H) minimum body mass ($\log_{10}$). The black reference line represents a 1 to 1 ratio. Linear regression lines shown in gray (N = 319).

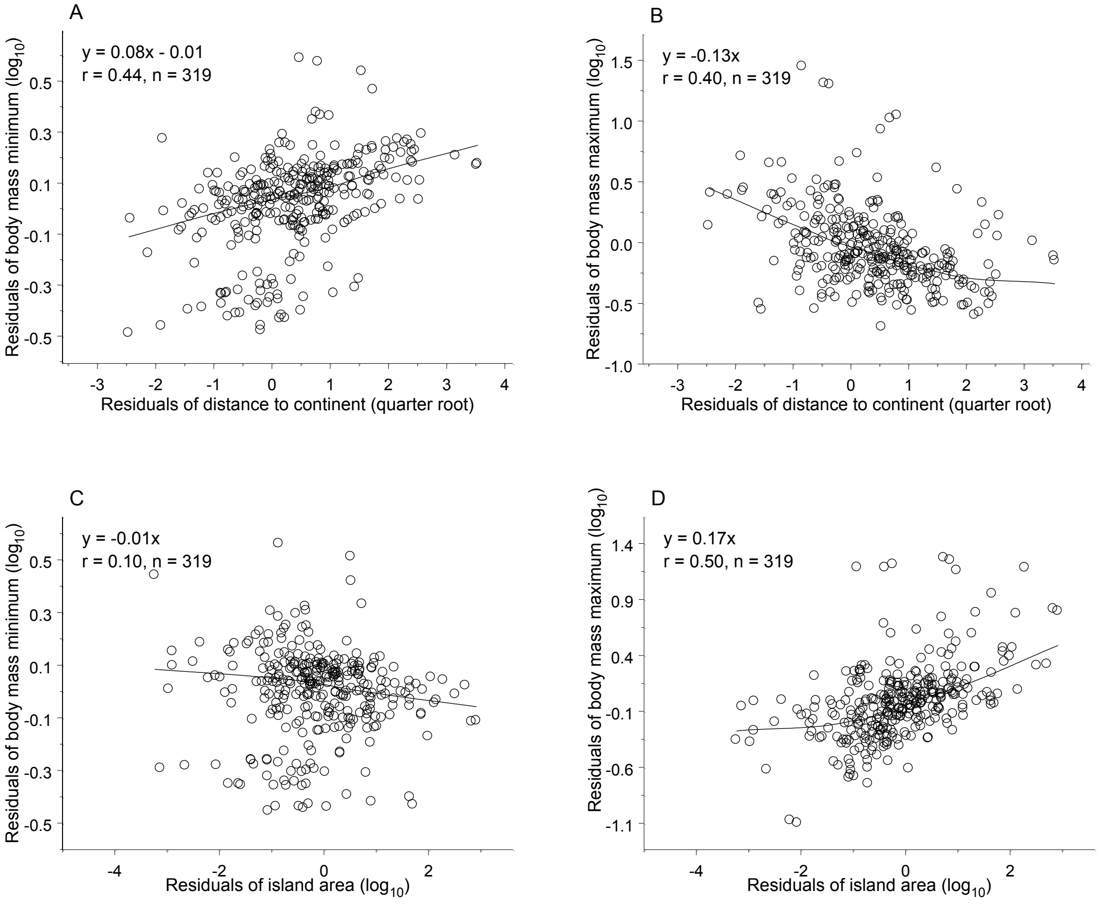


Figure 2.4. Partial correlation between island isolation and area on mass extremes. The axes represent residuals after statistically controlling for climate (and isolation and area respectively). (A and C) body mass minimum ($\log_{10}$). (B and D) body mass maximum ($\log_{10}$). LOWESS lines shown, tension 0.80.

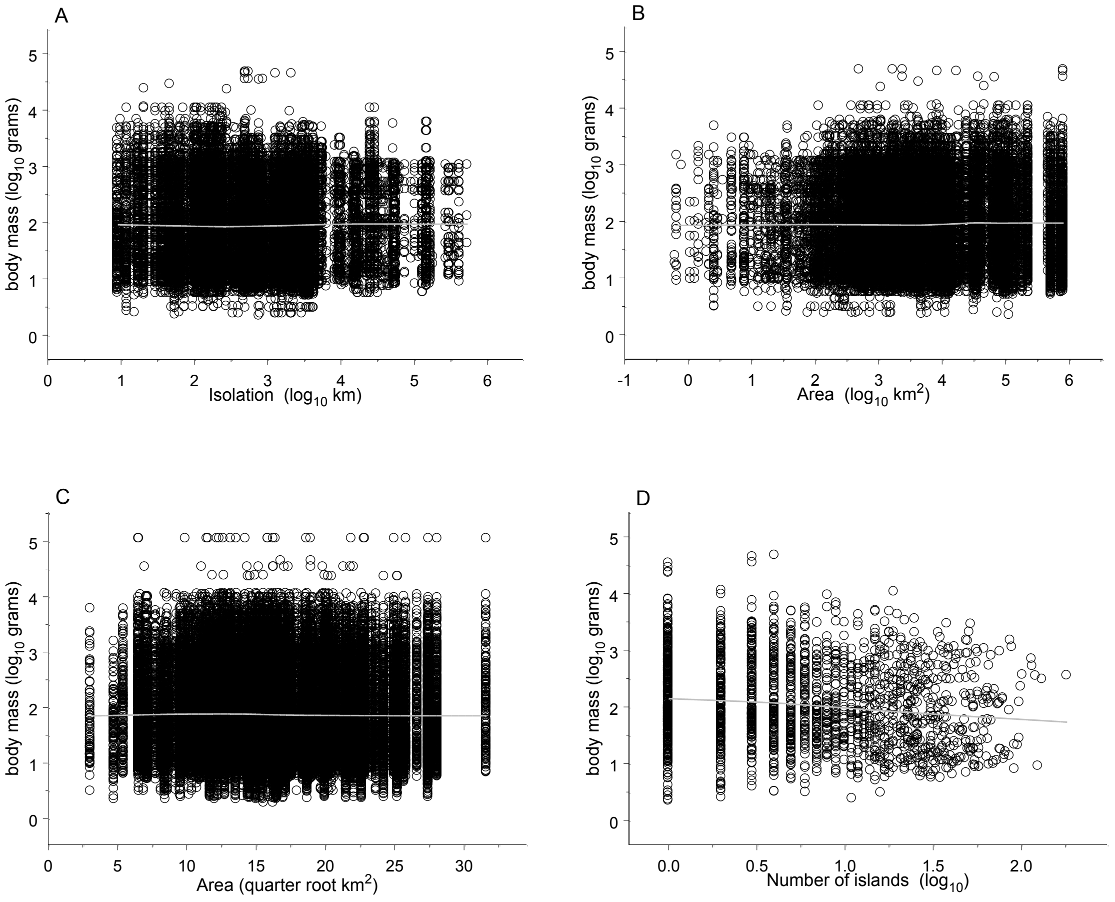


Figure 2.5. Body size-incidence, island area, and island isolation relationship for birds among islands and continents worldwide. (A) body mass incidences ($\log_{10}$) as a function of island isolation ($\log_{10}$), N = 21873. (B) body mass incidences ($\log_{10}$) as a function of island area ($\log_{10}$), N = 22636. (C) body mass incidences ($\log_{10}$) as a function of continental area (quarter root), N = 2032. (D) body mass incidences ($\log_{10}$) as a function of number of island occurrences ($\log_{10}$), N = 2032.

3. Chapter 3: Geographic gradients of diversity driven by gradients of the rarest species

Abstract

Geographic variation in species diversity correlates strongly with climate, but a mechanistic understanding of this relationship has remained elusive. A half-century ago, Preston observed that the number of individuals per species in species assemblages is log-normally distributed (with parameters I, the total number of individuals, and m, the number of individuals of the rarest species). Here, I show that both m and ϕ (the proportion of species represented by a single individual in samples of species assemblages) are strongly related to climate. Moreover, global variation in species richness is more strongly related to these measures of rarity than to climate. I propose that variation in the shape of the log-normal species abundance distribution is responsible for global gradients of species richness: rare species (reflected in m and ϕ) persist better in benign climates. These results conceptually unify two of the most prominent patterns in nature – log-normal abundance distributions and latitudinal diversity gradients. Further, my findings have important implications regarding the impact of climate extremes on diversity.

Introduction

One of the most fundamental problems in biology is to understand why some areas of the Earth accommodate very many species, and other areas, very few. Generally, the number of species in a region decreases from the equator to the poles, and from low to high elevation (Grytnes 2003; Willig *et al.* 2003; Hawkins & Felizola Diniz-Filho 2004; Hillebrand 2004; McCain 2007). On both of these gradients, richness correlates strongly with temperature and/or precipitation in most broad taxonomic groups (Currie 1991; O'Brien *et al.* 2000; Francis & Currie 2003; Hawkins *et al.* 2003; Kalmar & Currie 2007; Field *et al.* 2009). These correlations remain consistent as climatic variables change, both seasonally, and over long periods (Brown *et al.* 2001; H-Acevedo & Currie 2003). This suggests that the richness-climate correlation reflects a causal relationship, but exactly what mechanism/s is/are involved remains obscure, despite decades of research on the subject.

Frank Preston suggested the core of a mechanism in the 1960’s. Examining local assemblages, Preston found that the number of individuals per species in species assemblages could be described by a log-normal distribution with two parameters (Preston 1962b, a): *I,* the total number of individuals in the assemblage (individual density), and *m*, as the number of individuals of the rarest species. Preston’s model can be solved for SR, the total number of species in an assemblage, yielding equation (1):

$$SR = 2.075 * (I / m)^{0.262} \quad (1)$$

Preston pointed out that this model accounts for the very commonly observed relationship between species richness and area, because larger areas contain more individuals (Table C1 in Appendix). Yet, Preston was silent on the subject of latitudinal or elevational gradients of richness.

Building from Preston's species-area relationship, the energy-richness hypothesis (Table C1) postulated that species richness depends on the number of individuals, which in turn depends on both sampling area and primary productivity (Hutchinson 1959; Wright 1983). If highly productive areas such as the wet tropics support high densities of individuals, they should therefore have many species. However, subsequent work showed that this causal pathway is incorrect: the number of individuals (*I*) does not vary sufficiently to account for observed richness gradients (Currie *et al.* 2004; Borregaard & Rahbek 2010; McGlynn *et al.* 2010).

This leaves the number of individuals of the rarest (*m*), or the shape of the individuals/species abundance distribution, as the source of geographical variation in species richness. Preston argued, and subsequent literature largely observed (Connolly *et al.* 2005; Dornelas *et al.* 2006; Ulrich *et al.* 2010), but see (Hubbell *et al.* 2008), that the variation in abundance among species in most assemblages at least approximately conform to a log-normal distribution. Regarding *m*, Preston said little: "So far as the present paper is concerned it [interspecific competition] drives the value of 'm' down to the lowest level" (Preston 1962b). Preston clearly assumed that *m* might vary spatially, and he speculated that *m* should decrease as the number of species for a given area increases. However, Preston did not test this nor did he (or subsequent literature) discuss further about spatial variation in *m*.

If the log-normal distribution of individuals (equation [1]) is more or less universal, and given that *SR* covaries strongly with climate but *I* does not, then *m* must depend upon climate. This suggests a new hypothesis to explain biodiversity gradients (Table C1): geographic gradients of species richness arise because the ability of species to persist at low densities (reflected in *m*), rather than the total number of individuals (reflected in *I*), depends strongly on climate.

The Metabolic Theory of Ecology (MTE; (Allen *et al.* 2002)) proposed something quite similar (Table C1). First, Allen and collaborators assumed that the "Energy Equivalence Rule" is universal: that is, the total metabolic rate of all individuals of a given species in any given area (i.e., W·individual^{-1} * individuals·km^{-2}) is approximately constant, irrespective of body size or climate. Since individual metabolic rates are higher at higher temperatures, there must be fewer individuals per species in warm places for total metabolism to remain constant. It had been observed that the total number of individuals of all species per unit area is approximately independent of climate. Therefore, if there are fewer individuals per species in warm areas, then there must be more species. The MTE predicted geographic variation in richness remarkably similar to observed patterns; however, closer examination showed systematic departures from the predictions (regarding slope of richness and temperature relationship) and assumptions (regarding energetic equivalence) of metabolic theory (Hayward *et al.* ; Clarke 2006; Algar *et al.* 2007; Carbone *et al.* 2007; Hawkins *et al.* 2007). The MTE gets close, but it misses something.

I propose instead that geographic gradients in richness arise from climate-dependent variation in the persistence of rare species. I test three predictions of this hypothesis. First, if climate influences the persistence of rare species, which in turn influences richness, then the proximal correlations (climate-rarity, rarity-richness) should be stronger than the distal correlation (climate-richness). This is a very strong prediction, because it is already known that climate-richness correlations are very strong. Second, if the tendency of rare species to persist is the driver of species richness gradients, then it should not matter how gradients of rarity arise. The climate-rarity relationship observed on an elevational gradient should be consistent with the climate-rarity relationship observed over latitudinal gradients. Third, structural equation modeling (path analysis) should show stronger support for models in which climate affects species richness via a measure of the persistence of rare species, rather than directly.

Materials and Methods

I used two data sets to test my predictions (Figure 3.1). The first data set consisted of a global set of sites sampled by Alwyn Gentry (Phillips & Miller 2004) (albeit mainly in the Neotropics). From Gentry's data, I culled 195 sites that were 0.1 hectares in area, and at which mean annual temperature and total annual precipitation could be obtained from WorldClim and from (Phillips & Miller 2004).

The second data set included eleven 1-ha sites along the Volcan Barva elevational transect (Costa Rica) studied by Lieberman et al. (Lieberman *et al.* 1996). For each of the 11 sites, Lieberman et al. reported the total number of individuals and species richness for all trees with a diameter at breast height (d.b.h.) greater than or equal to 10 cm (see (Lieberman *et al.* 1996) for site details). Note that the plot size difference between the global data and the Lierbman data will not affect my analysis since equation (1) simply accounts for differences in I, m, and SR as plot size changes.

Good climatic data are very difficult to obtain in mountainous areas: climate varies over short distances, and weather stations are few. I therefore estimated temperature at Lieberman's sites by assuming a lapse rate of 6° C decrease per 1000 meter increase in elevation (Lieberman *et al.* 1996). Temperature at sea level was estimated from (Holdridge *et al.* 1971). Precipitation estimates were obtained from (Kluge *et al.* 2006).

Hypotheses about m are difficult to assess because the number of individuals in the least abundant population in a region is impossible to observe directly. Consequently, I estimated m indirectly by two means. First, I created a proxy for m: ϕ, the proportion of species represented by a single individual (i.e., singletons) in standard-sized samples from species assemblages, ϕ. To verify that ϕ is an appropriate surrogate for m, I also calculated the predicted value of m at each site in both the global data and the Barva data. Given observed SR and I, re-arranging equation (1) yields:

$$m = (16.2 * I) / SR^{3.817} \qquad (2)$$

where the variables in equation (2) are similar to those in equation (1). I found that m and ϕ are strongly correlated (r^2=0.60, Figure 3.2).

To test my first prediction (that richness should relate to rarity more strongly than it relates to climate), I examined the relationships among species (SR) per quadrat, ϕ, and individual density (I). Most published models of broad-scale variation in tree richness relates richness to some variant of a temperature x precipitation interaction (Currie 1991; O'Brien 1998; O'Brien *et al.* 2000; Francis & Currie 2003). I therefore tested regression models involving mean annual temperature (°C), total annual precipitation (meters), and the interaction of the two variables. I also included squared terms of the three variables to allow for non-linearities in the relationships. For all analyses, I used the following transformations to normalize their distributions: $\log_{10}(SR)$, $\log_{10}(I)$, and $P^{0.5}$ (square root transformation). I found that, the best-supported models included only the temperature • precipitation interaction (and sometimes its square), e.g.:

$$log_{10}(SR) \sim T \bullet P^{0.5} + (T \bullet P^{0.5})^2 \qquad (3)$$

The quadratic term was dropped from models in which it was not statistically significant. I also tested whether the addition of individual density (I) to the models significantly improved the relationships. Further, I first related species richness as functions of proportion of singletons (ϕ) separately and then included individual density (I), equation (4).

$$log_{10}\,SR = \phi + (log_{10}\,I) \tag{4}$$

To test my second prediction (that rarity-climate gradients should be the same on elevational or latitudinal gradients), when I modeled ϕ or m as functions the interaction between mean annual temperature and annual precipitation ($T{\bullet}P$). I used:

$$log_{10}\,(\phi \text{ or } m) \sim T \bullet P^{0.5} + (T \bullet P^{0.5})^2 \tag{5}$$

Once again, the quadratic term, which was added to test for non-linearity in the relationship between rarity and climate, was dropped from models in which it was not statistically significant. To test whether the observed patterns among the various regression models were similar between the two gradients, I repeated the regression models that included a binary categorical variable distinguishing between the two types of gradients. The categorical variable was added alone (to allow the intercepts to vary), and was added interacting with each independent variables (to allow the slopes to vary).

To test my third prediction, I constructed competing path models, and I compared which model(s) were most consistent with the observed correlations among the variables. All statistical analyses were conducted using S-Plus ver. 8.0 while the path models were conducted using Amos ver. 5.01.

Results

Consistent with earlier work (Currie 1991; O'Brien *et al.* 2000; Francis & Currie 2003; Hawkins *et al.* 2003; Kalmar & Currie 2007; Field *et al.* 2009), I found species richness to be strongly correlated with climate (specifically, an interaction between mean annual temperature and precipitation) on both the Barva and global gradients (Table 3.1). Individual density relates only weakly with climate on the geographic (global data) gradient, and non-significantly on the elevational (Barva) gradient (Table 3.1). Although richness does depend upon the density of individuals (*I*) (Table 3.1), *I* does not vary enough geographically (by less than two orders of magnitude in the global data and approximately one order of magnitude in the Barva data, Table C.2) to have much influence on gradients of richness (Currie *et al.* 2004; Borregaard & Rahbek 2010; McGlynn *et al.* 2010). In contrast, *m* varies by six orders of magnitude in the global data and nearly three orders of magnitude on the Barva transect (Figure 3.2, Table C.2). Similarly, the proportion of singletons ϕ varies from 0.07 to 0.83 in the global data and from 0.17 to 0.48 in the Barva data Table C.2).

When I relate *SR* as a function of ϕ, I found ϕ explained from 0.57 and 0.47 of the variation in richness across the global and Barva data respectively and indistinguishably between the two data sets (Figure C.1, $p = 0.07$ for the intercept, $p = 0.74$ for the slope). When I include density of individuals (*I*) to equation (4), I found that global variation in richness of the global data was more strongly related to ϕ and *I* (my hypothesized proximal link: $R^2=0.83$) than to climate (the hypothesized indirect link; $R^2=0.74$) (Table 3.1). These results are consistent with the first prediction (re: Climate → ϕ →SR), global variation in richness should be more strongly related to ϕ than to climate. However, when using only the Barva data, the results were inconsistent with my first prediction where richness was more strongly related to climate ($R^2=0.94$) than to ϕ ($R^2=0.52$). Reasons for this inconsistency will be discussed below. Lastly, global variation in ϕ (the second hypothesized proximal link) was not more strongly related to climate than was richness: Gentry $R^2=0.46$ for ϕ, $R^2=0.66$ for *SR*), Barva $R^2=0.75$ for ϕ and $R^2=0.95$ for *SR*.

Consistent with my second prediction, both ϕ and *m* relate strongly to climate (Table 3.1). Moreover, they do so indistinguishably on the two gradients (Figure 3.3). The relationship between *m* and $T \bullet P$ (Figure 3.3A) was statistically similar between the two gradients ($p = 0.81$

for intercept, p = 0.97 for $T{\bullet}P$, and p = 0.94 for $T{\bullet}P^2$). Regarding ϕ, its relationship with $T{\bullet}P$ was also similar between the two gradient types (p = 0.36 for intercept, p = 0.19 for $T{\bullet}P$, and p = 0.20 for $T{\bullet}P^2$). This "natural experiment" – climatic gradients originating in two different ways, but having the same effect on ϕ, m and richness, is consistent with a direct effect of climate.

A path analysis of ϕ, m, richness, and climate revealed a more complicated set of interactions than my initial hypothesis proposed (Figure 3.4). I used a path analysis to test whether the observed correlations are more consistent with a model in which species richness is linked to climate via rarity, or one in which richness relates by another path to temperature and precipitation. Note that a path analysis is an extension of multiple regressions that allows one to examine more than one dependent variable at a time and allows for variables to be dependent with respect to some variables and independent with respect to others (Shipley 1997). I constructed three path models that include the temperature • precipitation interaction, proportion of singletons, density of individuals, and species richness (Figure 3.4). If species richness is causally linked to rarity, then a model connecting richness and ϕ (Figure 3.4, path-model *A*) should out-perform a model that does not contain that path (path-model *B*). However, if temperature and precipitation influence richness through some other mechanism, then path-model *B* should perform better than *A*. Model *C* causally links species richness with both rarity and temperature • precipitation. I evaluated model performance and goodness of fit using the variation explained in species richness as well as Bayes's information criterion (BIC) (Bollen & Long 1993). I found that Model *A* outperformed Model *B* and I also found that model *C* was the best out of the three, explaining 86% of the variation of species richness, and having by far the lowest BIC (Figure 3.4*C*). These results indicate that temperature and precipitation influence species richness primarily through ϕ (note path coefficients from ϕ to *SR* is much higher than temp•precip to *SR*). Subsequently, there is a smaller effect through some other mechanism. Therefore, these results are mostly consistent with the third prediction.

Discussion

My results are consistent with the hypothesis that richness varies along climatic gradients principally because species persist at lower densities in places with benign climates (high temperature and precipitation). Richness is also related to variation in the density of individuals, which is only weakly dependent on climate. Finally, there is also a smaller effect of climate that is mediated neither by the persistence of rare species nor by the total number of individuals. However, my predictions for the proximal correlations (climate-rarity, rarity-richness) and the distal correlation (climate-richness) were consistent among the global data and less so for the Barva data. This disparity could possibly result from the small sample size and possibly the larger sampling unit (1 ha vs. 0.1 ha for global data) associated with the Barva data. This will require further testing. Despite finding this difference in my prediction however, I found that most relationships between the dependent variables and the independent variables were statistically indistinguishably from the two types of gradients. Subsequently, rare species persist at much lower densities in areas with high temperatures and high precipitation on both types of gradients.

Why would species persist at lower densities in warm wet regions? It is known that population extinction risk varies inversely with population size (Pimm *et al.* 1988). The slope of that relationship may depend upon climate, such that low-density populations have a higher probability of persisting in benign climates. Benign climates typically vary less seasonally than more extreme climates, both on elevational gradients (Figure C.2) and on latitudinal gradients (Figure C.3) (Janzen 1967). Plant mortality rates are strongly linked to variation in temperature and precipitation, especially with extreme weather events such as prolonged droughts (van Mantgem & Stephenson 2007; Adams *et al.* 2009; Allen *et al.* 2010; Lines *et al.* 2010; Phillips *et al.* 2010). Thus, I would expect that trees occurring in regions with stable climates would have, on average, lower mortality rates, and therefore species could persist at low densities. Areas that have higher mortality rates should have few rare species or rare species with much higher population s (i.e., on average, higher values of m and lower values of ϕ). Direct tests of this prediction are rare; however, based on a limited amount of data from forests (Swaine *et al.* 1987), I found the expected relationship is consistent with the predicted one (Figure 3.5).

I cannot exclude the possibility that richness responds to some other aspect of the log-normal distribution. Since the total number of individuals in species assemblages varies relatively little with climate (Table 3.1), and if species assemblages globally conform (at least approximately, cf. (McGill *et al.* 2007; Hubbell *et al.* 2008)) to Preston's log canonical log normal, then persistence of rare species in benign climates must shift the entire canonical log normal distribution to the left (Figure C.4). One would therefore expect a negative relationship between average population density and the temperature • precipitation interaction (T•P), which is what I observed (Figure C.5). One would also expect that the density of the most abundant species to vary negatively with T*P (Figure C.6). Further, as the average number of individuals per species decreases, the maximum density of individuals of species should also decrease and the number of rare species should increase (i.e. more singletons). I found that my observed patterns are in agreement with the predicted ones (Figure C.7A and B, Figure C.8A and B). Finally, variation in species richness among quadrats must be related to any descriptor of the position of the log normal distribution. Therefore, as the average density of individuals and maximum individual density increases species richness must decrease. Once again, the observed pattern is consistent with the predicted pattern (Figure C.7C and Figure C.8B).

My hypothesis, along with my proposed mechanism, offers the potential to predict how tree community characteristics (i.e. number of species and species abundance distributions) will change with future climate change. If for example, regions experience less benign climates, compared to their contemporary climates, my mechanism predicts that the lognormal species abundance distribution of the community will shift right (Figure C.4). Consequently, this shifting will cause the average individual density to increase thereby causing the extinction of species with the lowest densities (reflected in m). This process should ultimately decrease the number of species, irrespective of species adapting to future climatic changes.

Preston's model of the distribution of individuals among species explained why larger areas have more species: because they have more individuals. My evidence is consistent with Preston's prediction; however, I found that the density of individuals varies too little geographically to produce strong geographical richness gradients. Rather, my evidence suggests that Preston's model can also account for geographical gradients of richness when it is coupled with one assumption: that species persist in benign climates at lower densities (reflected in m and ϕ). In different words, the relationship between extinction probability and population abundance must be climate dependent. This interaction generates gradients of species richness along climatic gradients, be they latitudinal or elevational. This hypothesis provides a conceptual unification of two of the most striking patterns in nature: log-normal abundance distributions, and geographical patterns of richness.

Tables

Table 3.1. Models relating species richness (SR), the number of individuals per quadrat (I), or the number of singletons (species represented by a single individual in the sample, ϕ) to the interaction between mean annual temperature and the square root of annual precipitation ($T \cdot P^{0.5}$). Non-significant terms ($p > 0.05$) are surrounded by square brackets. All other terms are significant at $p \leq 0.05$. Two data sets were used: an elevational gradient on the Barva volcano in Costa Rica, and global data set (with a Neotropical emphasis) gathered by Alan Gentry. nr – not relevant.

Model	R^2	AIC	Gradient
$\log_{10} SR_{B1} \sim T \cdot P^{0.5}$	0.94	-25.62	Barva
$\log_{10} SR_{B2} \sim T \cdot P^{0.5}$ $[+ (T \cdot P^{0.5})^2]$	0.95	-23.00	Barva
$\log_{10} SR \sim T \cdot P^{0.5}$ $[+ \log_{10} I]$	0.94	-22.00	Barva
$\log_{10} SR \sim \phi$	0.47	-4.07	Barva
$\log_{10} SR \sim \phi$ $[+ \log_{10} I]$	0.52	-3.14	Barva
$\log_{10} m \sim T \cdot P^{0.5}$	0.94	6.39	Barva
$\log_{10} m \sim T \cdot P^{0.5}$ $[+ (T \cdot P^{0.5})^2]$	0.94	8.86	Barva
$\phi_B \sim (T \cdot P^{0.5})^2$ $[+ T \cdot P^{0.5}]$	0.72	-20.72	Barva
$\phi_B \sim T \cdot P^{0.5}$	0.55	-19.37	Barva
$\log_{10} I \sim$ $[T \cdot P^{0.5} + (T \cdot P^{0.5})^2]$	0.00	nr	Barva
$\log_{10} SR \sim T \cdot P^{0.5} + (T \cdot P^{0.5})^2$	0.66	-62.00	World
$\log_{10} m \sim T \cdot P^{0.5} + (T \cdot P^{0.5})^2$	0.66	425.67	World
$\log_{10} SR \sim T \cdot P^{0.5} + (T \cdot P^{0.5})^2 + \log_{10} I$	0.74	-115.49	World
$\log_{10} SR \sim \phi$	0.57	-15.44	World

$\log_{10} SR \sim \log_{10} I + \phi$	0.83	-190.16	World
$\phi \sim T \cdot P^{0.5} + (T \cdot P^{0.5})^{2}$	0.46	nr	World
$\log_{10} I \sim T \cdot P^{0.5} + (T \cdot P^{0.5})^{2}$	0.26	nr	World

Figures

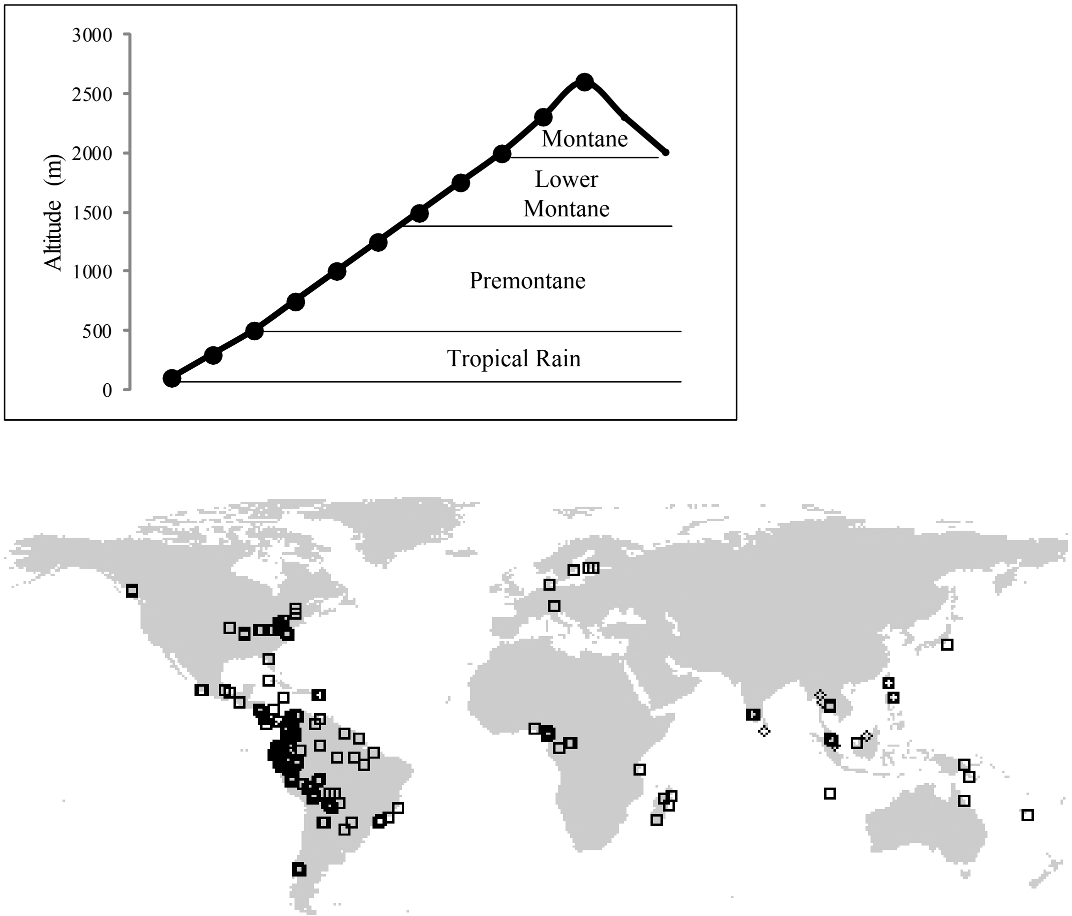


Figure 3.1. The sample sites used in our analysis. The top panel represents an elevational gradient on the Barva volcano in Costa Rica (Libermann et al. 1996); forest types were obtained from http://www.bio.miami.edu/carlos/projects.html. The world map shows sites from a data set compiled by Alywn Gentry (Phillips and Miller 2004).

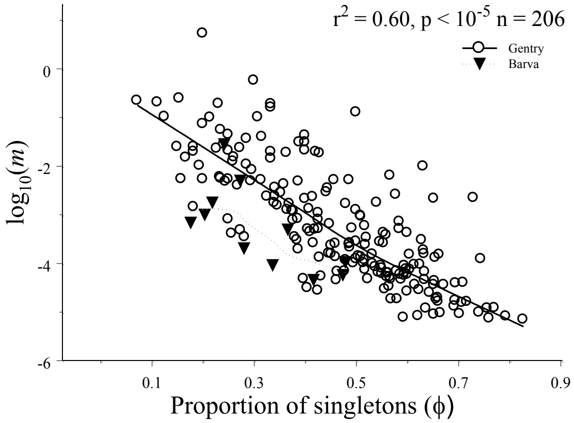


Figure 3.2. The number of individuals of the rarest (m) as a function of proportion of singletons (World and Barva sites); *m* was estimated from number of individuals and species richness (Equation (2) in materials and methods). LOWESS line shown with a tension of 0.80.

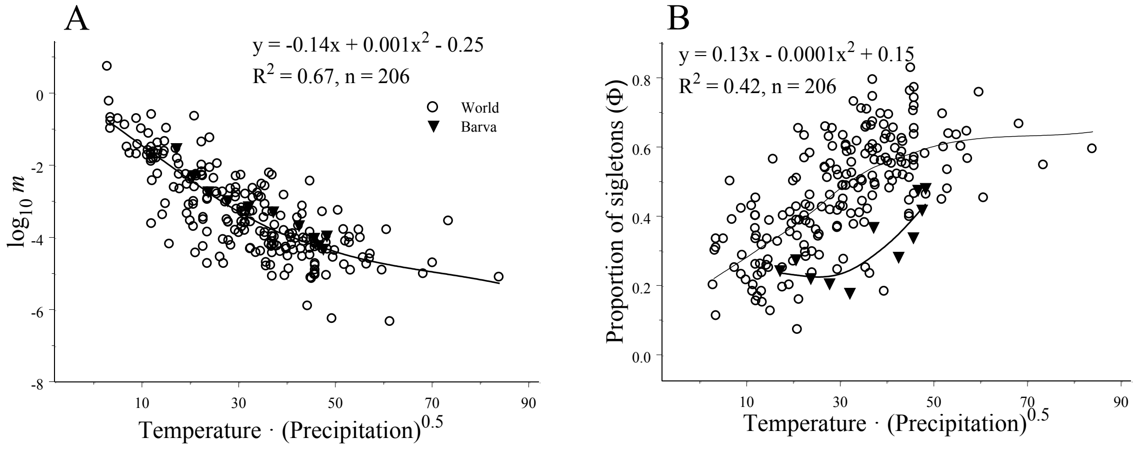


Figure 3.3. A) The number of individuals of the rarest species (*m*) as a function of the temperature (K) and precipitation interaction (meters) in two data sets: an elevational transect (inverted triangles) on the Barva Volcano in Costa Rica, and a global data set (Gentry, open circles) in which sites vary in latitude. I included a second-degree polynomial for our analysis. Precipitation (meters) was square root transformed. B) The proportion of singletons per site also relates strongly to climate. The proportion of singletons on the Barva transect is lower than in the Gentry data because the Barva quadrats were larger than the world quadrats. The difference in the number of individuals that results from the differing quadrat size was controlled in the estimation of *m*, but not for ϕ (which was observed directly).

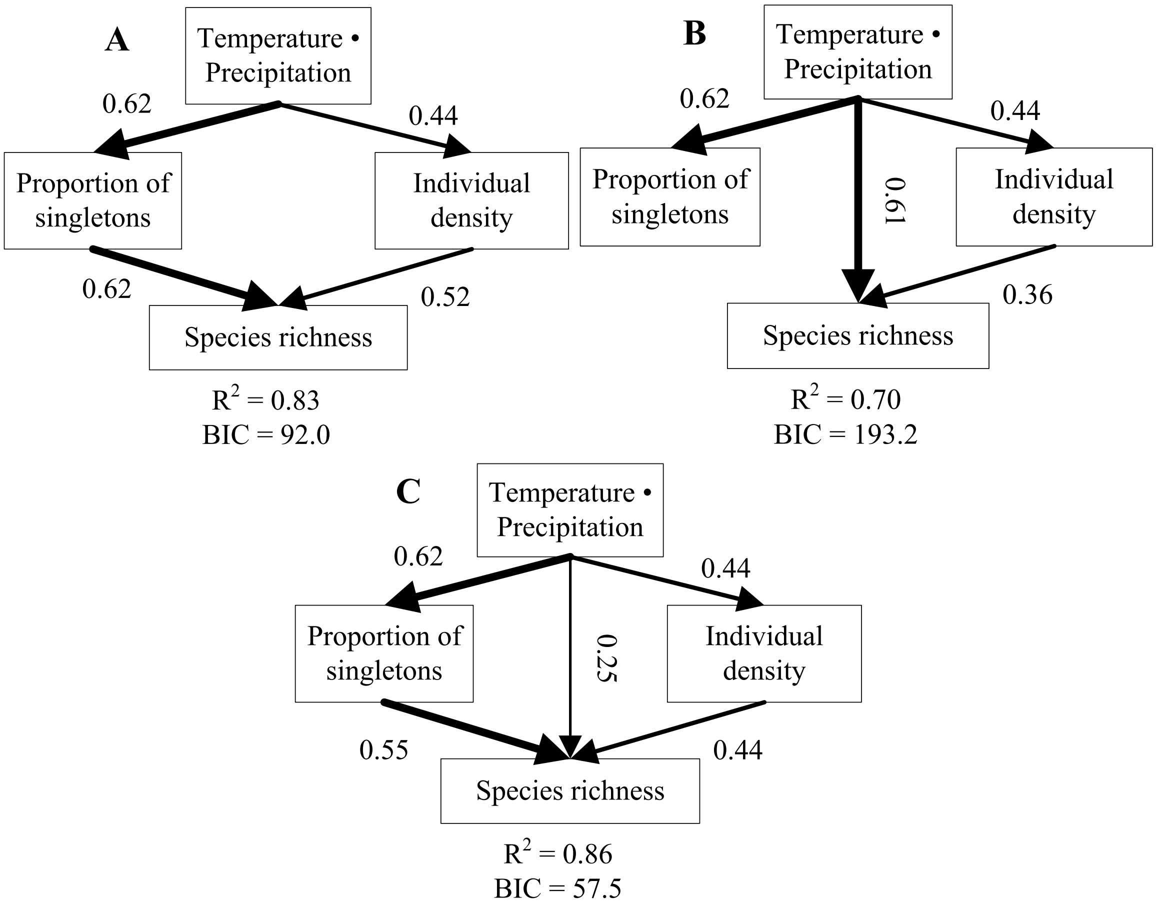


Figure 3.4. Three competing path models with standardized coefficients, goodness of fit (R^2), and model performance (BIC, Bayes's Information Criterion). Arrow width is proportional to the strength of the effect. Model *C* provides higher explained variance and considerably higher likelihood than the other two models. A path analysis with a (Temperature • Precipitation)^2 term yielded qualitatively similar results, and accounted for slightly more variance (average increase of 2.3%), but caused coefficient estimates to have inflated variance. Path analysis conducted using only the global data set of Gentry.

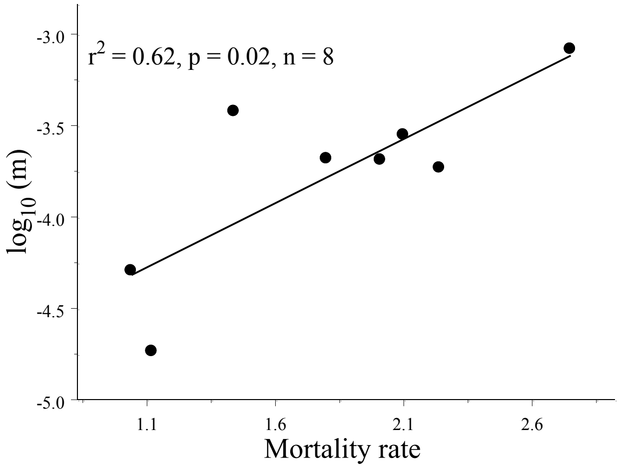


Figure 3.5. The number of individuals of the rarest species (*m*) as a function of mortality rate. Data were obtained from (Swaine *et al.* 1987). The number of individuals of the rarest species was estimated from density of individuals and species richness (equation [2] in Methods). Linear regression line shown. I chose sites that had published results for the number of species, number of individuals and mortality rates. Mortality rate was defined as $\lambda = (\log_e n_0 - \text{loge } n_1) / t$ where n_0 is the number of trees at the first time interval, n_1 is the number of surviving at the second time interval, t years later. The number of individuals of the rarest species (m) was estimated using $m = (16.2 * I) / SR^{3.817}$ where *I* is the number of individuals and *SR* is the number of species.

4. Chapter 4: The required minimum area and the financial cost to protect the rarest species

Abstract

Protecting species from habitat loss is one of the pressing conservation problems of this century (M.E.A. 2005). While there are different methods for protecting species and habitats (Dudley 2009), one of the more common methods involves the protection of natural habitat. Based on the species area relationship, scientists know that larger areas will protect more species, (May 1976; Simberloff 1992; Wilson *et al.* 2006; Wilson *et al.* 2007; Guilhaumon *et al.* 2008). Though successful for protecting many species, this method does not take into account abundances of the protected species. As is well known, within species communities, there are only a few common species and many more rare ones, now recognized as the principle of species abundance distribution (Preston 1948). Although many species in a protected area will be rare, (inherent rarity (Maina & Howe 2000)), it is likely that these rare species will not have sustainable viable population sizes (Shaffer 1981) which, despite being protected, would make them susceptible to extinction. By using Frank Preston's (Preston 1962b, a) observation that species abundance distributions follow a canonical log normal distribution, and to better protect the rare species, I estimated the minimum area the rarest species need to have "viable" population sizes. This estimation showed that across continents and latitudes, the required minimum area of the rarest species relates consistently to temperature and precipitation. Lastly, based on area, I estimated the financial cost of protecting the rarest species and found a weak negative relationship (r^2 =

0.05, p = 0.003) between the cost to protect the rarest species and a country's gross domestic product.

Introduction

Although laws in ecology that explain or describe the first order variation of the distribution of life across our planet are rare, two patterns considered as ecological "laws" are: species abundance distribution (SAD) and the species-area relationship (SAR) (Rosenzweig 1995; McGill *et al.* 2007). One of the most common patterns of the SAD is that natural species assemblages nearly always consist of a few common species and many rare ones (Preston 1948; McGill *et al.* 2007). Despite occurring for nearly all taxa worldwide (Ulrich *et al.* 2010), the mechanisms responsible for this near universal pattern are still unknown (see (McGill *et al.* 2007) for a review). The other ecological "law," the SAR, simply states that as sampling area increases so does the number of species. This pattern has also been observed in nearly every taxonomic group worldwide (Gleason 1922; Preston 1962a; MacArthur & Wilson 1963; Connor & McCoy 1979; Rosenzweig 1995). While both the SAD and SAR are nearly universal, the SAR is more commonly used for conservation purposes. By using the SARs, scientist commonly view habitat loss and alteration as primary causes of species extinction, specifically from areas of natural landscapes converted to the area of human-dominated landscapes (M.E.A. 2005). However, additional studies have shown that the number of species lost using the SAR approach consistently overestimates the number of extinctions from loss of habitat (Simberloff 1992; May *et al.* 1995; Pimm & Askins 1995; He & Hubbell 2011). If models then fail to estimate accurately species loss as a function of habitat loss, then they could possibly fail in estimating how much land area is needed to protect a given number of species, particularly the rare[3] ones.

The SAR has been used to prioritize protected areas since larger areas will protect more species (May 1976; Desmet & Cowling 2004; Wilson *et al.* 2006; Wilson *et al.* 2007; Guilhaumon *et al.* 2008). However, using the SAR to establish protected areas for a given size does not consider SADs. Consequently, despite being in a protected area, some species may have only a few individuals in the protected area, which makes it likely that these rare species could go extinct (Maina & Howe 2000). Ideally, knowing the number of individuals of the rarest species in a given area would provide a baseline to better estimate how much area is needed to protect all species in the community. Although determining this in the field would be difficult to determine, time intensive, and costly (Bruner *et al.* 2004), I ask, using Preston's model, whether it can mathematically estimate the minimum area the rarest species needed for a "viable"[4] population. One may question the utility or the accuracy of using Preston's question towards estimating the minimum area for the rarest species. However, elsewhere, I showed that his model could predict richness (based on rarity, Chapter 3) across different types of spatial gradients, which suggests that his model and coefficients represent observed abundance distributions patterns across space. In addition, Preston's model assumes that SADs follow a log-normal distribution. Although other types of distributions describe the SAD (Fisher *et al.* 1943; Hubbell 2001; McGill *et al.* 2007), Preston's log-normal distribution describes SADs reasonably well (Connolly *et al.* 2005; Dornelas *et al.* 2006; Ulrich *et al.* 2010).

---

[3] Rare species in this analysis can take on one of the seven forms of rarity outlined by (Rabinowitz *et al.* 1986) based on their range size, habitat breadth, and abundances.

[4] Note that 'viable' in this case is not directly related to the minimum viable population size of the rarest species (Shaffer 1981).

Preston, examining local assemblages, found that the abundances of different species could be described by a log-normal distribution with two parameters (Preston 1962b, a), one parameter is the total number of individuals in the assemblage (individual density) and the other is the number of individuals of the rarest species. Deducing from his model that species richness should covary with area, because larger areas contain more individuals, Preston predicted the richness-area relationships and species richness based on his two parameters, which lead to equation 1:

$$SR = 2.075 * (I / m)^{0.262} \tag{1}$$

Where SR is species richness, I is individual density and m is the total number of individuals of the rarest species.

To estimate the minimum sampling area required for the rarest species, I solved for m rather than SR in equation 1; this resulted in equation 2

$$m = (16.2 * I) / SR^{3.817} \tag{2}$$

Because m represents the total number of individuals of the rarest species in a given area, I could then estimate the minimum sampling area needed for at least two individuals of the rarest species. Based on Preston's assumption that m must be greater than or equal to two (Preston 1962b), I chose two individuals as a 'viable' population size. Although a more realistic viable population size must be greater than two, once the minimum sampling area for two individuals is known, the area needed to increase the number of individuals observed to approximate a more realistic viable population size can be scaled (e.g. 5000 individuals (Traill *et al.* 2007; Traill *et al.* 2010), but see Flather et al. (2011). Using the Alwyn Gentry tree transect data from Phillips and Miller (2004), I estimated the minimum sampling area needed to capture at least two individuals of the rarest species by multiplying an appropriate scaling factor in hectares to *m,* for 196 sites around the world, so that the smallest *m* within a given site was approximately equal to 2 (ranged among sites at: 2.1, to 2.3). Note that using that using approximately two individuals of the rarest across regions assumes that the minimum “viable population” size is constant. This is likely unrealistic based on the work of Silva and Downing (1994) where they found smaller minimum viable population sizes in tropical areas. In addition, Chapter 3 also suggests that the minimum viable population sizes can be much lower in regions with benign climates. However, if minimum viable population sizes are lower in regions with more benign climates, it is likely that estimated sampling area needed to capture at least two individuals will be overestimated. In other words, the estimated minimum sampling area will likely protect more individuals of the rarest.

I found that across continents and latitude, the required minimum area was explained consistently by temperature and precipitation. Based on area, I estimated the financial cost of protecting the rarest species and found a weak negative relationship ($r^2 = 0.05$, $p = 0.003$) between the cost to protect the rarest species and a country’s gross domestic product.

Methods Summary

I used Alwyn Gentry’s tree transect data, 220 sites (0.1 hectare) located on most continents but concentrated in the tropical Americas (Phillips & Miller 2004), I first compared how the minimum area varies across the different regions. I used a $\log_{10}$ transformation of the minimum area required for the rarest species to normalize the distribution. I removed sites that were less than 0.1 hectare and sites where temperature and precipitation could not be accurately estimated, which left 196 sites for the analysis. Because temperature and precipitation relate with many ecological patterns (see

Introduction), I wanted to determine if and how the minimum area of the rarest species relates with these two variables. To determine the relationship between the minimum area of the rarest species and temperature, precipitation, and the interaction between temperature and precipitation, I used bi-variate scatter plots and linear regression models. I used mean annual temperature (C) and total annual precipitation (mm) estimates reported in Phillips and Miller (2004). Treating each region as a categorical variable, I then used an ANOVA and Tukey's Honestly-Significant-Difference Test. I used a square root transformation for total annual precipitation and temperature and precipitation interaction, although I did not transform mean annual temperature.

To calculate the minimum area for the rarest species, and the costs in US dollars required to purchase such areas across various countries, I first converted the minimum area from hectares to square kilometers. Using James' *et al* data (1999) including financial shortfalls (e.g. the amount by which a financial requirement exceeds the amount of cash that is available) in US dollars budgeted among 38 different countries; I then multiplied the minimum area (km^2) by the average annual cost per km^2. For countries not reported in James *et al.* (1999), I used the region's average cost per km^2 including financial shortfalls[5]. The results of these calculations established the total budget needed to purchase the minimum area of the rarest species. To normalize the distribution of the total budget to purchase the minimum area of the rarest species for each country, I used a $\log_{10}$ transformation.

To determine whether the cost needed to purchase the minimum area of the rarest species was significant across regions, I used an ANOVA where the cost needed to protect

---

[5] For example, since Germany had no reported budget cost for protected areas, I used the average cost per km^2 across Europe.

the minimum area was the dependent variable and region was the independent variable (categorical). I then tested for significant differences among the various regions using Tukey's Honestly-Significant-Difference Test. Lastly, because a country's gross domestic product (GDP) could potentially affect the resources allocated to protect areas (Antle & Heidebrink 1995; Balmford *et al.* 2003; McDonald & Boucher 2011), I examined the relationship between a country's GDP and the cost needed to purchase the minimum area of the rarest species. I obtained GDP data for each country from the International Monetary Fund Emerging and Developing Economies List (I.M.F. 2012) and used a $\log_{10}$ transformation for GDP to normalize its distribution. I checked residual plots for homoscedasticity and used S-Plus ver. 8.0 (Insightful, Inc., Seattle, Wash.) for all analyses.

Results

I found that the minimum area required for at least two individuals of the rarest tree species varies across continents (Figure 4.1) and by nearly six orders of magnitude. Interestingly, and alarmingly, rare species that require more area occur in regions that experience the heaviest habitat alteration (Butler 2011). Moreover, the minimum area of the rarest shows a pronounced negative relationship with absolute latitude (Figure 4.2) and explained 58% in the variation of the required minimum area. In summary, rare species occurring in equatorial regions require more area for 'viable' population sizes compared to species that occur farther north or south.

Showing the geographical variation in the minimum area needed for the rarest species to have 'viable' population is only pertinent if one can explain or predict such variation. Because I am using tree data and because tree types (Kleidon & Mooney 2000), tree height (Kempes *et al.* 2011), tree abundance (Sun *et al.* 2007; Kleidon *et al.* 2009), and tree diversity (O'Brien 1998; Kleidon & Mooney 2000; O'Brien *et al.* 2000; Francis & Currie 2003) relate to temperature, precipitation, and their interaction, I related the minimum area of the rarest to these variables. In other words, I am asking if environmental variables that explain gradients in other characteristics of tree assemblages, might also explain gradients in the minimum area rare species requiring at least two individuals.

The results indicate that variation in the minimum sampling area needed for the rarest is explained by variation in temperature, precipitation, and their interaction (Figure 4.3a-c). While temperature explained more of the variation in the minimum area compared to precipitation, albeit slightly, it was the interaction between the two that explained most of the variation (Figure 4.3c). Subsequently, rare species that occur in warm wet regions require a much larger sampling area to include a minimum of two individuals than do species that occur in cold dry ones. The largest minimum area for the rarest across all sites was approximately 31,000 hectares (in South America), an area about twice the size of Washington DC. In contrast, the smallest area of the rarest in Europe (0.04 ha) was about the size of two tennis courts. Consequently, the rarest tropical species require a much larger area for a “viable” population than do northern temperate ones.

The average financial cost to establish protected areas for the rarest among Africa, Europe, and North America was significantly lower ($P < 0.05$) than the cost estimated in Mesoamerica and South America (Figure 4.4). Tropical Asia had the highest cost for establishing protected areas; generally, the more developed regions (e.g. Europe and North America) have the lowest cost for protecting the rarest. Interestingly, despite this trend, there was a weak negative relationship between cost to protect the rarest and GDP (Figure 4.5). While significant ($p < 0.05$), GDP explains only 5% of the variation in cost to establish protected areas for the rarest.

Discussion

It is estimated that are over 100,000 protected sites across our world comprising approximately 12.9% of the global terrestrial area (Chape *et al.* 2005; Jenkins & Joppa 2009). Among most countries, the distribution of the protected areas among the six categories defined by the International Union for Conservation of Nature (IUCN) occur in Categories II (national park) and VI (managed resource protected areas (Chape *et al.* 2005)). Because the analysis is dealing the area to protect the rarest species, the results from this analysis are most relevant to the IUCN categories in strict nature reserves (Category Ia), wilderness areas (Category Ib), national parks (Category II), protected landscapes (Category V), and managed resource protected areas (Category VI) (Dudley 2009). Although the remainder of the discussion applies to categories more relevant to the analysis, there is little doubt that the protection of sites under the other IUCN categories (Categories III—natural moment, Category IV—habitat/species management area) have been seminal in protecting thousands of species covering millions of square kilometers (Chape *et al.* 2005; Jenkins & Joppa 2009).

While the majority of the variation of the minimum sampling area of the rarest requiring at least two individuals is explained by the temperature and precipitation interaction, why rare species occurring in warm wet regions require more area is not entirely clear. Perhaps, warm wet regions (or regions with benign climates), allow for lower population densities than do cold dry regions (see Chapter 3). Although based on equation 1 the relationship between minimum area and temperature and precipitation might simply reflect variation in richness, this does not appear to be the case. Elsewhere (Chapter 3), I proposed that gradients of richness are causally determined by gradients in *m*, which in turn are driven by gradients in temperature and precipitation. Moreover, by using equation 2, one can monitor the temporal variation in *m* at local sites to estimate variation in *m* across broader regional scales and also relate this change in *m* to variation in temperature and precipitation. Although *m* will vary naturally due to random stochastic processes (Hubbell 2001), if *m* increased, by say, an order of magnitude, then this suggests that the rarest species within a given area has likely gone extinct.

It is known that population extinction risk varies inversely with population size (Pimm *et al.* 1988). I propose that the slope of that relationship depends upon climate. Population extinction risks can be affected by extreme weather events such as prolonged droughts or an increase in temperature which can accelerate plant mortality (van Mantgem & Stephenson 2007; Adams *et al.* 2009; Allen *et al.* 2010; Lines *et al.* 2010; Phillips *et al.* 2010). Thus, it is expected that trees, particularly the rare ones, occurring in regions with stable climates would have, on average, lower mortality rates, and therefore species could persist at low densities. However, this needs further testing. Despite not knowing exactly how or why temperature and precipitation cause the geographical variation in the minimum area rare species require, future climate change will most likely affect the rarest species. It is also likely that variation in climate will be less predictable as climate changes thus increasing the likelihood that the rarest species could possibly go extinct.

Knowing the minimum area for the rarest could help agencies establish protected areas that reduce the likelihood of the rarest species (and all other species) from becoming extinct. If one knows the minimum area needed to protect the rarest species, then this area essentially encompasses all other species and if such area is protected then the likelihood of extinction for all species is reduced. In other words, if one wanted to protect as many species (trees for this analysis) as possible, then one would essentially protect natural areas that are as large as or equal to the minimum area of the rarest tree species. Theoretically, the area needed to protect the most species equates to the minimum area needed for the rarest. While this area will encompass two individuals of the rarest, it is very likely that it will encompass more individuals of other rare species.

Although the assumption that at least two individuals (based on Preston) are sufficient for a viable population is unrealistic, my results can estimate the minimum area needed for a more reasonable viable population size. In Mexico for example, the minimum area required for two individuals is 750 ha. If one assumes that a minimum viable population size for a sustainable population is approximately 5000 individuals (Traill *et al.* 2007; Traill *et al.* 2010), then the area would need to increase to approximately 1,875,000 hectares or approximately 18750 square kilometers. Based on James *et al*. (1999), the financial cost, including shortfalls would be around five and half million US dollars. This approximates the cost to protect the rarest species based on a minimal viable population size of 5000 individuals. If minimal viable populations can be much lower (Flather *et al.* 2011), then the cost to protect the rarest will necessarily decrease.

The results also demonstrated that the cost per km^2 to finance the minimum area of the rarest also varied among the different regions with Tropical Asia having the largest cost. Despite varying across regions and countries, there was only a weak relationship between the cost per km^2 and a country's GDP, perhaps because developing countries have a much lower cost per km^2 than the cost observed in developed countries (James *et al.* 1999; James *et al.* 2001; Balmford *et al.* 2003; Bruner *et al.* 2004). Thus, in developing countries, many rare species require more area for at least two individuals of the rarest; such increased costs may be offset by having a lower cost per km^2. The one major exception is New Caledonia which requires 85 thousand dollars including financial shortfalls (James *et al.* 1999), to protect one square mile of protected area.

The estimated cost to establish protected areas in this study did not consider associated costs many of which can exceed that of the cost to that of purchasing the protected area (James *et al.* 2001; Bruner *et al.* 2004). These can include but are not limited to expenses for management, inventory surveys, system wide support of protected networks, damage and others (Bruner *et al.* 2004; Naidoo *et al.* 2006; Wilson *et al.* 2007). Moreover, even if agencies had the necessary funds to establish and monitor newly protected areas, Eklund *et al*. (2011) found that governance factors, corrupt vs. non-corrupt, and economic development can impact how funds are allocated to protected areas Even when considering such factors impacting the success of newly established protected areas, the cost needed to protect the rarest species in this study (in Peru) with an area that captures 5000 individuals was approximately 12 million US dollars. This cost is approximately 0.002% of what Americans spent on carbonated soft drinks in 2009 (http://www.beverage-digest.com/editorial/datastats.html). However, the financial cost to protect the most expensive ‘species’ (based on the minimum area and the country’s per km^2 cost and 5000 individuals) which occurs in New Caledonia was estimated to be around 10.7 billion US dollars or just 14% of what Americans spent on soft drinks (http://www.beverage-digest.com/editorial/datastats.html). While the cost to protect the rarest does vary across countries, it is encouraging to find that in many countries, the total cost to protect the rarest may not be out of reach.

Figures

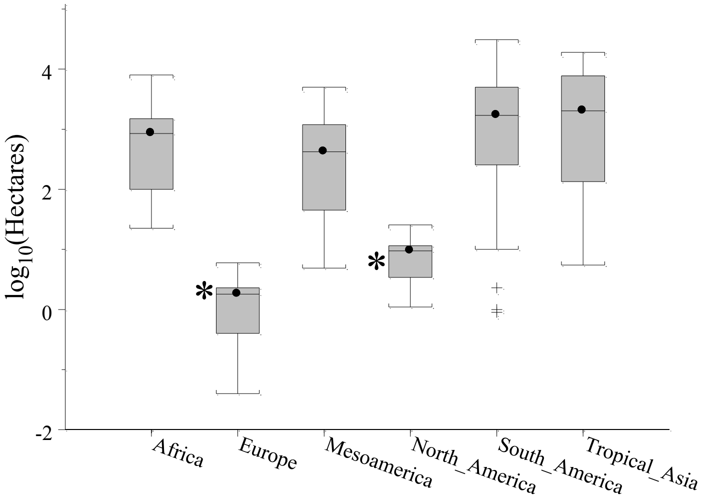


Figure 4.1. Median and quartile range for the minimum area ($\log_{10}$) of the rarest across different continents. Outliers are represented by plus signs, N = 196. Asterisks represent regions with values significantly lower ($p < 0.05$) compared to the other regions.

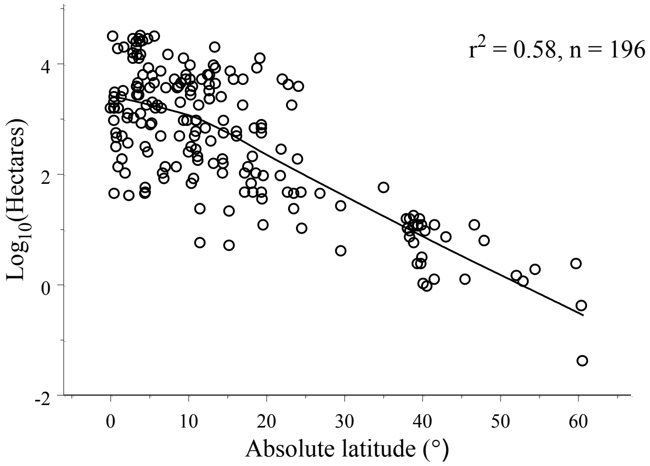


Figure 4.2. Minimum area ($\log_{10}$ hectares) of the rarest as function absolute latitude. Lines are LOESS trend lines, tension = 0.80, N = 196.

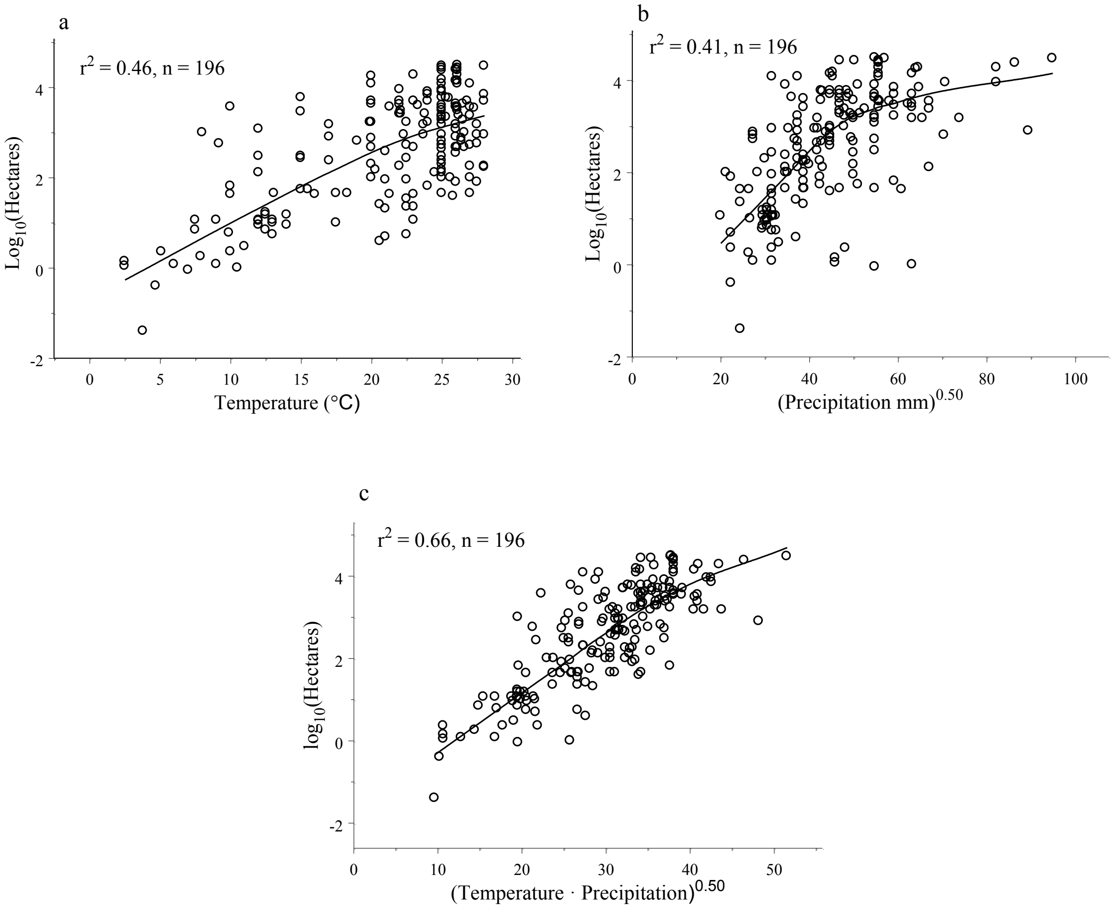


Figure 4.3. Minimum area ($\log_{10}$ hectares) of the rarest as function of environmental variables. a), mean annual temperature (°C); b), total annual precipitation (mm, square root transformation); c), mean annual temperature (°C) and total annual precipitation interaction (square root transformation). Lines are LOESS trend lines, tension = 0.80, N = 196.

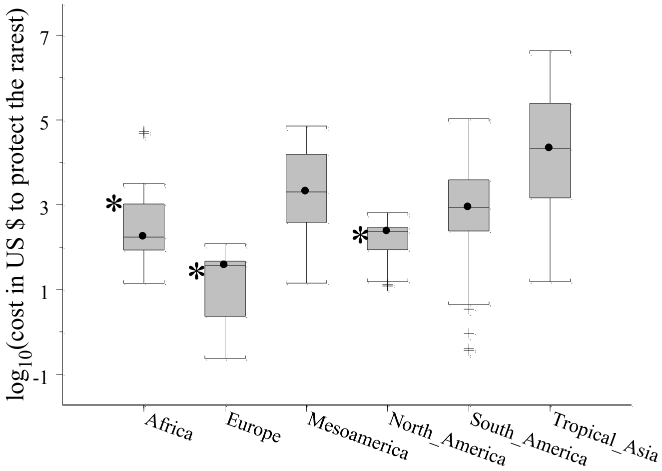


Figure 4.4. Median and quartile range for the cost in US dollars (log$_{10}$) to establish protected areas for the rarest species (based on two individuals). Outliers are represented by plus signs, N = 196. Asterisks represent regions with values significantly lower ($p < 0.05$) compared to the other regions.

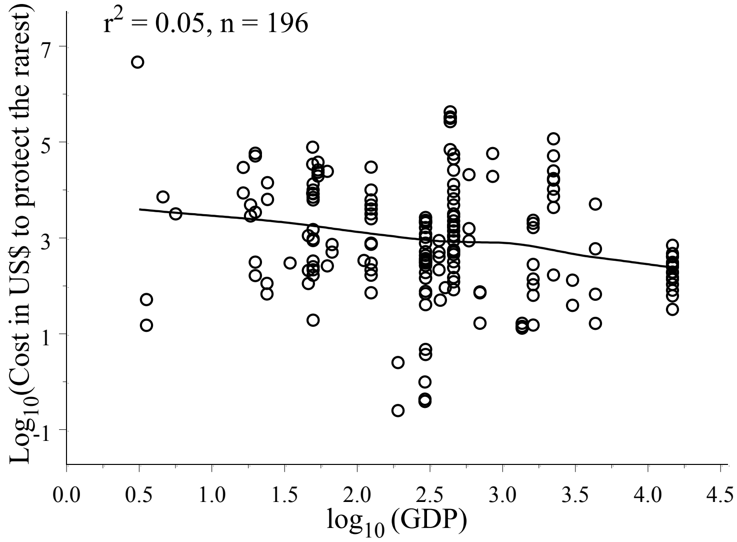


Figure 4.5. Cost in US dollars to establish a protected area to for the rarest species among 38 countries as a function of the country's GDP. The cost was estimated by multiplying the country's cost per km^2 cost times the minimum area (based on two individuals) required for the rarest species. Lines are LOESS trend lines, tension = 0.80, p = 0.003, N = 196.

5. Chapter 5: Bergmann up-dated: A closer look at how mammalian body size varies geographically

Abstract

Aim: Bergmann's rule and several more recent hypotheses predict that a higher proportion of species at high latitudes (or, more generally, in cold climates) are large-bodied. Tests of this prediction have nearly always focused on mean body-size, rather than examining changes in the shape of the entire body-size distribution. Here, I test: A) whether geographic variation in body size is as simple as a shift toward larger species in cold regions, B) to what extent these distributions also depend upon other climatic variables, C) to test the specific predictions from the heat conservation, resource seasonality hypotheses, and the evaporative water loss hypotheses

Location: The Western Hemisphere

Methods: I tallied the number of species in ten body size categories in 200 x 200 km^2 grid cells (n=1196) across the Americas, resulting in a sample size of 11960 size category × grid cell combinations. For each quadrat, I determined mean annual temperature (K), mean annual precipitation (mm), resource seasonality (maximum monthly net primary productivity minus minimum monthly net primary productivity). I used ANCOVAs to test the interactions between climate and body size.

Results:

1. Species of all sizes occur across the entire temperature gradient.
2. Mean body mass of mammalian assemblages captures only 2% of the geographical variation in mammalian body sizes.

3. The specific predictions from the various hypotheses that attempt to explain body mass distribution were not supported.
4. The number of species observed in different size categories responded differently to the environmental variables. Small- and large-bodied species responded most strongly to mean annual temperature and mean annual precipitation while medium-bodied species responded most strongly to resource seasonality.

Main Conclusion: The focus on mean body-size, and on latitude or temperature, in most studies of Bergmann's rule (or related hypotheses) misses most of the geographical variation in mammalian body sizes. Body size is not dependent on a single climatic variable. These results are not consistent with any of the hypotheses proposed to explain the geographical variation of species among size categories. It is not clear what process(es) generate(s) these patterns, but it seems unlikely that they will be explained by any single mechanism.

Introduction

Ten years before *On the Origin of Species* was published by Charles Darwin, Carl Bergmann (Bergmann 1847) published, "Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse", which described one of ecology's first generalizations, the tendency for homeotherms to increase in body mass at higher latitudes (Figure 5.1). Moreover, Bergmann provided a mechanistic explanation as to why species become larger as latitude increases. He developed the heat conservation hypothesis, which suggests that cold climates should have more large-bodied species and fewer small-bodied species. Bergmann's mechanism was based on the notion that larger species have smaller surface area to volume ratios compared to smaller bodied species, allowing larger species to conserve heat more effectively compared to smaller ones. Thus, large-bodied species should be better able to persist in cold regions, while small-bodied species should have an advantage in low latitudes or regions with warmer temperatures. James (James 1970) proposed the flip side of this argument: small-bodied species radiate excess heat more effectively due to high surface-area:volume ratios, and therefore can tolerate -- and be more common in -- hot areas. Because Bergmann's and James's hypotheses predict the same patterns of spatial variation in body size, discussion below will be limited to Bergmann's heat conservation hypothesis .

While Bergmann provided a simple explanation to describe the pattern of increasing body size in colder regions, the resolution at which Bergmann's hypothesis should be tested is still contentious (Blackburn *et al.* 1999; Meiri 2010; Watt *et al.* 2010). Studies that report intra-specific variation in body-size, or the geographic variation in closely related species, often provide evidence that is consistent with Bergmann's proposed pattern and the heat conservation hypothesis (Ashton *et al.* 2000; Ashton 2002; Freckleton *et al.* 2003; Hayes 2003; Meiri & Dayan 2003; Lucherini *et al.* 2006) but see (Meiri *et al.* 2009). However, when Bergmann's rule is tested by examining variation in species assemblages across broad-spatial extents, the results are not as consistent (Cotgreave & Stockley 1994; Blackburn & Gaston 1996; Blackburn *et al.* 1999; Blackburn & Hawkins 2004; Rodriguez *et al.* 2006; Rodríguez *et al.* 2008; Morales-Castilla *et al.* 2012). Recent studies have suggested that Bergmann's rule, at the level of regional species assemblages, is restricted to northern temperate assemblages (Blackburn & Hawkins 2004; Rodriguez *et al.* 2006; Rodríguez *et al.* 2008). Here, I focus on regional species assemblages, not local communities of individuals.

In more recent times, other hypotheses (or mechanisms) have also been proposed to explain the geographical variation in the distribution of body sizes. The resource availability hypothesis (referred to as variation in resources hypothesis in the remainder text) proposes that large-bodied species are favored in areas with seasonal changes in resources or in areas of low productivity (Dunbrack & Ramsay 1993; Rodríguez *et al.* 2008). This hypothesis relies on the fact that large-bodied species have lower mass-specific metabolic rates and have higher fat reserves compared to smaller ones. Consequently, larger animals can survive starvation longer compared to smaller animals, migrate over long distances to track seasonal fluctuations in resources, and require fewer resources for a given mass (Calder 1984). In addition, because small-bodied species have higher rates of mass-specific metabolism, small species require more resources per mass per unit time compared to large-bodied species. The variation in resources hypothesis predicts that the number of small-bodied species occurring in an assemblage should decrease as resources become more seasonal.

While temperature has been the leading contender towards explaining the geographical variation of body sizes, I propose that geographic variation in the distribution of body sizes is also dependent on water availability. Small-bodied species experience higher rates of water loss per unit mass compared to larger species (Calder, 1984). Therefore, physiological adaptations to dehydration may be more important than temperature in governing the abundance and distribution of animals (Louw 1993). If small-bodied species experience greater demand for water compared to large-bodied species, then small-bodied species should also respond to precipitation. I will refer to this idea as the evaporative water loss hypothesis. While water availability has been proposed to influence the geographical variation in amphibian body sizes (Olalla-Tárraga *et al.* 2009), to the best of my knowledge, no study has attempted to show a statistical relationship between the distribution of mammalian body sizes and water availability.

Why is it important to identify environmental variables that relate strongly to the geographical variation of body sizes? First, many life-history traits such as metabolism, population density, range size, and more relate strongly to body size (Peters 1983; Schmidt-Nielsen 1984; Brown *et al.* 2004). In addition, body size is also thought to constrain community assembly among various taxa (Diamond 1975). Identifying the environmental variables that describe the first order variation of body size distribution is an important step in making ecology a predictive science. Second, hypotheses that predict patterns of body size can be tested by observing those patterns.

The Bergmann, variation in resource, and the evaporative water loss hypotheses all predict that body size distributions change shape in a quite simple way: increased frequency of larger species, and decreased frequency of smaller species. Many studies have tested these hypotheses by looking at variations in means or medians (Blackburn & Hawkins

2004; Rodriguez *et al.* 2006; Rodríguez *et al.* 2008; Morales-Castilla *et al.* 2012). Few studies have examined whether the entire distribution simply shifts toward larger species. Is it true that the number of the smallest species in regional assemblages increases most strongly with temperature and water, and that each larger size class responds progressively less strongly (Figure 5.1b)?

Methods

I generated a grid with equal area cells, 200 x 200 km^2, covering the Americas. This cell size was used instead of a smaller size to minimize the potential effects of insufficient sampling in some South American regions. I superimposed the geographic ranges of the 1759 mammal species indigenous to the Americas (Patterson *et al*. 2007). I excluded all off-shore islands and any coastal grid cells <50% filled with land. This resulted in 1196 grid cells and a total of 1754 mammalian species. Because Bergmann's rule applies to homeotherms, I included all mammal species in the analysis including volant species.

Species' body masses (g) were obtained primarily from (Nowak 1999b, a). I supplemented this source with (Smith *et al.* 2003). When both male and female masses were given, the mean of the two was used. I organized the data into a matrix of species presence/absence (1/0) for each grid cell. I then replaced each presence with the average mass of the species resulting in a sample size of 112,300 body size x grid cell combinations.

It is undoubtedly true that there is intraspecific variation in body mass along latitudinal gradients (Ashton *et al.* 2000; Ashton 2002; Freckleton *et al.* 2003; Hayes 2003; Meiri & Dayan 2003; Lucherini *et al.* 2006) . However, interspecific variation of body mass is several orders of magnitude greater than intraspecific variation. I assume that, in the present context, the error introduced by geographic intra-specific variation in body size is negligibly small.

To characterize body size frequency distributions, I used two types of body size indices described below. First, because there are fewer large-bodied species than small-bodied species, I defined body size categories by taking all mammal species that occur in the Americas, ordering their body sizes, and dividing these into 10 categories with equal numbers of species (but unequal ranges of body sizes, (see Table 5.1) for details and see Table D.1 for an example). Second, I also defined ten categories of equal width on a logarithmic scale of body mass, but with different total numbers of species per category. This was accomplished using $\log_{3.6}$-transformed body sizes (see Table D.2 for statistical summary). The $\log_{3.6}$ was chosen because it created 10 size categories. These two procedures each resulted in a sample size of 11,960 size category × grid cell combinations. I then tallied the number of species in each given size category, in each grid cell. The two techniques of binning yielded qualitatively similar empirical results in subsequent analyses. Below, I present and discuss the results only from the first binning procedure. Results from the second binning procedure can be found in appendices.

To test the competing hypotheses, I chose independent variables that reflect each of the different hypotheses. Mean annual temperature (K), minimum monthly temperature (K), and mean annual precipitation (mm) were taken from WOLRDCLIM (Hijmans *et al.* 2005) at 30 arc-seconds (~1 km) resolution. These data are climate normals based on data from 1960-1990. I used maximum net primary productivity minus minimum primary productivity to estimate resource seasonally (Rodríguez *et al.* 2008). Net primary productivity (kg C m^{-2} $year^{-1}$) data were obtained from Moderate Resolution Imaging

Spectroradiometer, MODIS (http://daac.ornl.gov/MODIS/MODIS-menu/products.html, ~ 1 km, (MODIS 2000)). I standardized all environmental variables by subtracting the mean from the observed value, divided by the standard deviation.

The dependent variable was the number of species in a given body size category in a given grid cell. Bivariate scatter plots indicated the numbers of species varied as approximately linear, homoscedastic functions of the environmental variables, with slopes and intercepts that differed among the ten size categories. I therefore fitted a model of the following form:

$$SR_{ij} = c_0 + c_{00}\theta_j + c_{10}T_j + c_{11}T_j\theta_i + c_{20}P_i + c_{21}P_i\theta_j + c_{30}S + C_{31}S_i\theta_j \qquad \text{eq. 1a}$$

and 1b

where SR_{ij} is the number of species of a given size category *j* in a given grid cell *i*, The c_0, c_1, etc. are fitted regression coefficients; *T, P,* and *S* represent mean annual temperature (K), mean annual precipitation (mm) and resource seasonality (maximum NPP minus minimum NPP), and θ represents the different body size categories. I carried out this analysis first treating θ as a continuous variable (eq. 1a), which assumes (based on the hypotheses mentioned above) that the slopes of environmental variables vary linearly across body-size categories.

To allow the slope-coefficients to vary non-linearly among body-size categories, I used a multiple regression that included polynomial terms:

$$SR_{ij} = c_0 + c_{00}\theta_j + c_{10}T_j + c_{11}T_j\theta_i + c_{12}T_j\theta_i^2 + c_{20}P_i + c_{21}P_i\theta_j + c_{22}P_i\theta_j^2 + c_{30}S + C_{31}S_i\theta_j + C_{32}S_i\theta_j^2 + C_{33}S_i\theta_j^3 \qquad \text{eq. 2}$$

The variables used in equation 2 are similar to those used in equation 1a, except for the polynomial functions and similar to equation 1a, body size was treated as a continuous variable. Finally, to allow more complex, non-monotonic variation of the slope coefficients, I repeated the analysis described in equation 1a, but treating θ as a categorical variable (equation 1b); this is an ANCOVA. I then compared the performance of these three models using the Akaike information criterion (AIC) as well as the amount of the variation explained (Burnham and Anderson 2002).

I did not use the proportion of species in a given size category ($SR_{ij}/\ total\ SR_i$) since proportions have undesirable statistical properties and since size categories were constructed to have equal numbers of species in the continental species pool. The heat conservation hypothesis predicts, for example, that small-bodied species should have a stronger response (larger slope-coefficient) to temperature compared to those of large-bodied species. Statistical analyses were conducted using Splus ver. 8 (Insightful, Inc., Seattle, Wash.). All geographic system analyses were conducted using Arc/Info version 8.3 (ESRI 2003).

Results

Mean body size is a very poor descriptor of the spatial variation in body size distributions. Mean body size of an assemblage captures only 2% of the spatial variation in the distribution of $\log_2$ body size 0ccurrences (Figure 5.2a, Table 5.2). Species of most body sizes occur across the entire temperature and latitude range (Figure 5.2b, c). The distribution of body sizes of species that occur in a given region is nowhere near Gaussian, nor even unimodal. Thus, the mean body size of an assemblage is a poor descriptor of the geographical variation of body sizes. Given this fact, there seems little point in seeking mechanistic hypotheses about the mean body size of regional species pools.

Latitude and minimum monthly temperature explain very little of the geographic variation in species' body size. Latitude (absolute) and minimum monthly temperature explain only approximately 2% of the variation (Table 5.2). However, as other studies have noted (Blackburn & Hawkins 2004; Rodriguez *et al.* 2006; Rodríguez *et al.* 2008; Morales-Castilla *et al.* 2012) latitude and temperature do explain~65% of the geographic variation in mean body size of species in regional assemblages, with cooler areas tending to have slightly larger species. When the analysis is done without the bats (e.g., (Blackburn & Hawkins 2004; Rodriguez *et al.* 2006; Rodríguez *et al.* 2008; Morales-Castilla *et al.* 2012), this relationship nearly disappears: temperature explained only 8% of the variance of mean body size with slightly *smaller* species in cool areas. The fact that the sign and strength of the mean body size - temperature relationship depend so strongly on which taxa are included argues against any general explanation of geographic variation in mean body size.

Even though mammal species of all sizes occur across all latitudes, the proportion of species within particular size categories does vary considerably across space (Figure 5.3). The proportion of small-bodied species is generally greater at low latitudes, and the proportion of large-bodied species greater at higher latitudes (Figure 5.3). This much is the pattern predicted by Bergmann's rule (Figure 5.1a). However, the proportion of the smallest species is highest in temperate regions. This, and other patterns described below, is inconsistent with Bergmann and the other hypotheses.

Species richness in different size categories relates to climate very differently, and it does so in a much more complex way than simple hypotheses such as Bergmann's rule predict (Figure 5.4a-c; see also Figure D.2 for analyses based on $\log_{3.6}$ categories). Rather than the progressively shallower (less strongly positive) richness-temperature relationships from the small to the largest size categories predicted by extant hypotheses, I observe multi-modal, or at least U-shaped variation for mean annual temperature and mean annual precipitation (Figure 5.4b, Figure D.3) and third-degree polynomial variation for resource seasonality (Figure 5.4c). When I compared the various fitted models (equations 1a, 2 and 1b), the most complex model (eq. 1), the ANCOVA in which slope coefficients varied non-monotonically (Figure 5.4) was by far the best of the three (Table 5.4). In other words, the simple predictions of Bergmann's rule and related hypotheses were once again not empirically supported.

Discussion

Virtually all hypotheses about geographic variation in body size assume that body sizes vary with climate (or latitude) in a very simple manner: more large species and fewer smaller one in cold places. If this were the case, then mean body size should capture this variation well. The goal of the present study was to test: 1) is this simple pattern actually true? 2) If not, how does the number of species in different body size categories actually relate to climate? To address these objectives, I wanted to develop a more complete method to test the geographical variation in the distribution of mammalian body sizes as a function of climatic variables. By looking at the complete body-size distributions of regional mammal species assemblages, I found that the mean of the distributions is a poor descriptor of the geographical variation of body sizes. Mean body size is reasonably strongly related to mean annual temperature, mean annual precipitation, and resource seasonality in the manner predicted by Bergmann's rule and related hypotheses (Table 5.3). However, when bats are omitted, the pattern reverses. Moreover, looking at the complete distribution, the slope-coefficients are not in accordance with the simple predicted pattern. I conclude that the results are inconsistent with all of the hypotheses. Yet, the numbers of species in all size categories do relate to mean annual temperature, resource seasonality, and mean annual precipitation. Clearly, climate does somehow affect body size distributions.

Exactly why the results did not match the predictions from each hypothesis is unknown, but there might be several explanations. First, the variation in resources and the evaporative water loss hypotheses rely on the relationship body size has with metabolism. Is it possible that mammals, of all sizes, have evolved physiologically in relation to their contemporary climates such that mammals of all sizes can occur in essentially all types of climates? I will discuss this below.

The heat conservation hypothesis, the variation in resources hypothesis, and the water availability hypothesis attempt to explain mechanistically the distribution of mammalian body sizes by using the allometric relationship body size has with either surface area or metabolic processes. Because my results found no evidence in support of the heat conservation hypothesis and because this hypothesis relies on surface area to volume ratios, not metabolism, I limit the remainder discussion to the variation in resources hypothesis and the water availability hypothesis. These two hypotheses argue that the predicted patterns of body size distributions depend on size-dependent metabolic rates in relation with resource availability (food or water).

Why the variation in resources and the evaporative water loss hypotheses fail to explain the geographic distribution of mammalian body sizes may depend on the assumption that mammals' daily metabolic requirements is a simple allometric relationship with body size (Peters 1983; Calder 1984; Dunbrack & Ramsay 1993; Brown *et al.* 2004). Resting metabolic rate or basal metabolic rate (BMR) is often used to predict an organism's daily resource requirements (Peters 1983; Calder 1984; Dunbrack & Ramsay 1993; Brown *et al.* 2004) which has been used to develop mechanistic hypotheses about the geographical variation of body sizes (Rodríguez *et al.* 2008). However, resting metabolic rate is the minimal energy expenditure of an organism that fails to include daily activities an organism experiences. A more accurate estimate of an organism's daily resource requirements can be estimated by using field metabolic rate (FMR, KJ/day). Field metabolic rate is the total energetic cost a wild animal incurs during the course of a day. FMR includes the costs of basal metabolism, thermoregulation, locomotion, feeding, predator avoidance, digestion, posture, etc. (Nagy 1987). Therefore, FMR may predict more accurately the daily-required resource requirements of species living in the wild, particularly since BMR is not directly related to FMR (Nagy 2005). In addition, it has been shown that an organism's FMR will depend on the type of environment it occupies such that animals in xeric environments have a much lower FMR compared to animals in mesic environments (Nagy *et al.* 1999).

To examine further, why the predictions of the variation in resources hypothesis and the evaporative water loss were rejected, I estimated the dry matter intake (DMI, g/day of mammals in both xeric and mesic environments using the FMR equations of (Nagy *et al.* 1999). DMI represents the amount of food energy (g) that an organism requires to balance its daily metabolic flux, which is determined by dividing FMR by the metabolizable energy content of species' diet in units of metabolizable kJ/g dry matter (Nagy *et al.* 1999). The following FMR equations were used to calculate DMI: xeric herbivores (non-ruminants) $3.18M^{0.785}/10$ KJ/g of D.M.; mesic herbivores (non-ruminants) $8.18M^{0.639}/10$KJ/g of D.M.; xeric herbivores (ruminants) $3.18M^{0.785}/11.5$ KJ/g of D.M, mesic herbivores (ruminants) $8.18M^{0.639}/11.5$ KJ/day of D.M. Mass (in grams) is represented by M, and D.M. represents the gross energy content of animal's forage.

Dry matter intake (DMI, g/day) of wild herbivorous mammals in xeric and mesic environments varies as a function of body size and as a function of water availability (Figure 5.5a). As a first approximation, small-bodied herbivores (both ruminants and non-ruminants) in xeric environments (low productivity) require less metabolizable energy than herbivores in mesic environments. This pattern results from xeric species having a lower FMR compared to mesic species (Nagy *et al.* 1999). In contrast, DMI for xeric herbivores is higher compared to that of mesic herbivores for the larger size categories. Moreover, for a given DMI, the data suggest that small-bodied desert species should survive longer compared to mesic species (Figure 5.5b). This relationship changes as body size increases such that for a given DMI, large-bodied mesic species survive longer compared to those in desert regions. This relationship not only predicts that the largest herbivores should occur in mesic environments, but it may also explain why some of the largest herbivores are common in mesic environments and are rare in xeric environments.

While the discussion above addresses physiological adaptations with respect to different climates, I ask whether there are other processes involved that could explain why body size distributions relate consistently to climate, but inconsistently with the hypotheses. I propose the following; most mammalian physiological processes depend upon temperature (Berry & Bjorkman 1980; Gillooly *et al.* 2001; Brown *et al.* 2004) and available moisture (Nagy 1987; Lovegrove 2003; Tieleman *et al.* 2003; Reichstein *et al.* 2007). Kleidon & Mooney (2000) showed that different sets of physiological configurations (for trees) were constrained by temperature and precipitation. They found that the number of viable physiological combinations increased in warm, wet climates and decreased in cold or dry ones. The physiological processes used in their model also depend upon body size (Peters 1983; Calder 1984; Schmidt-Nielsen 1984; West *et al.* 1999; Sibly

& Brown 2007; Hendriks & Mulder 2008). If body size differences reflect different physiological combinations then it therefore follows that the number of species of a given body mass might also depend on climatic conditions. This leads to the prediction that the number of species among the different size categories and within the size categories should increase in warm wet regions. Subsequently, following Kleidon and Mooney, more species of different body size should increase in relation to temperature and precipitation. The predicted pattern appears to be consistent with the observed one (Figure 5.6b-d). In addition, assemblages that lack species in a given size category (fewer physiological combinations) should occur in cold, dry regions, which is shown in Figure 5.6b-d. Interestingly, temperature has a much stronger relationship with respect to the number of species within and among the various categories (Figure 5.6b). This pattern suggests that temperature could be an important factor, more so than precipitation and resource seasonality, in determining the number of different physiological combinations (e.g. different body sizes) that can occur in region. I will attempt to examine this further in future work.

Conclusion

Traditional techniques of using mean body size for assemblages captures very little of the overall geographical variation of body sizes. In addition, such techniques can create spurious relationships between the observed patterns and the potential mechanism(s). My statistical technique attempted to provide a more accurate description of the geographical variation of mammalian body sizes. Consequently, my results fail to provide support for each of the different mechanisms. However, as a first approximation, the pattern predicted by Bergmann, more large-bodied and fewer small-bodied species at higher latitudes was supported. It is clear however, that different body sizes do respond to the different climate variables, but not in the predicted pattern. The processes that generate the geographical variation of body sizes do include, but are not limited to temperature, precipitation, and variation in resources. Moreover, I attempted to demonstrate that mammals have evolved physiologies with respect to environmental conditions (Figure 5.5a, b). Mammals of all sizes are found nearly everywhere across the planet, but the number of species for a given size does vary geographically and varies in response to temperature and precipitation (Figure 5.6b-d). In other words, the distribution of mammalian body sizes may simply reflect the number of different physiological combinations (different body sizes) that can persist under climatic constraints (Kleidon & Mooney 2000).

Tables

Table 5.1. Statistical summary of the body masses (kg) for the 10 body size categories. Each size category has approximately 169 species. Standard deviation is represented by STDV. Occurrences represent the total occurrences observed for each size category. Species represents the number of species in each size category.

Size category	Average	Median	STDV	Minimum	Maximum	Occurrences	Species
1	0.006	0.006	0.002	0.002	0.01	16017	171
2	0.014	0.014	0.002	0.01	0.018	15657	171
3	0.022	0.022	0.003	0.019	0.027	11513	168
4	0.034	0.035	0.004	0.028	0.041	9619	166
5	0.054	0.055	0.008	0.041	0.067	6873	166
6	0.083	0.078	0.013	0.068	0.117	5562	168
7	0.191	0.191	0.046	0.118	0.283	6034	168
8	0.403	0.4	0.091	0.285	0.6	5206	172
9	1.243	1.139	0.533	0.615	2.682	10931	170
10	30.784	7	72.844	2.7	579.25	25723	174

Table 5.2. Top panel: regressions predicting the $\log_2$ (mass) of individual species occurring in 4 x10^4 km^2 quadrats covering the Americas, as functions of absolute latitude, minimum monthly temperature (min. mont temp.), and the average body mass of an assemblage (N = 112,300). Bottom panel: similar regressions predicting average $\log_2$ (body mass) of all species occurring in a grid cell (N=1196). All relationships are significant ($p < 10^{-5}$).

Dependent variable	Independent variable	intercept or slope	std error	r^2	N
Mass ($\log_2$)					
	intercept	-3.40	0.019	0.02	112,300
	latitude (absolute)	0.04	0.001		
				0.02	
	intercept	-2.39	0.013		112,300
	min. mont temp.	-0.38	0.001		
	intercept	-4.75	0.041		112,300
	mean body size (ln)	1.07	0.020	0.02	
Average mass ($\log_2$)					
	intercept	6.43	0.019		1196
	latitude (absolute)	0.04	0.001	0.68	
	intercept	26.70	0.013		1196
	min. mont. temp.	-0.07	0.001	0.65	

Table 5.3. Mean body mass ($\log_2$) in relation to each climate variable separately. All variables are significant at $p < 0.05$.

Independent variable	slope-coefficient	r^2
Mean annual temperature	-0.066	0.65
Minimum monthly temperature	-0.043	0.61
Resource seasonality	-0.024	0.49
Mean annual precipitation	-0.17	0.34

Table 5.4. Models accounting for the variation in the number of species (species richness) in body size categories, as a function of climate and its interaction with body size. For models 1a, body size was treated as continuous variable, and the slope of the richness-climate relationship was assumed to change linearly among body size categories. Model 2 was similar, but the slope of the richness-climate relationship could change non-linearly among body size categories. Model 1a, or a monotonic non-linear relationship is the simple relationship predicted by Bergmann's rule and related hypotheses. In model 1b, body size was treated as a categorical variable, and the richness-climate slope could change in any manner among body size categories. Adjusted r^2 and adjusted AIC are presented. These results are inconsistent with a simple increase in body size toward colder climates. A more detailed description of the results is presented in the appendix (Equation D1, Equation D2, Equation D3).

Model	Form	r^2	AIC
Eq. 1b	Complex	0.76	1530
Eq. 2	Polynomial	0.71	5896
Eq. 1a	Linear	0.44	11758

Figures

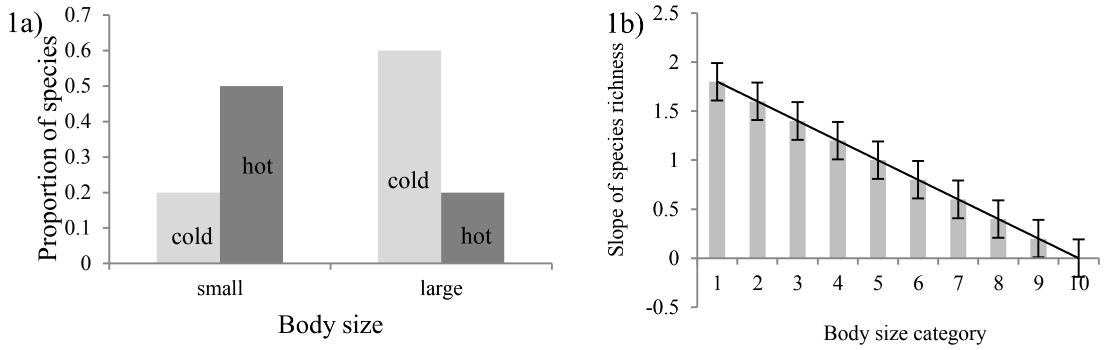


Figure 5.1. 1a) An example of the variation in the proportions of small- and large-bodied species in hot, versus cold geographic regions, as predicted from Bergmann's rule, the heat-conservation hypothesis, the variation in resource hypothesis, and the evaporative water loss hypothesis. 1b) As a corollary, the number of species a body size category is predicted to increase with temperature (water, seasonality) most strongly in the smallest body size category (number 1), and progressively less strongly in larger categories (2-10). Note that all hypotheses predict a monotonically negative relationship for panel 1b. However, the predicted relationships are not necessarily linear, nor is there a specific predicted intercept or slope.

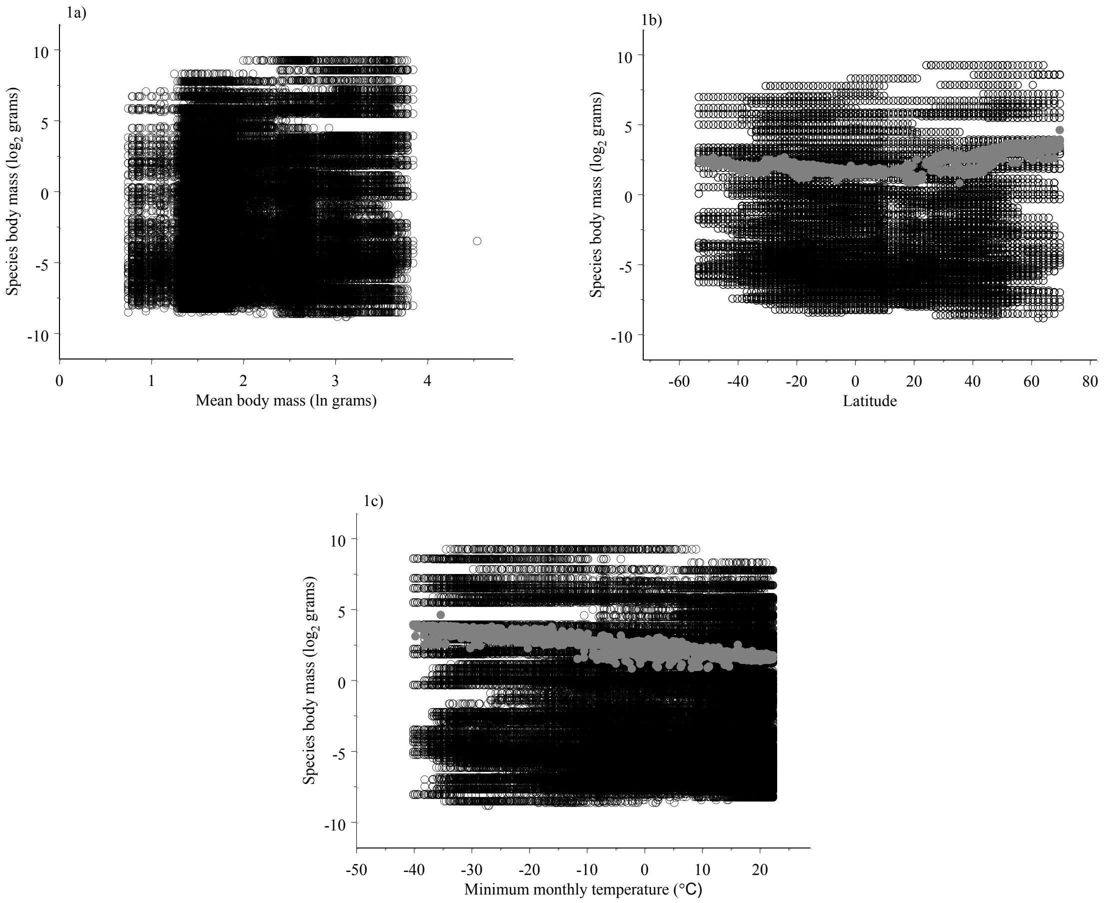


Figure 5.2. Log_2 occurrences of species as a function of a) mean body size of an assemblage (N = 112,300); b) latitude; c) minimum monthly temperature. Each point represents a species occurrence at a temperature or latitude at which it occurs. Species of essentially all sizes occur at all temperatures and latitudes even though the mean body mass of an assemblage does vary somewhat. Gray data points represent the average mass for each grid cell.

3

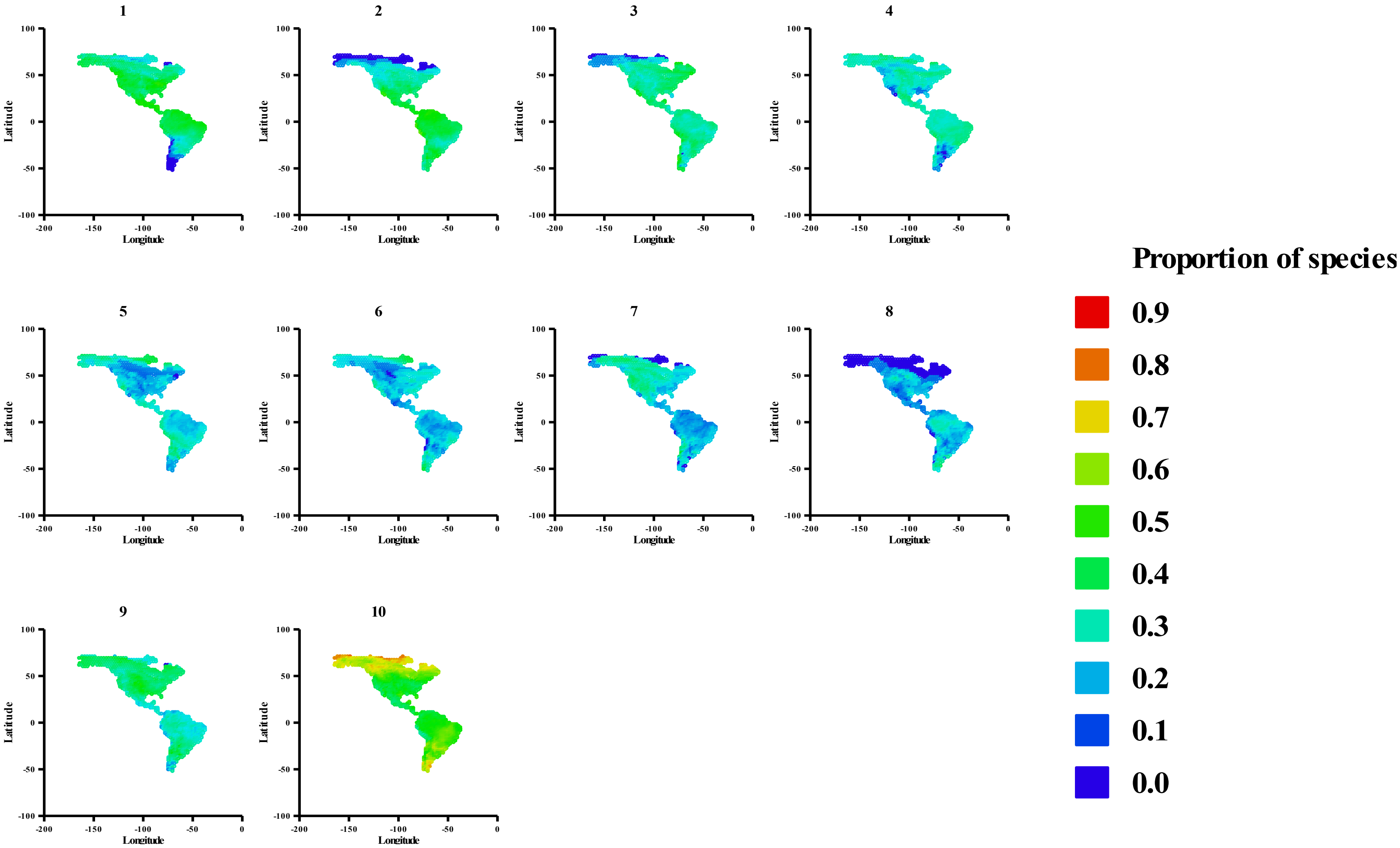


Figure 5.3. Proportion (arc-sin square root) of species observed among the 10 size categories. See Table 5.1 for body size ranges within each size category.

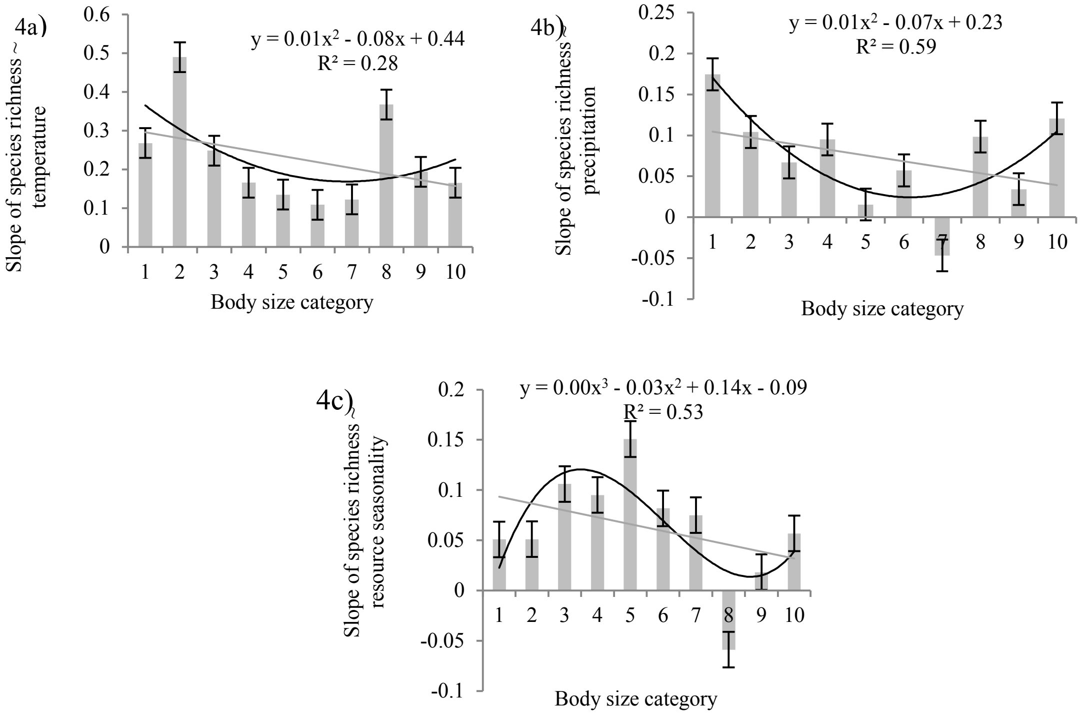


Figure 5.4. Slope of species richness (+/- SE) for the various size categories as a function of a) mean annual temperature; b) mean annual precipitation; c) resource seasonality. Slope coefficients were generated from equation 1. Linear and polynomial fits were added to depict the general shape of the coefficients. Linear regression line shown in gray.

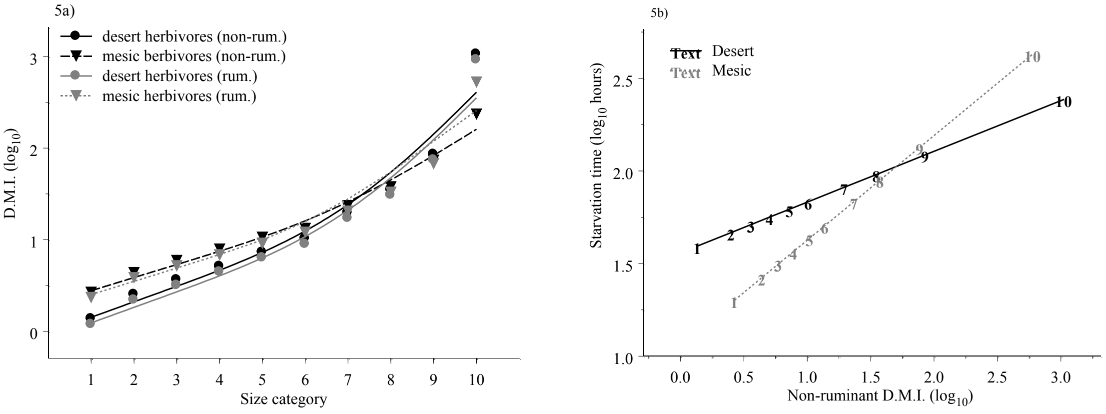


Figure 5.5. a) Dry mater intake ($\log_{10}$ D.M. I., g of D.M. /day) for non-ruminant and ruminant herbivores in relation to the body size categories in xeric and mesic environments. Dry matter intake was estimated by dividing field metabolic rate (KJ/day) by metabolizable energy (KJ/g) following Nagy *et al,* .1999 using the average body size for each size category. The following equations were used: xeric herbivores (non-ruminants) $3.18M^{0.785}/10$ KJ/g of D.M.; mesic herbivores (non-ruminants) $8.18M^{0.639}/10$KJ/day of D.M.; xeric herbivores (ruminants) $3.18M^{0.785}/11.5$ KJ/g of D.M, mesic herbivores (ruminants) $8.18M^{0.639}/11.5$ KJ/day of D.M. where M equals mass (g); b) Starvation time ($\log_{10}$ hours) in relation to the dry matter intake ($\log_{10}$ D.M g/day). Starvation time was estimated using the following equation: xeric species: $(0.5 * 7\text{KJ/g} * M) / 3.18M^{0.785} = 1.10M^{0.215}$ days; mesic species $(0.5 * 7\text{KJ/g} * M) / 8.18M^{0.639} = 0.428M^{0.361}$ days, where M equals mass (g), 0.5 represents a 50% reduction of tissue mass, 7KJ/g represents energy content of tissue (Peters, 1983).

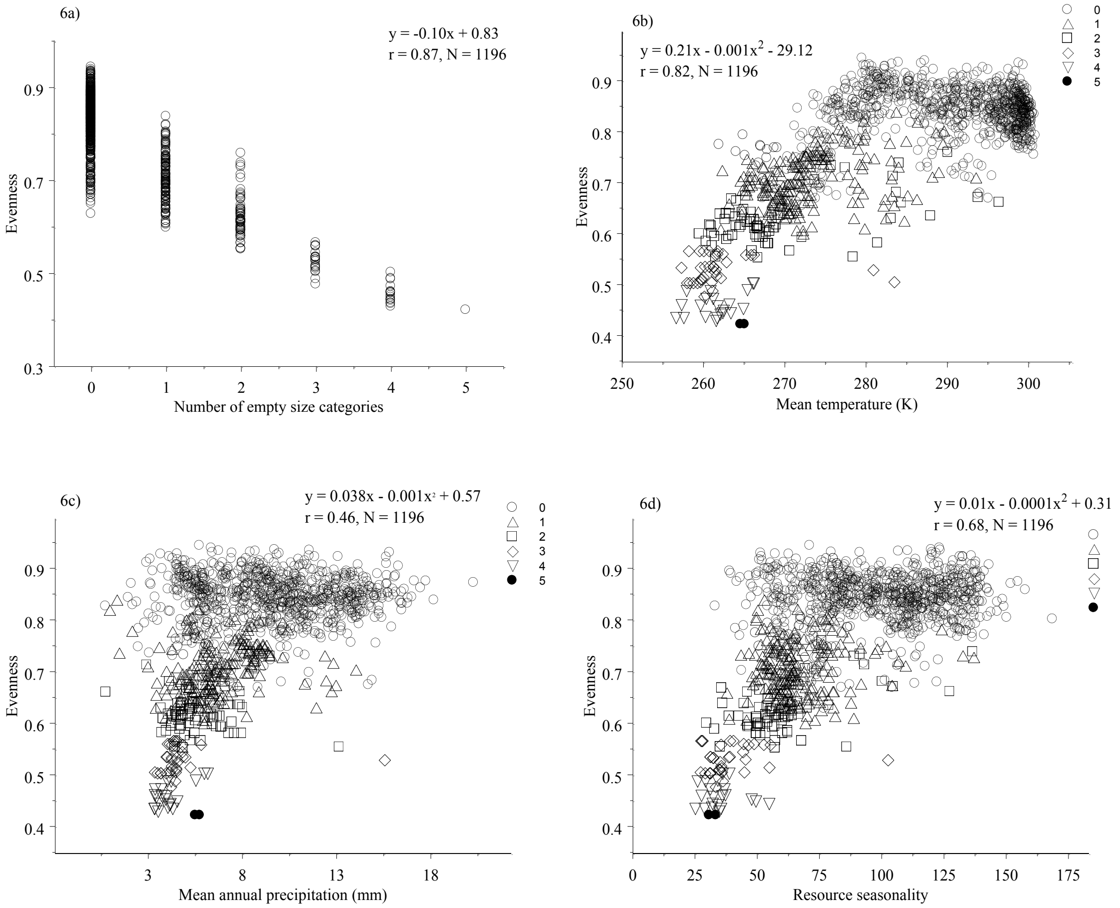


Figure 5.6. Evenness of the number of species observed among the ten size categories in relation to: a) number of empty size categories, evenness decreases as the number of empty size categories increase; b) mean annual temperature; c) mean annual precipitation; d) resource seasonality. The different symbols represent the number of empty size categories. Evenness was calculated for each grid cell using the following equation: $G = e^H / S$ where e is the natural log base, H is the Shannon index for an individual grid cell, and S is the number of size categories (10 in this case).

6. Chapter 6: Resource requirements and metabolic efficiency: size convergence of island giants and dwarfs

Abstract

Ecologists have speculated on the peculiarities of body size evolution of insular species in their clades; giant endemic birds (e.g. elephant birds) and dwarf mammals (e.g. elephants), now mostly extinct, evolved extreme sizes on isolated oceanic islands. "Islands" of habitat also occur on mountaintops in the southwestern Unites States, where species' ranges often extend much beyond these "pseudo-islands". The body masses of the largest mammalian herbivores in these assemblages are predictable from "pseudo-island" area, which is also true for the maximal body size of mammals on land-bridge islands across the Japanese archipelago, Mediterranean islands, and the Sea of Cortez. Based on resource requirements of a constrained area and metabolic efficiency of individuals, body mass evolution of species on oceanic, continental, and land-bridge islands yields strikingly convergent results. This chapter shows that body masses of extinct island bird giants and mammalian dwarfs are quite similar to extant, unremarkable mammals in mountaintop and land-bridge islands of equal area.

Introduction

With respect to their continental sister clades, unique species of giant endemic birds (e.g. dodos, (Cheke & Hume 2008)) and dwarf mammals (dwarf elephants (Ferretti 2008)), once occurred on isolated oceanic islands as the largest herbivores in their respective species assemblages. Maximum body size of animals (bird or mammal) in isolated and pseudo-isolated islands is predictable from habitat area (Burness *et al.* 2001; Millien & Gonzalez 2011). The body size of the largest mammal species in mountaintop "pseudo-islands" also relates strongly with continental "pseudo-island" area (Marquet & Taper 1998). However, despite these relationships, Meiri *et al*. (2011) found that the largest birds, when compared between continents and islands, were observed more often on islands than on continents, independent of area. Contrarily, the largest species of mammals showed no obvious trend of being insular or continental (Meiri *et al.* 2011). In addition, Raia and Meiri (2011) also found that body size evolution on islands is clade specific and independent of island area. These results suggest that the maximum size of insular species should relate to different factors than those of the largest continental species. Nevertheless, the question remains as to why some insular species evolved such unique sizes, compared to their continental relatives and whether they are in fact evolutionary oddities. It is often observed that small-bodied insular species evolve towards larger sizes while large-bodied species evolve towards small ones (Foster 1964; Van Valen 1973; Case 1978; Lomolino 2005; Meiri *et al.* 2011; Lomolino *et al.* 2012). Thus, insular species will have body sizes quite different to those of their continental relatives. This evolutionary change of body sizes is known as "the island role". The objective of this analysis is not to explain "the island rule", but to determine whether the largest insular herbivorous species, either bird giants or mammal dwarfs have similar sizes compared to the largest species of continental and land-bridge faunas in comparable areas.

To address why island giants and island dwarfs evolved such extreme sizes, one must consider that body size relates allometrically to required resources for growth, maintenance, and reproduction, as such larger species and individuals require more resources (Peters 1983; Schmidt-Nielsen 1984). This is particularly true for both birds and mammals, which have similar relationships between body size and metabolic rate (Peters 1983; Schmidt-Nielsen 1984; Brown *et al.* 2004). In the same manner that the total available resources will be limited by habitat area (Rosenzweig 1995), smaller areas have fewer resources and can only support species of a given maximal size. Once an individual colonizes an isolated island, selection will favour body sizes adapted to the availability of resources given island area. If a large-bodied species colonizes an island with an area much smaller than its original continental habitat, selection will favour the evolution of reduced body sizes or insular dwarfism.

On the other hand, island gigantism can result from two, non-mutually exclusive processes--selection to utilize more resources and selection to escape the necessity of high-quality resources. First, known as the Jarman-Bell principle, digestive and metabolic efficiencies in herbivores increase with body size, allowing larger species to utilize a greater range of plant resources (Bell 1971; Jarman 1971; Geist 1974). This principle is based on the notion that retention time of food particles within the digestive system scales allometrically with body mass at a slope of -0.25 (Bell 1971; Jarman 1971; Geist 1974; Demment & Soest 1985) and also dictates that as retention time increases, the efficiency with which plant material is broken down also increases. As a result, compared to smaller species, larger herbivorous species are more efficient in breaking down plant material and having a longer retention time allows larger species to metabolize a greater variety of plant resources, both of low and high quality. Because of their high mass-specific metabolic rate, small-bodied species need higher quality resources requiring shorter retention times relative to their size (Peters 1983; Demment & Soest 1985). If high quality resources are rare on isolated islands, selection should favour the evolution of larger body sizes. Subsequently, small-bodied species should selectively evolve towards larger sizes (e.g. gigantism) either to utilize a greater range of different plant resources or to escape the necessity of relying on high-quality resources, Thus, I hypothesize that maximum body size on islands represents a convergence of resource requirement and metabolic efficiency.

Since mammalian communities of mountaintop and land-bridge island (e.g. "pseudo islands") are composed of species whose geographic ranges often extend far beyond their mountains and their land-bridge islands, it is likely that these species are not truly isolated from other populations. Therefore, it is likely that genetic exchange can occur with populations at lower elevations farther north among mountaintop islands and with continental populations on land-bridge islands and that these species can extend beyond their range in order to obtain the necessary resources for growth and reproduction.

In contrast, on isolated oceanic islands with endemic populations necessarily isolated relative to their mainland congeners, selection should favor body sizes that approach the resource requirement-metabolic efficiency optimum. However, on "pseudo islands" with soft boundaries, selection would be somewhat relaxed for an optimal body size for a given area. Moreover, if genetic mixing occurs in these populations, evolutionary changes in body size would likely occur more slowly than those of insular species (Gingerich 2001; Lenormand 2002; Evans *et al.* 2012). In contrast, oceanic islands having hard boundaries, selection for the optimal body size should be stronger thereby increasing the rate of evolution of insular species (Millien 2006; Millien 2011; Evans *et al.* 2012), but see (Raia & Meiri 2011). The increase in body size evolution would also be likely if species on mountaintops were truly isolated. Selection for an optimal size in a given area would lead to the evolution of unusual body sizes, relative to mainland species in the same clades and would also lead to body size convergent patterns across continental, land-bridge pseudo islands, and isolated insular ones. The resource requirement-metabolic efficiency hypothesis posits that for a given area, oceanic island giants and dwarfs are simply the largest herbivores in their assemblages, with body sizes similar to those of the maximum body sizes on "pseudo islands".

The results from this analysis strongly suggest that body masses of extinct island bird giants and mammalian dwarfs are predictable from extant mammals in mountaintop and land-bridge islands of equal area.

Materials and Methods

To test my hypothesis, I used Marquet and Taper's (1998) and Millien and Gonzalez's (2011) data to develop a single regression model (equation (1)) that compares the body mass of the largest mammals to 'pseudo-island' area (see Figure 6.1A).

$$\log_{10}(\text{body mass (g)}) = 0.53 \log_{10}(\text{area (km}^2)) + 2.31 \qquad (1)$$

I chose this data because of its unique fauna, unique evolutionary and ecological histories, different geologies, and topographic heterogeneities. If such factors are important for influencing the maximum body sizes for a given area, then these differences should be apparent in the analysis. Marquet and Taper's data (extracted using Engauge Digitizer ver. 4.1) relate body size maximum of mammals across 'pseudo islands' of mountaintops of the South West United States. In contrast, Millien and Gonzalez's data, covering all trophic guilds, relate maximum body size of mammals across land bridge islands of the Japanese archipelagos, the Sea of Cortes, and Southwest Asia. Because my interest was in predicting the largest extinct herbivores across ocean islands, I disregarded data not relevant to herbivores.

I used equation (1) to calculate the expected body mass of the extinct bird giants and mammalian dwarfs (see Table 6.1 for species and references). Where body masses could be obtained from the primary literature, I used data of the largest extinct endemic herbivorous bird and mammal faunas on oceanic islands. I transformed body mass (g) using a $\log_{10}$ transformation to normalize their distribution. As mentioned, my hypothesis involves the advantage versus disadvantage between metabolic efficiency and the total amount of resources required for growth, maintenance and reproduction, both of which relate with body size for birds and mammals in similar ways (Jarman 1971; Peters 1983; Schmidt-Nielsen 1984; Demment & Soest 1985; Brown *et al.* 2004). Since the extinct birds in my data are all flightless herbivores, it is likely that the giant bird species in my analysis would have physiologies similar to herbivorous mammals, extant or extinct (Peters 1983). I included the bird giants and mammalian dwarfs to determine whether their sizes relate convergently to island area. Any apparent physiological differences that might exist between birds and mammals will be apparent in the analysis. For example, because birds typically have an elevated metabolic rate compared to mammals of a similar size (Peters 1983; Schmidt-Nielsen 1984), the predicted maximum bird mass should be slightly smaller when using mammalian data. To test for differences between the predicted and observed values for the extinct bird giants and mammal dwarfs, I conducted an ANCOVA where I regressed observed values as a function of predicted values and included a categorical variable distinguishing between mammals and birds. I included the categorical variable to allow the intercepts to differ. I also included the categorical-predicted mass interaction variable to test for slope differences between birds and mammals.

To determine if the intercept between predicted extinct mass (from equation 1) and observed extinct mass in Figure 6.2A, is significantly different from zero, I first centered the data by subtracting the predicted values from the predicted mean. I then subtracted the observed values subtracted from the predicted mean. Using a linear regression model, I tested for significant difference between observed mean and the predicted mean allowing the regression analysis to reduce the residual error attributed to the slope. All analyses were conducted using S-Plus ver. 8.0 (Insightful, Inc., Seattle, Wash.).

For clarity, I define a bird giant as a species larger than its continental sister clade and mammalian dwarfs as species smaller than its continental sister clade. For the purpose of this study, the maximum body size of a species for a given island can be an island giant, a mammalian dwarf, or both.

Because body masses can be phylogenetically conserved among congeneric taxa (Smith *et al*. 2004, Lyons & Smith 2010), it is quite possible that the evolutionary change of body sizes of the extinct bird giants and mammalian dwarfs could simply depend on their body masses being phylogenetically conserved and independent of any process or factors associated with the island habitats. However, for reason discussed below, I did not take phylogeny into account for the analysis. First, the ‘extinct’ dwarfs and ‘giants’ are given the appropriate adjectives as a direct reference to their sister clades. If their body sizes were phylogenetically conserved and independent of any process or factors associated with island habitat, then these extinct species would not be designated as either a ‘dwarf’ or a ‘giant’. Subsequently, they would have retained names synonymous to their continental relatives (e.g. elephant vs. dwarf elephant). For example, the dodo bird (*Raphus* *cucullatus*) belong to the family Raphinae, which contains doves, pigeons, quail etc. It is commonly known that body masses of dodos was substantially larger than its closest relatives. Thus, the evolutionary change in body sizes of the island dwarfs and giants cannot reflect phylogenetically conserved body sizes, and thus it is not necessary to take phylogeny into account for the analysis.

A proper phylogenetic test for this analysis requires reasonable accurate phylogenetic trees, particularly at the species level. The correct phylogenies for most of the extinct birds used in the analysis is still uncertain, and this is particularly true for the ratites (van Tuinen *et al.* 1998; Harshman *et al.* 2008), which include many birds species in the analysis. Moreover, for some species (e.g. the elephant bird, *Aepyornis maximus*) recent phylogenetic analysis could not identify its closest relative (Cooper *et al.* 2001). Attempting to statistically remove any effect of phylogeny depends on reasonable estimates of the correct phylogenetic tree, particularly at the species level for my anlysis. However, the correct phylogenetic tree is still being debated (van Tuinen *et al.* 1998; Cooper *et al.* 2001; Harshman *et al.* 2008) and thus any phylogenetic analysis might give spurious results. Lastly, because I use both extinct bird giants and dwarfs in the analysis, any phylogenetic effect should be apparent in the model residuals. If the evolutionary change of these insular giants and dwarfs was strictly dependent on body size being phylogenetically conserved, convergent patterns should not be observed. As mentioned, the main objective of this analysis is to determine if these extinct insular giants and dwarfs show convergent patterns of body size in relation to extant mammals habituating 'pseudo island'.

Because of the uncertainty in knowing how island size changed with changing climates or sea level changes, I chose contemporary island size rather than historical island size. Depending on the period in which the species inhabited the islands, such a choice will either underestimate or overestimate island area. However, the residual variation of the regression analysis should reveal any measurement error. Island area was obtained from Burnes *et al*. (Burness *et al.* 2001) I transformed land area (km^2) using a $\log_{10}$ transformation to normalize their distribution.

Results and Discussion

The once extinct bird giant and mammalian dwarf have body sizes similar to species on 'pseudo-islands' given area. Despite having variability around the regression line (Figure 6.1A), equation (1), applied to continental mountaintops and land-bridge islands successfully predicts the body mass of extinct endemic bird giants and mammalian dwarfs on oceanic islands (Figure 6.2A; r^2=75%). The slope In Figure 6.2A is not significantly different from 1.0 (95% confidence interval 0.75, 1.49). In addition, the intercept at the data mean is not significantly different from zero (Figure 6.2B, $p = 0.31$). Visually, the dwarfs and giants fall within the variability of the mountaintop and land-bridge data (Figure 6.1B).

If island area limits available resources and if metabolic rate determines the amount of resources required for growth and reproduction and because birds have a slightly higher metabolic rate for a given mass compared to mammals (Peters 1983), then the bird giants should have a slightly smaller mass when predicted from mammal assemblages[6]. I found that predicted bird mass was not only consistently lower than observed mass, but the majority of predicted bird mass was in fact larger than observed mass. I also found that

---

[6] Birds typically have an elevated metabolic rate compared to mammals of a similar size

both the slope and intercept were slightly, but significantly different for the bird giants and mammal dwarfs (p = 0.04 for slope, p = 0.02 for intercept).

Although equation (1) successfully predicted extinct insular giants and dwarfs as a function of habitat area in mountaintop islands of the S.W. U.S.A and a number of different land-bridge islands, it is possible that the positive relationship between land area and maximum body mass results from other variables collinear with land area. That larger land areas contain more species (Rosenzweig 1995), which would increase the probability of having a larger species in an assemblage by chance alone, is such a possibility. Kalmar and Currie (2007) showed and that species richness relates quite strongly to island isolation and that more distant islands have fewer species. If the relationship between maximum body mass and area results from variation of richness, then a strong negative relationship between island isolation and maximum body mass is expected. I found that the relationship between island isolation and maximum body mass of the dwarfs and giants was negative, but not significant (p = 0.22). Thus, the relationship between island area and maximum body mass of insular dwarfs and giants is not simply the result of species richness.

One possibility is that larger islands have larger species simply because larger islands, on average, are more productive and that more productive areas can support larger species. However, Olsen *et al* (2009), after controlling for species richness, found a negative relationship between productivity and median bird mass across the world. Moreover, since the largest land mammals, African elephants, occur in both the fringes of the Namib Desert, one of Africa's least productive areas, and in the Congolese rainforests, one of the most productive, it is unlikely that the positive relationship between island area and maximum body mass of the extinct insular species is the result of productivity.

Interestingly, despite each oceanic island or “pseudo-island’s” having its own unique fauna with different evolutionary and ecological histories, in respect to area, the maximum mass of extinct and extant herbivorous mammals shows remarkable convergent patterns: That the giant elephant bird (*A. maximus*) and the dwarf hippo (*H. lemerlei & H. madagascariensis)* of Madagascar evolved such extreme body sizes compared to other species in their clades, that the bird giant and the dwarf hippo would evolve very similar body masses for a given area. Such convergent patterns are surprising considering other studies have suggested that size evolution on islands is best understood on case by case fashion and by species specific competitive interaction (Raia & Meiri 2006; Palombo 2009; Raia & Meiri 2011).

Based on the resource requirement-metabolic efficiency hypothesis, macroevolution of body masses (Gingerich 2001; Kinnison & Hendry 2001; Evans *et al.* 2012) selects species with body masses near the maximal optimum for a given area and its available resources. By contrast, on isolated islands, with more intense selection pressures, microevolution (Evans *et al.* 2012) acts on whatever species that happens to be present, selecting their mass in the direction of the resource-requirement and metabolic efficiency optimum. From this perspective, the masses of dwarfs and giants species are not unexpected; rather, it is the clade from which particular size-defined niches were filled that is remarkable. In conclusion, I propose that the resource requirement-metabolic efficiency hypothesis might, given further testing, provide a new explanation for the evolution of extreme sizes, including, but not limited to the evolution of island giants and island dwarfs.

Table

Table 6.1. Insular species used in the analysis. I restricted the data to the largest endemic herbivorous bird and mammal faunas on oceanic islands where body masses could be obtained from the primary literature.

Scientific name	Common name	Size (kg)	Island	Island area (km^2)	Reference
Megapodius molistructor	Brush Turkey	3.5	Tongatapu	259	(Burness *et al.* 2001)
Anser sp.	Goose	2	Ibiza	577	(Burness *et al.* 2001)
Raphus cucullatus	Dodo	19	Mauritius	1874	(Burness *et al.* 2001)
Pezophaps solitaria	Rodrigues Solitaire	20	Mauritius	1874	(Cheke & Hume 2008)
Elephas cypriotes	Dwarf elephant	200	Cyprus	9248	(Palombo 2007)
Phanourios minutus	Dwarf hippo	200	Cyprus	9251	(Burness *et al.* 2001)
Moa-nalos	Hawaii goose	7.5	Hawaii	10434	(Burness *et al.* 2001)
Megavitiornis altirostris	Pigeon	15	VitiLevu	10531	(Burness *et al.* 2001)
Leptoptilos robustus	Flightless Stork	16	Flores	14154	(Meijer & Due 2010)
Sylviornis neocaldeoniae	Brush Turkey	40	New Caledonia	16648	(Steadman 1999)
Megaloceros cazioti	Deer	70	Sardinia	24090	(Burness *et al.* 2001)
Megalocnus zile	Giant ground sloth	150	Hispaniola	76192	(Burness *et al.* 2001)
Megalocnus rodens	Giant ground sloth	150	Cuba	110860	(Burness *et al.* 2001)
Dinornis novaezelandiae	Moa	230	New Zealand	270534	(Davies 2003)
Aepyornis maximus	Elephant bird	400	Madagascar	587040	(Burness *et al.* 2001)
Hippopotamus lemerlei	Dwarf hippo	374	Madagascar	587040	(Weston & Lister 2009)
Hippopotamus madagascariensis	Dwarf hippo	393	Madagascar	587041	(Weston & Lister 2009)

Figures

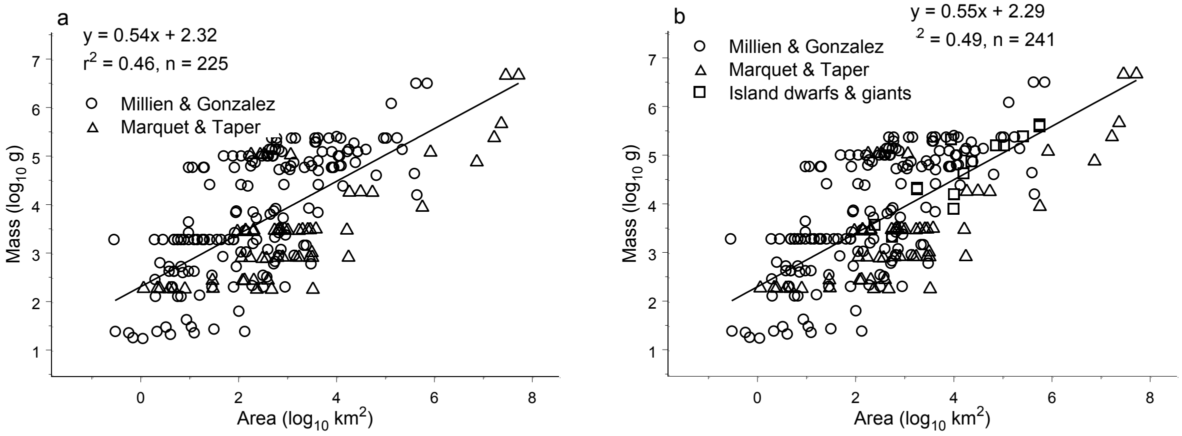


Figure 6.1. Body mass of birds and mammals as a function of land area. (a) Data from southwestern U.S.A mountaintops extracted from Marquet and Taper's (Marquet & Taper 1998). and from land-bridge islands of the Japanese archipelago, western Mediterranean, Sea of Cortes, and Southeast Asia from Millien and Gonzalez (Millien & Gonzalez 2011) (b) Body mass as a function of land area for all groups. Insular giants and dwarfs are squares, mammals of the S.W. U.S.A. are triangles, and mammals of the land-bridge islands are circles. See Table 6.1 for body size references for bird giants and mammal dwarfs. Linear regression line shown in black

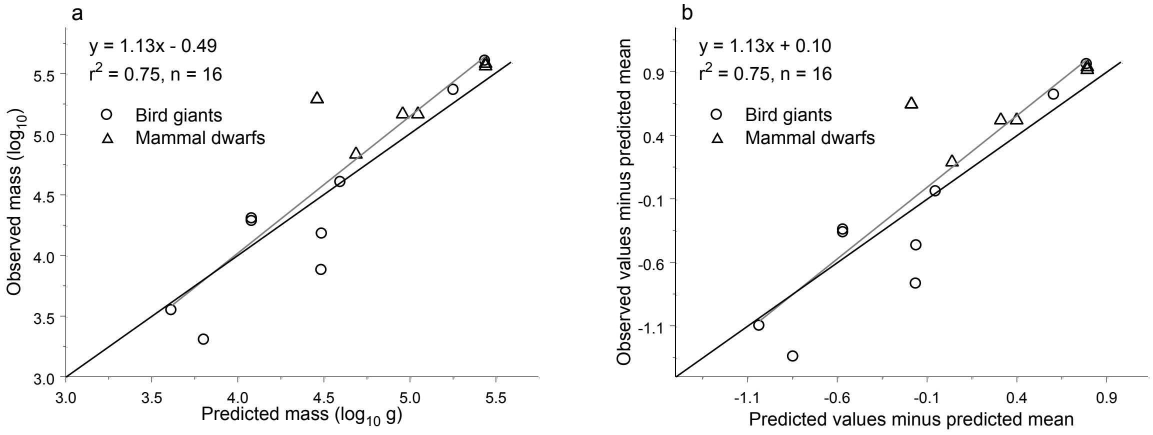


Figure 6.2. a) Observed body mass of insular bird giants (circles) and mammalian dwarfs (triangles) as a function of predicted body mass based on equation (1). 1). b) Observed body mass minus predicted body mass mean as a function of predicted body mass minus predicted body mass mean. This procedure is testing for the difference between the observed mean and the predicted mean, while allowing the regression to reduce the residual error that can be attributed to the slope. As a result, this procedure tests whether the intercept is significantly different from zero. Linear regression line shown in gray, one to one line shown in black. Bird giants are circles, mammal dwarfs are triangles. Note that equation (1) relates maximum body mass of extant mammals with 'pseudo-island' area across mountaintops of the SW U.S.A. and land-bridge islands including the Japanese archipelago, western Mediterranean, Sea of Cortes, and Southeast Asia.

Conclusions

For this thesis, I first set out to determine how assemblage structure varies across space and to determine whether it is related to a set of a few environmental variables in consistent ways across broad spatial scales. Because many assemblages have their own unique history, different geologies, and different independently evolved taxa, this thesis approximates the importance of regional processes (e.g. contemporary climatic variables) or local processes (e.g. species specific competitive interactions) in structuring species assemblages. Fundamentally, I attempted to test in this thesis whether much of assemblage structure across broad-spatial scales and across various taxa, in terms of body mass frequency distribution or species abundance distribution, is explained by a set of a few environmental variables, specifically: temperature and precipitation, in similar ways. Based on the idea of the convergence of assemblage structure, I then set out to develop a new hypothesis that attempts to explain mechanistically biodiversity gradients. I hypothesized that gradients of diversity are driven by gradients in the number of individuals of the rarest species, which in turn are themselves driven, by gradients in temperature and precipitation. By using the number of individuals of the rarest species, I set out to determine the minimum area needed to capture at least two individuals of the rarest and show that this minimum area varies across continental regions as well as with temperature and precipitation. I then determine the cost required to establish such a protected area and determine whether this relates with a country's gross domestic product.

I also set out to identify more accurately the geographical variation of mammalian body sizes, which led to the conclusion that using the mean size of an assemblage is not very useful when attempting to describe accurately the geographical variation of body sizes. I also tested and rejected the specific predictions of various hypotheses (including my own) that have been developed to explain the geographical distribution of body sizes. Lastly, I propose a new hypothesis that attempts to explain the evolution of extinct bird giants and mammalian dwarfs. I show that these unique taxa have body sizes similar to mammals observed on continental and land-bridge islands given area.

In this thesis, I have focused on the effects of climate in structuring species assemblages among different taxonomic groups globally. In doing so, I attempted to test that even though each assemblage has different local processes acting on individual species, each having its own unique biology, the effect of these processes towards structuring assemblages is minor compared to the effect(s) of climate. It is often taught that ecology is about the study of species interacting with one another and that local process (e.g. biotic interactions, predation, parasitism, etc.) are the primary factors towards structuring species assemblages. It appears that very little is taught or discussed about climate and its impact on assemblages. In fact, in Miller and Ricklefs (2000) Ecology textbook, they devote very little about how precipitation, temperature, and climate might influence species assemblages. For example, only two pages address the effect of precipitation (e.g. plant production), zero pages for temperature, and only seven pages about climate (effects on populations and plant distributions. Yet, they spend over one hundred pages (ca. 112) devoted to predators and or predation. I do not argue that local processes are not important. It is clear that these local processes are important, but their importance might be site or species specific. It is known that predators can affect prey abundances and even cause trophic cascades or that competition for common resources might restrict some species to specific areas. However, are these processes the primary ones towards structuring species assemblages? I argue they are not. To conclude, if one desires to predict assemblage structure across broad spatial scales, one must first account for a set of a few environmental variables, specifically:

temperature and precipitation. The results suggest that assemblage structure among different biotic assemblages look strikingly familiar, once climate is accounted for.

Chapter 1 outlines how I tested whether the body mass frequency distribution of trees and mammals relate in similar ways to temperature, precipitation, and habitat heterogeneity across the Americas. In general, my results suggest that assemblage structure is driven more by a set of a few environmental variables or regional processes rather than by resource partitioning, or biotic interactions. Although it is unclear why convergent assembly is observed for both trees and mammals, I provide a possible explanation that will require further testing.

In Chapter 2, which is similar in content to Chapter 1, I tested whether assemblage structure of bird communities relates similarly to a set of a few environmental variables across islands and continents. Similar to the findings of tests described in Chapter 1, I found that body mass frequency distribution of bird assemblages do relate similarly to temperature, precipitation, land area, and isolation globally. However, I did find that the body mass frequency distribution of island assemblages is somewhat different from continents in that island assemblages have a higher average mass, body mass variance, and body mass skew. In addition, island assemblages have slightly different patterns regarding the body size extremes (higher body mass minimum and lower body mass maximum). These patterns seem to suggest characteristics of islands, other than climate (e.g. island isolation) could influence the BMFD of insular assemblages. I explain these slight differences in relation to MacArthur and Wilson's theory of island biogeography (albeit slightly modified) based on the effect body size has on extinction probabilities.

In chapter 3, I introduce a new hypothesis that attempts to explain mechanistically gradients in biodiversity. I sought to find out if gradients of diversity are driven by gradients in the number of individuals of the rarest species, which in turn are driven, by gradients in temperature and precipitation. This hypothesis is based on Preston's canonical log distribution and assumes that species abundance distribution across space relate to temperature and precipitation in congruent ways. My analyses showed that both m and Φ (the proportion of species represented by a single individual in samples of species assemblages) are strongly related to climate. In addition, global variation in species richness was more strongly related to these measures of rarity than to climate. I proposed that variation in the shape of the log-normal species abundance distribution depends on climate and the change in shape of this abundance distribution is ultimately responsible for global gradients of species richness: rare species (reflected in m and Φ) persist better in benign climates. To the best of my knowledge, this is the first attempt to determine with the geographical variation of species richness is causally linked to the geographical variation in the number of individuals of the rarest species.

In Chapter 4, I use Preston model (from Chapter 3) to estimate the minimum sampling area needed to capture two individuals of the rarest species. I found that the minimum area varies across continents and latitude. These results suggest that the minimum area to protect the rarest specie varies geographically and this should be taken into account when establishing protected area to protect species from extinction. Despite this geographical variation, the minimum area does relate quite strongly to the interaction between temperature and precipitation ($r^2 = 0.66$). I also found that cost needed to establish the protected area of the rarest is marginally related to a country's gross domestic product.

In Chapter 5, I test whether using mean body size of regional assemblages is a useful technique (as often assumed in many macroecological studies) in describing the geographical variation of body sizes. Even though using mean body size has been widely used and are relatively easy to calculate among assemblages, they do not accurately represent the geographical variation of body sizes. Chapter 5 also outlines how I tested the specific predictions of various hypotheses (heat conservation hypothesis & resource seasonality hypothesis) that were developed to explain why some regions have larger species. All of the predictions of each hypothesis (including my own, the evaporative water loss hypothesis) were rejected. In summary, the focus on mean body-size, and on latitude or temperature, in most studies of Bergmann's rule and related hypotheses misses most of the geographical variation in mammalian body sizes. Body size is not dependent on a single climatic variable. The results from this chapter are not consistent with any of the hypotheses proposed to explain the geographical variation of species among size categories. It is not clear what process(es) generate(s) these patterns, but it seems unlikely that they will be explained by any single mechanism.

Chapter 6 focuses on whether the extinct herbivorous insular bird giants and mammalian dwarfs had evolved body sizes that are unique compared to the maximum mammalian size of continental and land bridge islands. Or, if they had similar body sizes one would expect based on the relationship maximum body size has with land area across mountaintops islands of the S.W. U.S.A and Mediterranean land bridge islands. I found that these now extinct giants and dwarfs had evolved body sizes one would expect among extant mammals in "pseudo-islands" of equal area. I propose that natural selection acted on these species, moving them in the direction of a resource requirement-metabolic efficiency optimum. Based on this proposition, the size of dwarf and giant species is not surprising.

Overall, I have attempted to test in this thesis whether climate e.g. temperature and precipitation, is the most important determining factor in how species assemblages are structured. The results of this thesis are consistent that climate is an important factor in structuring species assemblages, more so than biotic interactions or differences in regional specific histories. Although much of ecological studies have focused mainly on unique properties of particular biotic assemblages or of particular inter-specific interactions, the results from this thesis suggest that to understand characteristics of species assemblages, one must first account for temperature and precipitation: not the species' name, nor local processes such as biotic interactions. This perspective is somewhat at odds with mainstream ecological thinking. Perhaps, ecologists should consider the importance of climate and climate related variables towards structuring species assemblages and move away from local-scale processes and factors such as biotic interactions.

An important goal in macroecology is to identify broad-spatial scale commonalities or repeated patterns across various taxonomic groups. If the repeated patterns relate to a set of a few environmental variables rather than, for instance, species-specific biotic interactions, then ecologists must first account for these variables when attempting to predict assemblage structure. An important theme throughout this thesis is that characteristics of species assemblages look strikingly similar, once climate is accounted for. In summary, if ecologists desire to know or predict the size distribution of species, species abundance distributions, or the number of different species they must account for a set of a few environmental variables.

Exactly why assemblage structure show congruent patterns as a function of temperature and precipitation is not exactly clear. For each chapter, I attempted to introduce a possible mechanism or process for the observed patterns. A common element for the different mechanisms that I propose, involves some form of extinction risk. I hope that the results from this thesis will stimulate other ecologists (including myself) to test my proposed mechanisms.

The main conclusion of this thesis, that species assemblage structure depends on characteristics of the environment and not on biotic interactions, might give ecologists a new perspective about how species assemblages are structured. Climatic dependence of assemblage structure might possibly be a new general pattern that the field of ecology needs.

References

Abbott K.C. (2011). A dispersal-induced paradox: synchrony and stability in stochastic metapopulations. *Ecology Letters*, **14**, 1158-169.

Adams H.D., Guardiola-Claramonte M., Barron-Gafford G.A., Villegas J.C., Breshears D.D., Zou C.B., Troch P.A. & Huxman T.E. (2009). Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proceedings of the National Academy of Sciences*, **106**, 7063-7066.

Adler G.H. & Levins R. (1994). The Island Syndrome in Rodent Populations. *The Quarterly Review of Biology*, **69**, 473-490.

Algar A.C., Kerr J.T. & Currie D.J. (2007). A test of Metabolic Theory as the mechanism underlying broad-scale species-richness gradients. *Global Ecology and Biogeography*, **16**, 170-178.

Algar A.C., Kerr J.T. & Currie D.J. (2011). Quantifying the importance of regional and local filters for community trait structure in tropical and temperate zones. *Ecology*, **92**, 903-914.

Allen A.P., Brown J.H. & Gillooly J.F. (2002). Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, **297**, 1545-1548.

Allen C.D., Macalady A.K., Chenchouni H., Bachelet D., McDowell N., Vennetier M., Kitzberger T., Rigling A., Breshears D.D., Hogg E.H., Gonzalez P., Fensham R., Zhang Z., Castro J., Demidova N., Lim J.H., Allard G., Running S.W., Semerci A. & Cobb N. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660-684.

Allen C.R., Garmestani A.S., Havlicek T.D., Marquet P.A., Peterson G.D., Restrepo C., Stow C.A. & Weeks B.E. (2006). Patterns in body mass distributions: sifting among alternative hypotheses. *Ecology Letters*, **9**, 630-643.

Antle J.M. & Heidebrink G. (1995). Environment and Development: Theory and International Evidence. *Economic Development and Cultural Change*, **43**, 603-625.

Ashton K.G. (2002). Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Global Ecology and Biogeography*, **11**, 505-523.

Ashton K.G., Tracy M.C. & de Queiroz A. (2000). Is Bergmann's rule valid for mammals? *American Naturalist*, **156**, 390-415.

Bakker V.J. & Kelt D.A. (2000). Scale-dependent patterns in body size distributions of neotropical mammals. *Ecology*, **81**, 3530-3547.

Balmford A., Gaston K.J., Blyth S., James A. & Kapos V. (2003). Global variation in terrestrial conservation costs, conservation benefits, and unmet conservation needs. *Proceedings of the National Academy of Sciences*, **100**, 1046-1050.

Bell R.H.V. (1971). A grazing ecosystem in the Serengeti. *Scientific American*, **225**, 86-93.

Bergmann C. (1847). Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse: Göttinger Studien, v. 1.

Berry J. & Bjorkman O. (1980). Photosynthetic Response and Adaptation to Temperature in Higher Plants. *Annual Review of Plant Physiology*, **31**, 491-543.

Bjornstad O.N., Ims R.A. & Lambin X. (1999). Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology & Evolution*, **14**, 427-432.

Blackburn T.M. & Gaston K.J. (1996). Spatial patterns in the body sizes of bird species in the New World. *Oikos*, **77**, 436-446.

Blackburn T.M., Gaston K.J. & Loder N. (1999). Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and Distributions*, **5**, 165-174.

Blackburn T.M. & Hawkins B.A. (2004). Bergmann's rule and the mammal fauna of northern North America. *Ecography*, **27**, 715-724.

Blount Z.D., Borland C.Z. & Lenski R.E. (2008). Historical contingency and the evolution of a key innovation in an experimental population of Escherichia coli. *Proceedings of the National Academy of Sciences*, **105**, 7899-7906.

Blueweiss L., Fox H., Kudzma V., Nakashima D., Peters R. & Sams S. (1978). Relationships between body size and some life history parameters. *Oecologia*, **37**, 257-272.

Bollen K.A. & Long J.S. (1993). *Testing structural equation models*.Sage Publications, Inc., Newbury Park, CA.

Borregaard M.K. & Rahbek C. (2010). Causality of the relationship between geographic distribution and species abundance. *Quarterly Review of Biology*, **85**, 3-25.

Box E.O. (1981). *Macroclimate and plant forms: an introduction to predictive modeling in phytogeography*. 1st edn.Dr. W. Junk, The Hague, Boston, MA.

Brown J.H., Ernest S.K.M., Parody J.M. & Haskell J.P. (2001). Regulation of diversity: maintenance of species richness in changing environments. *Oecologia*, **126**, 321-332.

Brown J.H., Gillooly J.F., Allen A.P., Savage V.M. & West G.B. (2004). Toward a metabolic theory of ecology. *Ecology*, **85**, 1771-1789.

Brown J.H. & Maurer B.A. (1987). Evolution of Species Assemblages: Effects of Energetic Constraints and Species Dynamics on the Diversification of the North American Avifauna. *American Naturalist*, **130**, 1-17.

Brown J.H. & Nicoletto P.F. (1991). Spatial scaling of species composition - body masses of North-American land mammals. *American Naturalist*, **138**, 1478-1512.

Bruner A.G., Gullison R.E. & Balmford A. (2004). Financial Costs and Shortfalls of Managing and Expanding Protected-Area Systems in Developing Countries. *BioScience*, **54**, 1119-1126.

Buckley L.B. & Jetz W. (2007). Environmental and historical constraints on global patterns of amphibian richness. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 1167-1173.

Burness G.P., Diamond J. & Flannery T. (2001). Dinosaurs, dragons, and dwarfs: The evolution of maximal body size. *Proceedings of the National Academy of Sciences*, **98**, 14518-14523.

Burns K.C. (2007). Is tree diversity different in the Southern Hemisphere? *Journal of Vegetation Science*, **18**, 307-312.

Butler R.A. (2011). Tropical Rainforest Conservation. San Francisco URL http://www.mongabay.com/

Butt N., Malhi Y., Phillips O. & New M. (2008). Floristic and functional affiliations of woody plants with climate in western Amazonia. *Journal of Biogeography*, **35**, 939-950.

Buzas M.A. & Gibson T.G. (1969). Species diversity - benthonic foraminifera in Western North Atlantic. *Science*, **163**, 72-75.

Calder W.A. (1984). *Size, function, and life history*. 1st edn.vol.431 Harvard University Press Cambridge, MA.

California W.R.C.C. (2001). Western Regional Climate Center, CaliforniaURL http://www.wrcc.dri.edu/

Carbone C., Rowcliffe J.M., Cowlishaw G. & Isaac N.J.B. (2007). The scaling of abundance in consumers and their resources: implications for the energy equivalence rule. *American Naturalist*, **170**, 479-484.

Case T.J. (1978). A general explanation for insular body size trends in terrestrial vertebrates. *Ecology*, **59**, 1-18.

Chape S., Harrison J., Spalding M. & Lysenko I. (2005). Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **360**, 443-455.

Cheke A.S. & Hume J.P. (2008). *Lost land of the dodo : an ecological history of Mauritius, Réunion & Rodrigues*.Yale University Press, New Haven.

Clarke A. (2006). Temperature and the metabolic theory of ecology. *Functional Ecology*, **20**, 405-412.

Clauset A. & Erwin D.H. (2008). The Evolution and Distribution of Species Body Size. *Science*, **321**, 399-401.

Clegg S.M. & Owens I.P.F. (2002). The 'island rule' in birds: medium body size and its ecological explanation. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **269**, 1359-1365.

Clinebell R.R., Phillips O.L., Gentry A.H., Stark N. & Zuuring H. (1995). Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation*, **4**, 56-90.

Connolly S.R., Hughes T.P., Bellwood D.R. & Karlson R.H. (2005). Community structure of corals and reef fishes at multiple scales. *Science*, **309**, 1363.

Connor E.F. & McCoy E.D. (1979). Statistics and biology of the species-area relationship *American Naturalist*, **113**, 791-833.

Cooper A., Lalueza-Fox C., Anderson S., Rambaut A., Austin J. & Ward R. (2001). Complete mitochondrial genome sequences of two extinct moas clarify ratite evolution. *Nature*, **409**, 704-707.

Cornwell W.K., Schwilk D.W. & Ackerly D.D. (2006). A trait-based test for habitat filtering: convex hull volume. *Ecology*, **87**, 1465-1471.

Cotgreave P. & Stockley P. (1994). Body size, insectivory and abundance in assemblages of small mammals. *Oikos*, **71**, 89-96.

Croft D.A. (2001). Cenozoic environmental change in South America as indicated by mammalian body size distributions (cenograms). *Diversity and Distributions*, **7**, 271-287.

Currie D.J. (1991). Energy and large-scale patterns of animal-species and plant-species richness. *American Naturalist*, **137**, 27-49.

Currie D.J., Mittelbach G.G., Cornell H.V., Field R., Guegan J.F., Hawkins B.A., Kaufman D.M., Kerr J.T., Oberdorff T., O'Brien E. & Turner J.R.G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121-1134.

Organization for Tropical Studies: Meteorological and Hydrological Data (2011) http://www.ots.ac.cr/index.php?option=com_wrapper&Itemid=472

Davies S.J.J.F. (2003). *Moas*. 2nd edn. edn.vol.Vol. 8 Gale Group, Farmington Hills, MI.

USSR Committee for the International Hydrological Decade. (1977). Atlas of world water balance. UNESCO Press,Paris, France.

Deichmann U. (1991). ISRIC - World Soil Information Database.

Demment M.W. & Soest P.J.V. (1985). A Nutritional Explanation for Body-Size Patterns of Ruminant and Nonruminant Herbivores. *American Naturalist*, **125**, 641-672.

Desmet P. & Cowling R. (2004). Using the species-area relationship to set baseline targets for conservation. *Ecology and Society*, **9**, 11.

Diamond J.M. (1975). *Ecology and evolution of communities / Martin L. Cody and Jared M. Diamond, editors*. 1st edn.Belknap Press of Harvard University Press, Cambridge, Mass.

Dornelas M., Connolly S.R. & Hughes T.P. (2006). Coral reef diversity refutes the neutral theory of biodiversity. *Nature*, **440**, 80-82.

Dudley N. (2009). Guidelines for Applying Protected Area Management Categories. IUCN Publications Services. Gland, Switzerland.

Dunbrack R.L. & Ramsay M.A. (1993). The allometry of mammalian adaptations to seasonal environments: a critique of the fasting endurance hypothesis. *Oikos*, **66**, 336-342.

Eklund J., Arponen A., Visconti P. & Cabeza M. (2011). Governance factors in the identification of global conservation priorities for mammals. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **366**, 2661-2669.

Emerson B.C. & Gillespie R.G. (2008). Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology & Evolution*, **23**, 619-630.

Enquist B.J., Brown J.H. & West G.B. (1998). Allometric scaling of plant energetics and population density. *Nature*, **395**, 163-165.

Enquist B.J., Economo E.P., Huxman T.E., Allen A.P., Ignace D.D. & Gillooly J.F. (2003). Scaling metabolism from organisms to ecosystems. *Nature*, **423**, 639-642.

Enquist B.J. & Niklas K.J. (2001). Invariant scaling relations across tree-dominated communities. *Nature*, **410**, 655-660.

Enquist B.J. & Niklas K.J. (2002). Global allocation rules for patterns of biomass partitioning in seed plants. *Science*, **295**, 1517-1520.

ESRI (2003). Arc/Info, v. 8.2.3. In: *Environmental Systems Research Institute, Redlands.*

Evans A.R., Jones D., Boyer A.G., Brown J.H., Costa D.P., Ernest S.K.M., Fitzgerald E.M.G., Fortelius M., Gittleman J.L. & Hamilton M.J. (2012). The maximum rate of mammal evolution. *Proceedings of the National Academy of Sciences*, **109**, 4187-4190.

Falster D.S., Moles A.T. & Westoby M. (2008). A general model for the scaling of offspring size and adult size. *American Naturalist*, **172**, 299-317.

Ferretti M.P. (2008). The dwarf elephant Palaeoloxodon mnaidriensis from Puntali Cave, Carini (Sicily; late Middle Pleistocene): Anatomy, systematics and phylogenetic relationships. *Quaternary International*, **182**, 90-108.

Field R., Hawkins B.A., Cornell H.V., Currie D.J., Diniz-Filho J.A.F., Guegan J.F., Kaufman D.M., Kerr J.T., Mittelbach G.G., Oberdorff T., O'Brien E.M. & Turner J.R.G. (2009). Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132-147.

Fisher R.A., Corbet A.S. & Williams C.B. (1943). The relation between the number of species and the number of individuals in a random sample of an animal population. *The Journal of Animal Ecology*, 42-58.

Flather C.H., Hayward G.D., Beissinger S.R. & Stephens P.A. (2011). Minimum viable populations: is there a ‘magic number’ for conservation practitioners? *Trends in Ecology & Evolution*, **26**, 307-316.

Foster J.B. (1964). Evolution of mammals on islands *Nature*, **202**, 234-235.

Francis A.P. & Currie D.J. (2003). A globally consistent richness-climate relationship for angiosperms. *American Naturalist*, **161**, 523-536.

Freckleton R.P., Harvey P.H. & Pagel M. (2003). Bergmann's rule and body size in mammals. *American Naturalist*, **161**, 821-825.

Geist V. (1974). On the relationship of social evolution and ecology in ungulates. *American Zoologist*, **14**, 205-220.

Gentry A.H. (1982). Patterns of neotropical plant species diversity. *Evolutionary Biology*, **15**, 1-84.

Gillooly J.F., Brown J.H., West G.B., Savage V.M. & Charnov E.L. (2001). Effects of size and temperature on metabolic rate. *Science*, **293**, 2248-2251.

Gilpin M.E. & Diamond J.M. (1976). Calculation of immigration and extinction curves from the species-area-distance relation. *Proceedings of the National Academy of Sciences*, **73**, 4130-4134.

Gingerich P.D. (2001). Rates of evolution on the time scale of the evolutionary process. *Microevolution Rate, Pattern, Process*, 127-144.

Gleason H.A. (1922). On the relation between species and area. *Ecology*, **3**, 158-162.

Gould S.J. (1989). *Wonderful life: the Burgess Shale and the nature of history*. 1st edn.W.W. Norton, New York.

Graham C.H., Ron S.R., Santos J.C., Schneider C.J. & Moritz C. (2004). Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution*, **58**, 1781-1793.

Grytnes J.A. (2003). Species-richness patterns of vascular plants along several altitudinal transects in Norway. *Ecography*, **26**, 291-300.

Guilhaumon F., Gimenez O., Gaston K.J. & Mouillot D. (2008). Taxonomic and regional uncertainty in species-area relationships and the identification of richness hotspots. *Proceedings of the National Academy of Sciences*, **105**, 15458-15463.

H-Acevedo D. & Currie D.J. (2003). Does climate determine broad-scale patterns of species richness? A test of the causal link by natural experiment. *Global Ecology and Biogeography*, **12**, 461-473.

Hanski I. (1998). Metapopulation dynamics. *Nature*, **396**, 41-49.

Hanski I. (2001). Spatially realistic theory of metapopulation ecology. *Naturwissenschaften*, **88**, 372-381.

Hanski I. & Gilpin M. (1991). Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society*, **42**, 3-16.

Harrison S. & Cornell H. (2008). Toward a better understanding of the regional causes of local community richness. *Ecology Letters*, **11**, 969-979.

Harshman J., Braun E.L., Braun M.J., Huddleston C.J., Bowie R.C.K., Chojnowski J.L., Hackett S.J., Han K.-L., Kimball R.T., Marks B.D., Miglia K.J., Moore W.S., Reddy S., Sheldon F.H., Steadman D.W., Steppan S.J., Witt C.C. & Yuri T. (2008). Phylogenomic evidence for multiple losses of flight in ratite birds. *Proceedings of the National Academy of Sciences*, **105**, 13462-13467.

Hawkins B.A., Albuquerque F.S., Araujo M.B., Beck J., Bini L.M., Cabrero-Sanudo F.J., Castro-Parga I., Diniz J.A.F., Ferrer-Castan D., Field R., Gomez J.F., Hortal J., Kerr J.T., Kitching I.J., Leon-Cortes J.L., Lobo J.M., Montoya D., Moreno J.C., Olalla-Tarraga M.A., Pausas J.G., Qian H., Rahbek C., Rodriguez M.A., Sanders N.J. & Williams P.

(2007). A global evaluation of metabolic theory as an explanation for terrestrial species richness gradients. *Ecology*, **88**, 1877-1888.

Hawkins B.A. & Felizola Diniz-Filho J.A. (2004). ‘Latitude’ and geographic patterns in species richness. *Ecography*, **27**, 268-272.

Hawkins B.A., Field R., Cornell H.V., Currie D.J., Guegan J.F., Kaufman D.M., Kerr J.T., Mittelbach G.G., Oberdorff T., O'Brien E.M., Porter E.E. & Turner J.R.G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105-3117.

Hayes F.E. (2003). Geographic variation in the Great Pampa-Finch Embernagra platensis complex: evidence for two species. *Ardeola*, **50**, 223-235.

Hayward A., Kolasa J. & Stone J.R. The scale-dependence of population density-body mass allometry: Statistical artefact or biological mechanism? *Ecological Complexity*, **7**, 115-124.

He F., Gaston K.J., Connor E.F. & Srivastava D.S. (2005). The local-regional relationship: immigration, extinction, and scale. *Ecology*, **86**, 360-365.

He F. & Hubbell S.P. (2011). Species-area relationships always overestimate extinction rates from habitat loss. *Nature*, **473**, 368-371.

Hendriks A.J. & Mulder C. (2008). Scaling of offspring number and mass to plant and animal size: model and meta-analysis. *Oecologia*, **155**, 705-716.

Hijmans R.J., Cameron S.E., Parra J.L., Jones P.G. & Jarvis A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.

Hillebrand H. (2004). On the generality of the latitudinal diversity gradient. *American Naturalist*, **163**, 192-211.

Holdridge L., Grenke W.C., Hathway W.H., Ting T. & Tosi J.A. (1971). *Forest environments in tropical life zones: a pilot study*.Pergaman, New York, NY, USA.

Holling C.S. (1992). Cross-scale morphology, geometry, and dynamics of ecosystems *Ecological Monographs*, **62**, 447-502.

Houseman G. & Gross K. (2006). Does ecological filtering across a productivity gradient explain variation in species pool-richness relationships? *Oikos*, **115**, 148-154.

Hubbell S.P. (2001). *The unified neutral theory of biodiversity and biogeography*.Princeton University Press, Princeton.

Hubbell S.P., He F.L., Condit R., Borda-de-Agua L., Kellner J. & ter Steege H. (2008). How many tree species and how many of them are there in the Amazon will go extinct? *Proceedings of the National Academy of Sciences*, **105**, 11498-11504.

Huston M. (1979). General hypothesis of species-diversity. *American Naturalist*, **113**, 81-101.

Huston M.A. & Wolverton S. (2009). The global distribution of net primary production: resolving the paradox. *Ecological Monographs*, **79**, 343-377.

Huston M.A. & Wolverton S. (2011). Regulation of animal size by eNPP, Bergmann's rule, and related phenomena. *Ecological Monographs*, **81**, 349-405.

Hutchinson G.E. (1959). Homage to Santa-Rosalia or why are there so many kinds of animals. *American Naturalist*, **93**, 145-159.

I.M.F. (2012). International Monetary Fund Emerging and Developing Economies List. Database WEO Washington DC.

Ims R.A. & Andreassen H.P. (2005). Density-dependent dispersal and spatial population dynamics. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 913-918.

Ives A.R., Woody S.T., Nordheim E.V., Nelson C. & Andrews J.H. (2004). The synergistic effects of stochasticity and dispersal on population densities. *American Naturalist*, **163**, 375-387.

James A., Gaston K.J. & Balmford A. (2001). Can We Afford to Conserve Biodiversity? *BioScience*, **51**, 43-52.

James A.N., Green M.J.B. & Paine J.R. (1999). A global review of protected area budgets and staffing. Victoire Press. Conservation WW Cambridge, UK.

James F.C. (1970). Geographic size variation in birds and its relationship to climate. *Ecology*, **51**, 365-390.

Janzen D.H. (1967). Why Mountain Passes are Higher in the Tropics. *American Naturalist*, **101**, 233-249.

Jarman P.J. (1971). Diets of large mammals in the woodlands around Lake Kariba, Rhodesia. *Oecologia*, **8**, 157-178.

Jenkins C.N. & Joppa L. (2009). Expansion of the global terrestrial protected area system. *Biological Conservation*, **142**, 2166-2174.

Johst K. & Brandl R. (1997). Body size and extinction risk in a stochastic environment. *Oikos*, **78**, 612-617.

Kalmar A. & Currie D.J. (2006). A global model of island biogeography. *Global Ecology and Biogeography*, **15**, 72-81.

Kalmar A. & Currie D.J. (2007). A unified model of avian species richness on islands and continents. *Ecology*, **88**, 1309-1321.

Kelt D.A. & Meyer M.D. (2009). Body size frequency distributions in African mammals are bimodal at all spatial scales. *Global Ecology and Biogeography*, **18**, 19-29.

Kempes C.P., West G.B., Crowell K. & Girvan M. (2011). Predicting Maximum Tree Heights and Other Traits from Allometric Scaling and Resource Limitations. *PLoS ONE*, **6**, e20551.

Kerkhoff A.J. & Enquist B.J. (2006). Ecosystem allometry: the scaling of nutrient stocks and primary productivity across plant communities. *Ecology Letters*, **9**, 419-427.

Kerkhoff A.J., Enquist B.J., Elser J.J. & Fagan W.F. (2005). Plant allometry, stoichiometry and the temperature-dependence of primary productivity. *Global Ecology and Biogeography*, **14**, 585-598.

Kier G., Kreft H., Lee T.M., Jetz W., Ibisch P.L., Nowicki C., Mutke J. & Barthlott W. (2009). A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Sciences*, **106**, 9322-9327.

Kinnison M.T. & Hendry A.P. (2001). The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Microevolution Rate, Pattern, Process*, 145-164.

Kleidon A., Adams J., Pavlick R. & Reu B. (2009). Simulated geographic variations of plant species richness, evenness and abundance using climatic constraints on plant functional diversity. *Environmental Research Letters*, **4**, 1-5.

Kleidon A. & Mooney H.A. (2000). A global distribution of biodiversity inferred from climatic constraints: results from a process-based modelling study. *Global Change Biology*, **6**, 507-523.

Kluge J., Kessler M. & Dunn R.R. (2006). What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an elevational gradient in Costa Rica. *Global Ecology and Biogeography*, **15**, 358-371.

Kraft N.J.B., Comita L.S., Chase J.M., Sanders N.J., Swenson N.G., Crist T.O., Stegen J.C., Vellend M., Boyle B., Anderson M.J., Cornell H.V., Davies K.F., Freestone A.L., Inouye B.D., Harrison S.P. & Myers J.A. (2011). Disentangling the Drivers of β Diversity Along Latitudinal and Elevational Gradients. *Science*, **333**, 1755-1758.

Krug A.Z., Jablonski D. & Valentine J.W. (2009). Signature of the End-Cretaceous Mass Extinction in the Modern Biota. *Science*, **323**, 767-771.

Latham R.E. & Ricklefs R.E. (1993). Global Patterns of Tree Species Richness in Moist Forests - Energy-Diversity Theory Does Not Account for Variation in Species Richness. *Oikos*, **67**, 325-333.

Lebrija-Trejos E., Pérez-García E.A., Meave J.A., Bongers F. & Poorter L. (2010). Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology*, **91**, 386-398.

Legendre S. (1986). Analysis of mammalian communities from the late Eocene and Oligocene of southern France. *Palaeovertebrata*, **16**, 191-212.

Leith Helmut W.H. (1960). *Klimadiagramm-Weltatlas*.Veb Gustav Fischer, Jena, Germany.

Lenormand T. (2002). Gene flow and the limits to natural selection. *Trends in Ecology & Evolution*, **17**, 183-189.

Lieberman D., Lieberman M., Peralta R. & Hartshorn G.S. (1996). Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology*, **84**, 137-152.

Lines E.R., Coomes D.A. & Purves D.W. (2010). Influences of forest structure, climate and species composition on tree mortality across the Eastern US. *PloS one*, **5**, e13212.

Lomolino M.V. (1985). Body Size of Mammals on Islands: The Island Rule Reexamined. *The American Naturalist*, **125**, 310-316.

Lomolino M.V. (1990). The target area hypothesis: the influence of island area on immigration rates of non-volant mammals. *Oikos*, 297-300.

Lomolino M.V. (2005). Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography*, **32**, 1683-1699.

Lomolino M.V., Sax D.F., Palombo M.R. & van der Geer A.A. (2012). Of mice and mammoths: evaluations of causal explanations for body size evolution in insular mammals. *Journal of Biogeography*, **39**, 842-854.

Losos J.B. & Schluter D. (2000). Analysis of an evolutionary species–area relationship. *Nature*, **408**, 847-850.

Louw G. (1993). *Physiological animal ecology*.Longman Group UK Limited, Essex, England.

Lovegrove B.G. (2003). The influence of climate on the basal metabolic rate of small mammals: a slow-fast metabolic continuum. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, **173**, 87-112.

Lowenberg-Neto P., de Carvalho C.J.B. & Hawkins B.A. (2011). Tropical niche conservatism as a historical narrative hypothesis for the Neotropics: a case study using the fly family Muscidae. *Journal of Biogeography*, **38**, 1936-1947.

Lucherini M., Manfredi C., Luengos E., Mazim F.D., Soler L. & Casanave E.B. (2006). Body mass variation in the Geoffroy's cat (Oncifelis geoffroyi). *Revista chilena de historia natural*, **79**, 169-174.

Lyons S. & Smith F. (2010). Using macroecological approach to study geographic range, abundance and body size in the fossil record. *The Paleonotolgoical Society Papers*, **16**, 1-26.

M.E.A. (2005). *Ecosystems and Human Well-being: Biodiversity Synthesis*.World Resources Institute, Washington, DC.

MacArthur R.H. (1967). *The theory of island biogeography*.Princeton Univ Press, Princeton, N.J.

MacArthur R.H. & Wilson E.O. (1963). Equilibrium-theory of insular zoogeography. *Evolution*, **17**, 373-387.

Maina G.G. & Howe H.F. (2000). Inherent rarity in community restoration. *Conservation Biology*, **14**, 1335-1340.

Marquet P.A. & Cofre H. (1999). Large temporal and spatial scales in the structure of mammalian assemblages in South America: a macroecological approach. *Oikos*, **85**, 299-309.

Marquet P.A., Navarrete S.A. & Castilla J.C. (1995). Body size, population density, and the energetic equivalence rule. *Journal of Animal Ecology*, 325-332.

Marquet P.A. & Taper M. (1998). On size and area: Patterns of mammalian body size extremes across landmasses. *Evolutionary Ecology*, **12**, 127-139.

Matthysen E. (2005). Density dependent dispersal in birds and mammals. *Ecography*, **28**, 403-416.

May R.M. (1976). *Theoretical ecology: principles and applications*.Blackwell Scientific Publications.

May R.M. (1988). How Many Species Are There on Earth. *Science*, **241**, 1441-1449.

May R.M., Lawton J.H. & Stork N.E. (1995). *Extinction Rates*.Oxford University Press.

McCain C.M. (2007). Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography*, **16**, 1-13.

McDonald R.I. & Boucher T.M. (2011). Global development and the future of the protected area strategy. *Biological Conservation*, **144**, 383-392.

McGill B.J., Etienne R.S., Gray J.S., Alonso D., Anderson M.J., Benecha H.K., Dornelas M., Enquist B.J., Green J.L., He F.L., Hurlbert A.H., Magurran A.E., Marquet P.A., Maurer B.A., Ostling A., Soykan C.U., Ugland K.I. & White E.P. (2007). Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, **10**, 995-1015.

McGlynn T.P., Weiser M.D. & Dunn R.R. (2010). More individuals but fewer species: testing the 'more individuals hypothesis' in a diverse tropical fauna. *Biology Letters*, **23**, 490-493.

Meijer H.J.M. & Due R.A. (2010). A new species of giant marabou stork (Aves: Ciconiiformes) from the Pleistocene of Liang Bua, Flores (Indonesia). *Zoological Journal of the Linnean Society*, **160**, 707-724.

Meiri S. (2010). Bergmann's Rule – what's in a name? *Global Ecology and Biogeography*, **20**, 203-207.

Meiri S. & Dayan T. (2003). On the validity of Bergmann's rule. *Journal of Biogeography*, **30**, 331-351.

Meiri S., Dayan T. & Simberloff D. (2006). The generality of the island rule reexamined. *Journal of Biogeography*, **33**, 1571-1577.

Meiri S., Dayan T., Simberloff D. & Grenyer R. (2009). Life on the edge: carnivore body size variation is all over the place. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 1469-1476.

Meiri S., Raia P. & Phillimore A.B. (2011). Slaying dragons: limited evidence for unusual body size evolution on islands. *Journal of Biogeography*, **38**, 89-100.

Michalet R., Brooker R.W., Cavieres L.A., Kikvidze Z., Lortie C.J., Pugnaire F.I., Valiente-Banuet A. & Callaway R.M. (2006). Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*, **9**, 767-773.

Miller G.L. & Ricklefs R.E. (2000). *Ecology*. 4th edn.W. H. Freeman and Company, New York, New York.

Millien V. (2006). Morphological Evolution Is Accelerated among Island Mammals. *PLoS Biol*, **4**, e321.

Millien V. (2011). Mammals evolve faster on smaller islands *Evolution*, **65**, 1935-1944.

Millien V. & Gonzalez A. (2011). The maximal body mass–area relationship in island mammals. *Journal of Biogeography*, **38**, 2278–2285.

MODIS 2000.MODIS Terra Net Primary Production (NPP) Yearly L4 Global 1km SIN Grid. MOD17A3 http://daac.ornl.gov/MODIS/MODIS-menu/products.html.

Moles A.T., Warton D.I., Warman L., Swenson N.G., Laffan S.W., Zanne A.E., Pitman A., Hemmings F.A. & Leishman M.R. (2009). Global patterns in plant height. *Journal of Ecology*, **97**, 923-932.

Molino J.F. & Sabatier D. (2001). Tree diversity in tropical rain forests: A validation of the intermediate disturbance hypothesis. *Science*, **294**, 1702-1704.

Morales-Castilla I., Olalla-Tárraga M.Á., Purvis A., Hawkins B.A. & Rodríguez M.Á. (2012). The Imprint of Cenozoic Migrations and Evolutionary History on the Biogeographic Gradient of Body Size in New World Mammals. *American Naturalist*, **180**, 246-256.

Morris S.C. (2003). *Life's solution: inevitable humans in a lonely universe*.Cambridge University Press, Cambridge, UK.

Mouquet N., Munguia P., Kneitel J.M. & Miller T.E. (2003). Community assembly time and the relationship between local and regional species richness. *Oikos*, **103**, 618-626.

Mulder C.P.H., Uliassi D.D. & Doak D.F. (2001). Physical stress and diversity-productivity relationships: The role of positive interactions. *Proceedings of the National Academy of Sciences*, **98**, 6704-6708.

Nagy K.A. (1987). Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs*, **57**, 112-128.

Nagy K.A. (2005). Field metabolic rate and body size. *Journal of Experimental Biology*, **208**, 1621-1625.

Nagy K.A., Girard I.A. & Brown T.K. (1999). Energetics of free-ranging mammals, reptiles, and birds. *Annual review of nutrition*, **19**, 247-277.

Naidoo R., Balmford A., Ferraro P.J., Polasky S., Ricketts T.H. & Rouget M. (2006). Integrating economic costs into conservation planning. *Trends in Ecology & Evolution*, **21**, 681-687.

Niklas K.J., Midgley J.J. & Enquist B.J. (2003a). A general model for mass-growth-density relations across tree-dominated communities. *Evolutionary Ecology Research*, **5**, 459-468.

Niklas K.J., Midgley J.J. & Rand R.H. (2003b). Tree size frequency distributions, plant density, age and community disturbance. *Ecology Letters*, **6**, 405-411.

Nowak R.M. (1999a). *Walker's mammals of the world*. 6th edn.vol.2 Johns Hopkins University Press, Baltimore.

Nowak R.M. (1999b). *Walker's mammals of the world*. 6th edn.vol.1 Johns Hopkins University Press, Baltimore.

O'Brien E.M. (1998). Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. *Journal of Biogeography*, **25**, 379-398.

O'Brien E.M., Field R. & Whittaker R.J. (2000). Climatic gradients in woody plant (tree and shrub) diversity: water-energy dynamics, residual variation, and topography. *Oikos*, **89**, 588-600.

Okie J.G. & Brown J.H. (2009). Niches, body sizes, and the disassembly of mammal communities on the Sunda Shelf islands. *Proceedings of the National Academy of Sciences*, **106**, 19679.

Olalla-Tárraga M.Á., Diniz-Filho J.A.F., Bastos R.P. & Rodríguez M.Á. (2009). Geographic body size gradients in tropical regions: water deficit and anuran body size in the Brazilian Cerrado. *Ecography*, **32**, 581-590.

Olson V.A., Davies R.G., Orme C.D.L., Thomas G.H., Meiri S., Blackburn T.M., Gaston K.J., Owens I.P.F. & Bennett P.M. (2009). Global biogeography and ecology of body size in birds. *Ecology Letters*, **12**, 249-259.

Palkovacs E.P. (2003). Explaining adaptive shifts in body size on islands: a life history approach. *Oikos*, **103**, 37-44.

Palombo M.R. (2007). How can endemic proboscideans help us understand the "island rule"? A case study of Mediterranean islands. *Quaternary International*, **169-170**, 105-124.

Palombo M.R. (2009). Body size structure of Pleistocene mammalian communities: what support is there for the "island rule"? *Integrative Zoology*, **4**, 341-356.

Peters R.H. (1983). *The ecological implications of body size*.Cambridge Univ Press, Cambridge, New York.

Phillips O. & Miller J. (2004). *Global patterns of plant diversity: Alwyn H. Gentry's forest transect data set* Missouri Botanical Garden Press, St Louis, MO.

Phillips O.L., van der Heijden G., Lewis S.L., Lopez-Gonzalez G., Aragao L., Lloyd J., Malhi Y., Monteagudo A., Almeida S., Davila E.A., Amaral I., Andelman S., Andrade A., Arroyo L., Aymard G., Baker T.R., Blanc L., Bonal D., de Oliveira A.C.A., Chao K.J., Cardozo N.D., da Costa L., Feldpausch T.R., Fisher J.B., Fyllas N.M., Freitas M.A., Galbraith D., Gloor E., Higuchi N., Honorio E., Jimenez E., Keeling H., Killeen T.J., Lovett J.C., Meir P., Mendoza C., Morel A., Vargas P.N., Patino S., Peh K.S.H., Cruz A.P., Prieto A., Quesada C.A., Ramirez F., Ramirez H., Rudas A., Salamao R., Schwarz M., Silva J., Silveira M., Slik J.W.F., Sonke B., Thomas A.S., Stropp J., Taplin J.R.D., Vasquez R. & Vilanova E. (2010). Drought-mortality relationships for tropical forests. *New Phytologist*, **187**, 631-646.

Pimm S.L. & Askins R.A. (1995). Forest losses predict bird extinctions in eastern North America. *Proceedings of the National Academy of Sciences*, **92**, 9343-9347.

Pimm S.L., Jones H.L. & Diamond J. (1988). On the risk of extinction *American Naturalist*, **132**, 757-785.

Poulin R. & Morand S. (1997). Parasite body size distributions: interpreting patterns of skewness. *International Journal for Parasitology*, **27**, 959-964.

Preston F.W. (1948). The commonness, and rarity, of species. *Ecology*, **29**, 254-283.

Preston F.W. (1962a). Canonical Distribution of Commonness and Rarity: Part I. *Ecology*, **43**, 185-215.

Preston F.W. (1962b). Canonical Distribution of Commonness and Rarity: Part II. *Ecology*, **43**, 410-432.

Qian H. & Ricklefs R.E. (2000). Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature*, **407**, 180-182.

Rabinowitz D., Cairns S. & Dillon T. (1986). *Conservation biology: the science of scarcity and diversity.*Sinauer Associates, Sunderland, Massachusetts.

Raia P. & Meiri S. (2006). The island rule in large mammals: paleontology meets ecology. *Evolution*, **60**, 1731-1742.

Raia P. & Meiri S. (2011). The tempo and mode of evolution: body sizes of island mammals *Evolution*, **65**, 1927-1934.

Rajaniemi T.K., Goldberg D.E., Turkington R. & Dyer A.R. (2006). Quantitative partitioning of regional and local processes shaping regional diversity patterns. *Ecology Letters*, **9**, 121-128.

Rangel T., Diniz-Filho J.A.F. & Bini L.M. (2006). Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography*, **15**, 321-327.

Reichstein M., Ciais P., Papale D., Valentini R., Running S., Viovy N., Cramer W., Granier A., OgÉE J., Allard V., Aubinet M., Bernhofer C., Buchmann N., Carrara A., GrÜNwald T., Heimann M., Heinesch B., Knohl A., Kutsch W., Loustau D., Manca G., Matteucci G., Miglietta F., Ourcival J.M., Pilegaard K., Pumpanen J., Rambal S., Schaphoff S., Seufert G., Soussana J.F., Sanz M.J., Vesala T. & Zhao M. (2007). Reduction of ecosystem productivity and respiration during the European summer 2003 climate anomaly: a joint flux tower, remote sensing and modelling analysis. *Global Change Biology*, **13**, 634-651.

Ricklefs R.E. & Bermingham E. (2002). The concept of the taxon cycle in biogeography. *Global Ecology and Biogeography*, **11**, 353-361.

Ricklefs R.E. & Cox G.W. (1972). Taxon Cycles in the West Indian Avifauna. *American Naturalist*, **106**, 195-219.

Ricklefs R.E. & Schluter D. (1993). *Species diversity in ecological communities: historical and geographical perspectives*.Univ of Chicago Press, Chicago.

Rodriguez M.A., Lopez-Sanudo I.L. & Hawkins B.A. (2006). The geographic distribution of mammal body size in Europe. *Global Ecology and Biogeography*, **15**, 173-181.

Rodríguez M.Á., Olalla Tárraga M.Á. & Hawkins B.A. (2008). Bergmann's rule and the geography of mammal body size in the Western Hemisphere. *Global Ecology and Biogeography*, **17**, 274-283.

Rosenzweig M.L. (1995). *Species diversity in space and time*.Cambridge Univ Press, Cambridge, New York.

Schmidt-Nielsen K. (1984). *Scaling, why is animal size so important?*Cambridge Univ. Press, Cambridge, New York.

Scotese C.R. (2004). Cenozoic and Mesozoic paleogeography: changing terrestial biogeographic pathways. In: *Frontiers of biogeography: new directions in the geography of nature* (eds. Lomolino MV & Heaney LR). Sinauer Associates Sunderland, Massachusetts, pp. 9-26.

Shaffer M.L. (1981). Minimum Population Sizes for Species Conservation. *BioScience*, **31**, 131-134.

Shipley B. (1997). Exploratory path analysis with applications in ecology and evolution. *American Naturalist*, **149**, 1113-1138.

Sibly R.M. & Brown J.H. (2007). Effects of body size and lifestyle on evolution of mammal life histories. *Proceedings of the National Academy of Sciences*, **104**, 17707-17712.

Silva M. & Downing J.A. (1995). The allometric scaling of density and body mass: a nonlinear relationship for terrestrial mammals. *American Naturalist*, 704-727.

Simberloff D. (1992). Do species-area curves predict extinction in fragmented forest? In: *Tropical Deforestation and Species Extinction* (eds. Whitmore TC & Sayer JA). Chapman & Hall London, UK, pp. 75-89.

Smith Felisa A., Brown James H., Haskell John P., Lyons S.K., Alroy J., Charnov Eric L., Dayan T., Enquist Brian J., Ernest S.K.M., Hadly Elizabeth A., Jones Kate E., Kaufman Dawn M., Marquet Pablo A., Maurer Brian A., Niklas Karl J., Porter Warren P., Tiffney B. & Willig Michael R. (2004). Similarity of Mammalian Body Size across the Taxonomic Hierarchy and across Space and Time. *American Naturalist*, **163**, 672-691.

Smith F.A., Lyons S.K., Ernest S.K.M., Jones K.E., Kaufman D.M., Dayan T., Marquet P.A., Brown J.H. & Haskell J.P. (2003). Body mass of late quaternary mammals. *Ecology*, **84**, 3403-3403.

Steadman D. (1999). The biogeography and extinction of megapodes in Oceania. *Zoologische Verhandelingen*, **327**, 7-22.

Stevens R.D. (2011). Relative effects of time for speciation and tropical niche conservatism on the latitudinal diversity gradient of phyllostomid bats. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 2528-2536.

Stracey C.M. & Pimm S.L. (2009). Testing island biogeography theory with visitation rates of birds to British islands. *Journal of Biogeography*, **36**, 1532-1539.

Sun Z., Peng S. & Ou X. (2007). Rapid assessment and explanation of tree species abundance along the elevation gradient in Gaoligong Mountains, Yunnan, China. *Chinese Science Bulletin*, **52**, 225-231.

Sutherland G.D., Harestad A.S., Price K. & Lertzman K.P. (2000). Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology*, **4**, 1-16.

Svensson J.R., Lindegarth M., Jonsson P.R. & Pavia H. (2012). Disturbance-diversity models: what do they really predict and how are they tested? *Proceedings of the Royal Society B-Biological Sciences*, **279**, 2163-2170.

Swaine M.D., Lieberman D. & Putz F.E. (1987). The Dynamics of Tree Populations in Tropical Forest: A Review. *Journal of Tropical Ecology*, **3**, 359-366.

Tieleman B.I., Williams J.B. & Bloomer P. (2003). Adaptation of metabolism and evaporative water loss along an aridity gradient. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **270**, 207-214.

Tilman D. (1985). The resource-ratio hypothesis of plant succession. *American Naturalist*, **125**, 827-852.

Tittensor D.P., Mora C., Jetz W., Lotze H.K., Ricard D., Vanden Berghe E. & Worm B. (2010). Global patterns and predictors of marine biodiversity across taxa. *Nature*, **466**, 1098-1101.

Traill L.W., Bradshaw C.J.A. & Brook B.W. (2007). Minimum viable population size: A meta-analysis of 30 years of published estimates. *Biological Conservation*, **139**, 159-166.

Traill L.W., Brook B.W., Frankham R.R. & Bradshaw C.J.A. (2010). Pragmatic population viability targets in a rapidly changing world. *Biological Conservation*, **143**, 28-34.

Travis J.M.J., Murrell D.J. & Dytham C. (1999). The evolution of density–dependent dispersal. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **266**, 1837-1842.

Ulrich W., Ollik M. & Ugland K.I. (2010). A meta-analysis of species-abundance distributions. *Oikos*, **119**, 1149-1155.

Van Der Heijden G.M.F. & Phillips O.L. (2009). Environmental effects on Neotropical liana species richness. *Journal of Biogeography*, **36**, 1561-1572.

van Mantgem P.J. & Stephenson N.L. (2007). Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecology Letters*, **10**, 909-916.

van Tuinen M., Sibley C.G. & Hedges S.B. (1998). Phylogeny and biogeography of ratite birds inferred from DNA sequences of the mitochondrial ribosomal genes. *Molecular Biology and Evolution*, **15**, 370-376.

Van Valen L.M. (1973). Pattern and the balance of nature. *Evolutionary Theory*, **1**, 31-49.

Watt C., Mitchell S. & Salewski V. (2010). Bergmann's rule; a concept cluster? *Oikos*, **119**, 89-100.

Webb C.O., Ackerly D.D., McPeek M.A. & Donoghue M.J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475-505.

Weir J.T. & Schluter D. (2007). The Latitudinal Gradient in Recent Speciation and Extinction Rates of Birds and Mammals. *Science*, **315**, 1574-1576.

Wernstedt F.L. (1960). Climatic Fluctuation and Agriculture in the Great-Basin, 1931-56. *Journal of Range Management*, **13**, 173-178.

West G.B., Brown J.H. & Enquist B.J. (1999). A general model for the structure and allometry of plant vascular systems. *Nature*, **400**, 664-667.

Weston E.M. & Lister A.M. (2009). Insular dwarfism in hippos and a model for brain size reduction in Homo floresiensis. *Nature*, **459**, 85-88.

Whittaker R.J. & Field R. (2000). Tree species richness modelling: an approach of global applicability. *Oikos*, **89**, 399-402.

Whittaker R.J., Triantis K.A. & Ladle R.J. (2008). A general dynamic theory of oceanic island biogeography. *Journal of Biogeography*, **35**, 977-994.

Wiens J.J., Ackerly D.D., Allen A.P., Anacker B.L., Buckley L.B., Cornell H.V., Damschen E.I., Davies T.J., Grytnes J.A., Harrison S.P., Hawkins B.A., Holt R.D., McCain C.M. & Stephens P.R. (2005). Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, **13**, 1310-1324.

Wiens J.J. & Donoghue M.J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, **19**, 639-644.

Wiens J.J. & Graham C.H. (2005). Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annual Review of Ecology Evolution and Systematics*, **36**, 519-539.

Williams M.W. & Konovalov V.G. (2008). Central Asia Temperature and Precipitation Data, 1879–2003. Boulder, Colorado: USA National Snow and Ice Data Center. Accessed 2011. Digital media.

Willig M.R., Kaufman D.M. & Stevens R.D. (2003). Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual Review of Ecology Evolution and Systematics*, **34**, 273-309.

Wilson E.O. (1961). The Nature of the Taxon Cycle in the Melanesian Ant Fauna. *American Naturalist*, **95**, 169-193.

Wilson K.A., McBride M.F., Bode M. & Possingham H.P. (2006). Prioritizing global conservation efforts. *Nature*, **440**, 337-340.

Wilson K.A., Underwood E.C., Morrison S.A., Klausmeyer K.R., Murdoch W.W., Reyers B., Wardell-Johnson G., Marquet P.A., Rundel P.W., McBride M.F., Pressey R.L., Bode M., Hoekstra J.M., Andelman S., Looker M., Rondinini C., Kareiva P., Shaw M.R. & Possingham H.P. (2007). Conserving biodiversity efficiently: What to do, where, and when. *Plos Biology*, **5**, 1850-1861.

Wright D.H. (1983). Species-energy theory-An extension of species-area theory. *Oikos*, **41**, 496-506.

Wright S.J. (1985). How Isolation Affects Rates of Turnover of Species on Islands. *Oikos*, **44**, 331-340.

A. Appendix 1: Chapter 1 supplementary material

Tables

Table A.1. Statistical summary of the body masses (kg) for the 10 body size categories. Each size category has approximately 169 species. Standard deviation is represented by STDV. Occurrences represent the total occurrences observed for each size category. Species represents the number of species in each size category.

Size category	Average	Median	STDV	Minimum	Maximum	Occurrences	Species
1	0.006	0.006	0.002	0.002	0.010	16017	171
2	0.014	0.014	0.002	0.010	0.018	15657	171
3	0.022	0.022	0.003	0.019	0.027	11513	168
4	0.034	0.035	0.004	0.028	0.041	9619	166
5	0.054	0.055	0.008	0.041	0.067	6873	166
6	0.083	0.078	0.013	0.068	0.117	5562	168
7	0.191	0.191	0.046	0.118	0.283	6034	168
8	0.403	0.400	0.091	0.285	0.600	5206	172
9	1.243	1.139	0.533	0.615	2.682	10931	170
10	30.784	7.000	72.844	2.700	579.25	25723	174

Table A.2. Slope coefficients for mammals (generated from equation 3) for the proportion of species among the ten body size categories as a function of each environmental variable. All independent variables have been standardized with a mean of zero and a standard deviation of one. Bold values indicate significant variables, non-bold values represent significant values, $P < 0.10$; italic values represent non-significant values, $p > 0.10$

Size category	*T	†T^2	‡ T • P	§H
1	-0.22	-0.21	0.02	-0.01
2	0.39	-0.34	*0.000*	0.001
3	0.90	--0.90	0.01	0.001
4	-0.32	0.32	0.002	0.002
5	-1.40	1.42	-0.03	0.01
6	-0.37	0.35	0.01	0.003
7	0.72	-0.72	-0.01	*0.000*
8	1.37	-1.30	-0.004	0.01
9	0.67	-0.69	-0.002	-0.01
10	-1.78	1.73	-0.01	0.02

* Mean annual temperature (K)
† Mean annual temperature squared (K)
‡Mean annual temperature and mean annual precipitation interaction (mm)
§Habitat heterogeneity

Table A.3. Simultaneous autoregressive analysis (SAR) for each of the dependent variables. Models relating descriptors of the body mass frequency distribution, and species evenness as a function of temperature, precipitation, and habitat heterogeneity. Dependent variables were first modeled as functions of the environmental variables without distinguishing between continents, and then dummy independent variables were added. PC-1 is the first component of the proportion of mammalian species per $\log_2$ size classes while it is the first component of the proportion of individual trees in $\log_2$ size classes.

Mammals		Environmental variables	
Dependent variable	OLS	SAM predictor variables	SAM predictor variables+ space
Mean body size	0.71	0.70	0.68
Evenness	0.70	0..69	0.79
Body mass variance	0.66	0.65	0.60
Body mass skew	0.42	0.41	0.42
PC-1	0.74	0.72	0.89
Trees			
Mean d.b.h.	0.62	0.58	0.56
Evenness	0.49	0.45	0.52
d.b.h. variance	0.29	0.26	0.36
d.b.h. skew	0.48	0.44	0.50
PC-1	0.57	0.53	0.57

Table A.4. Regression coefficients (+- SE) of the dependent variables. Bold values represent significant effects ($P < 0.05$), * P value > 0.05 and < 0.10. All independent variables have been standardized with a mean of zero and a standard deviation of one.

Mammals	Temperature (K)	Temperature^2 (K)	Temperature (K) • Precipitation (mm)	Habitat heterogeneity
Mean body mass (log$_2$)	-12.43 (0.90)	11.75 (0.90)	-0.19 (0.02)	0.13 (0.02)
Body mass variance (log$_2$)	-38.43 (3.62)	35.31 (3.64)	0.19* (0.10)	0.19 (0.10)
Body mass skew (log$_2$)	4.27 (0.38)	-4.10 (0.38)	0.02* (0.01)	-0.03 (0.01)
Evenness	3.10 (0.08)	-3.17 (0.08)	-0.01 (0.002)	-0.02 (.001)
PC-1	-1.92 (0.09)	1.84 (0.09)	-0.02 (0.01)	0.02 (0.01)

Trees	Temperature (K)	Temperature^2 (K)	Temperature (K) • Precipitation (mm)	Habitat heterogeneity
Mean d.b.h. (cubrtlog$_2$)	-1.57 (0.35)	1.52 (0.35)	-0.01 (.001)	-0.01 (.003)
d.b.h. variance (cubrtlog$_2$)	-2.14 (0.76)	2.09 (0.76)	-0.004 (0.01)	-0.02 (0.01)
d.b.h. skew (log$_2$)	6.90 (2.60)	-6.64 (2.60)	0.04 (0.03)	0.08 (0.03)
Evenness	-1.89 (0.48)	1.84 (0.48)	-0.002* (0.005)	-0.015 (0.01)
PC-1	2.20 (0.68)	-2.12 (0.68)	0.01* (0.008)	0.03 (0.01)

Figures

Figure A.1. Gentry plots used in the analysis.

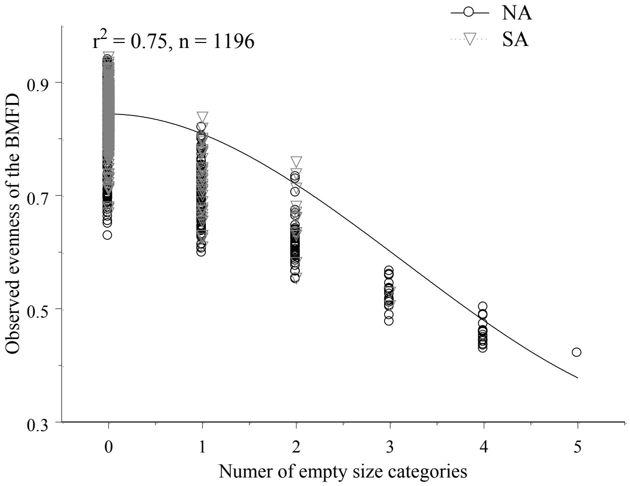


Figure A.2. Evenness of the body mass frequency distribution as a function of the number of empty size categories. LOWESS lines shown for both North and South America (tension 0.80). Note that the lines overlap across the range. The black circles and solid lines represent North America while the gray triangles and the hatched lines represent South America (N = 1196).

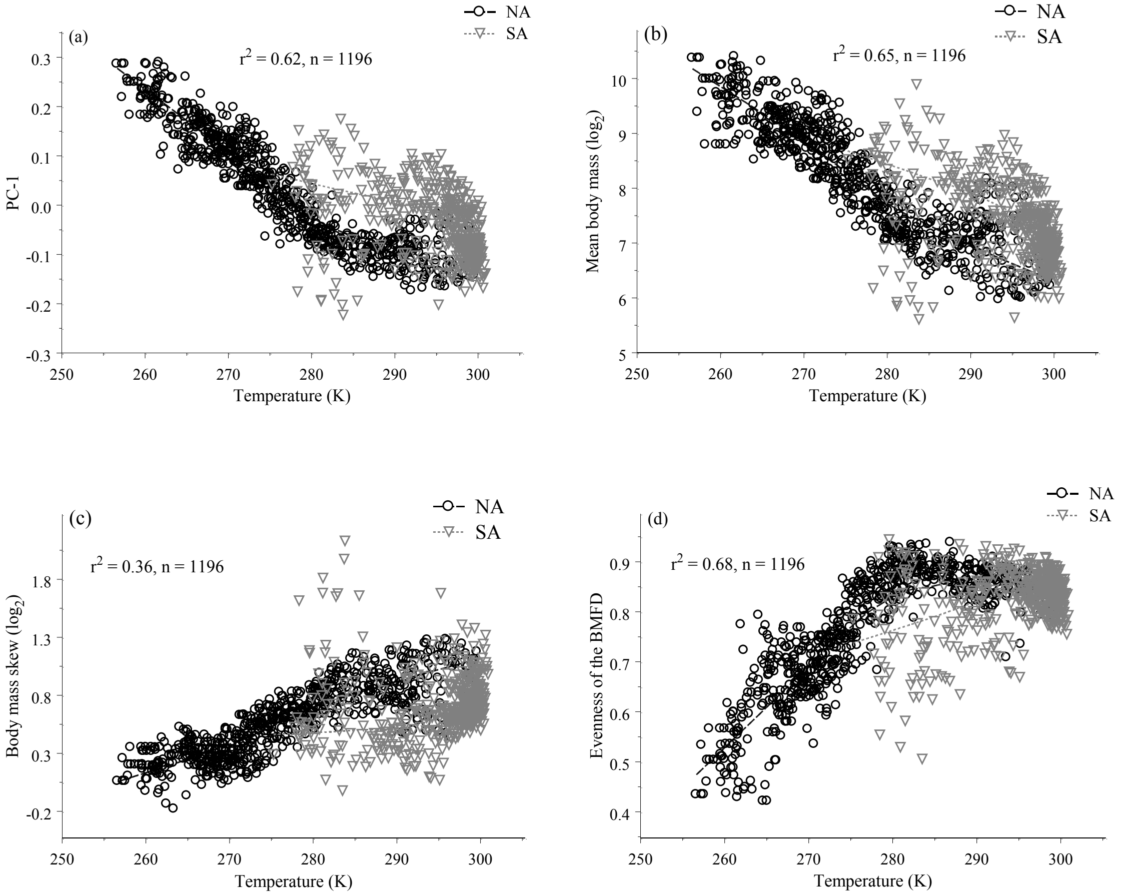


Figure A.3. Relationships among characteristics of species assemblages as a function of mean annual temperature. (a) principal component 1; (b) $\log_2$ average body mass; (c) body mass skew; (d) evenness of the body mass frequency distribution (BMFD), I included a second degree polynomial for temperature for the variable. The black circles and solid lines represent North America while the gray triangles and the hatched lines represent South America (N = 1196). Lines are LOWESS trend lines, tension = 0.80.

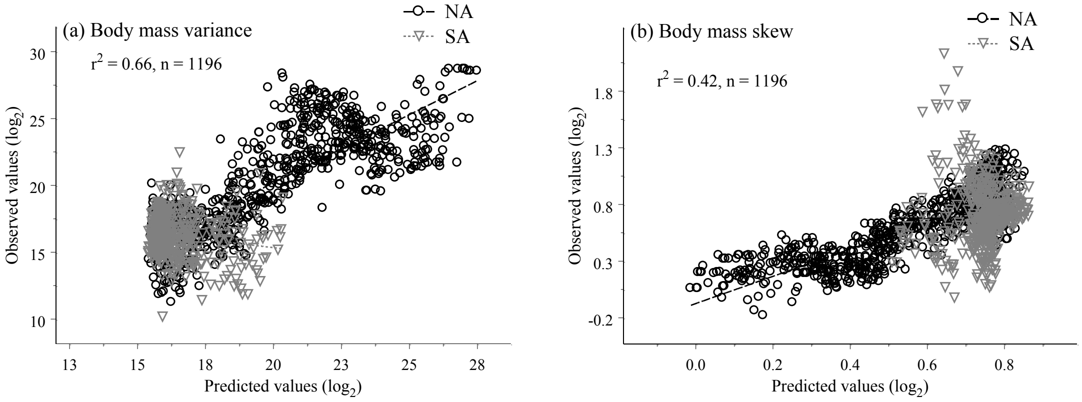


Figure A.4. Observed values as a function of the predicted values for mammals. (a) body mass of $\log_2$ variance; (b) $\log_2$ of body mass skew. The predicted values were calculated from the multiple regression models without continent. The black circles and solid lines represent North America while the gray triangles and the hatched lines represent South America (N = 1196). Linear regression lines shown for each continent.

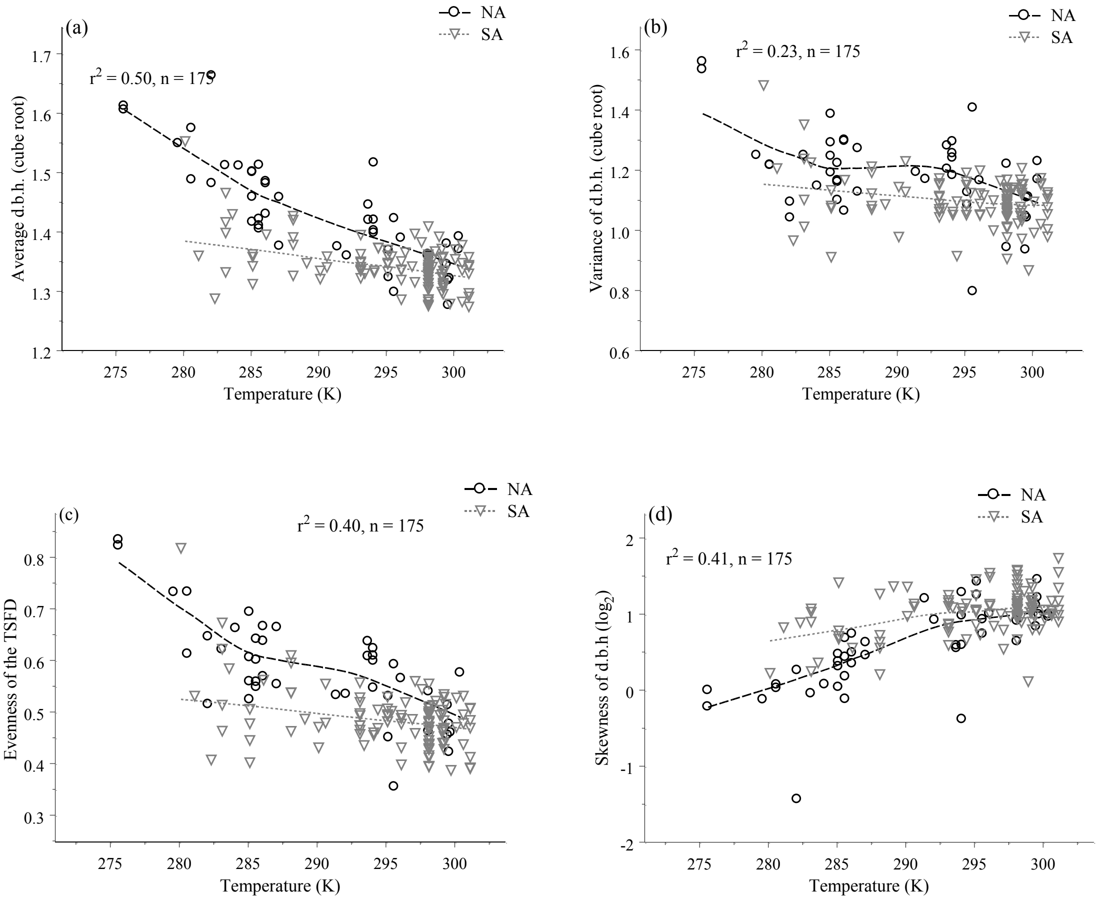


Figure A.5. Univariate relationships among characteristics of species assemblages among trees as a function of mean annual temperature. (a) log$_2$ average diameter at breast height (d.b.h. cube root transformation); (b) log$_2$ d.b.h. variance; (c) evenness of the tree size frequency distribution (TSFD) of d.b.h.; (d) log$_2$ d.b.h. skew. The black circles and solid lines represent North America while the gray triangles and the hatched lines represent South America (N = 175). LOWESS lines shown separately for each continent with a tension of 0.80.

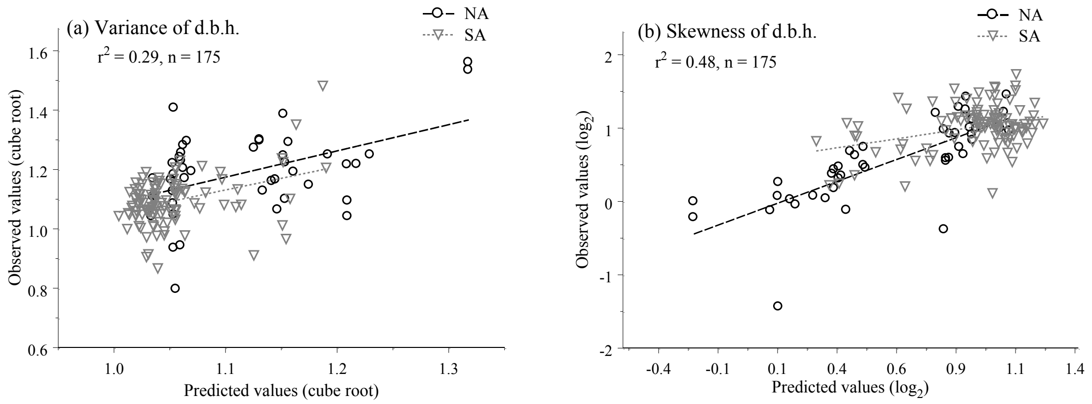
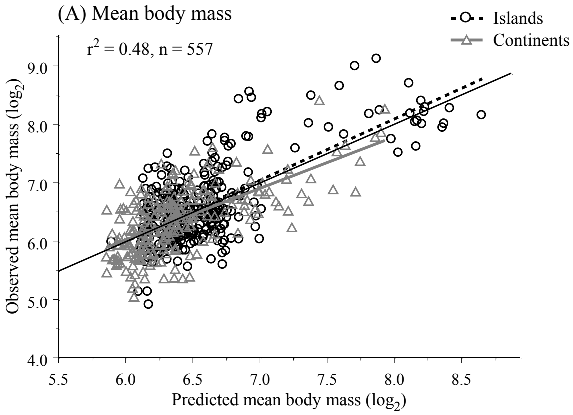


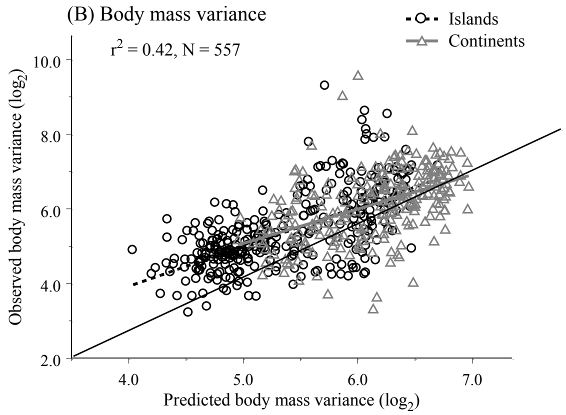
Figure A.6. Observed values as a function of the predicted values for trees. (a) $\log_2$ variance diameter at breast height (d.b.h. variance cube root transformation); (b) $\log_2$ d.b.h. skewness. The predicted values were calculated from the multiple regression models without continent. The black circles and solid lines represent North America while the gray triangles and the hatched lines represent South America (N = 175). Linear regression lines shown for each continent.

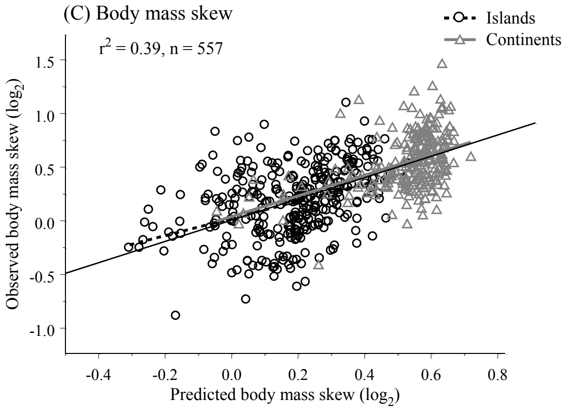
B. Chapter 2 Appendix: supplementary material

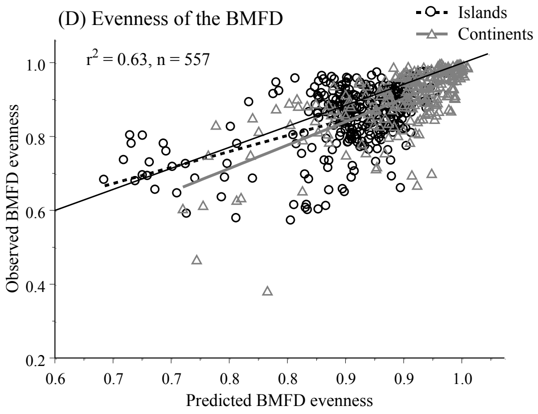
Figures

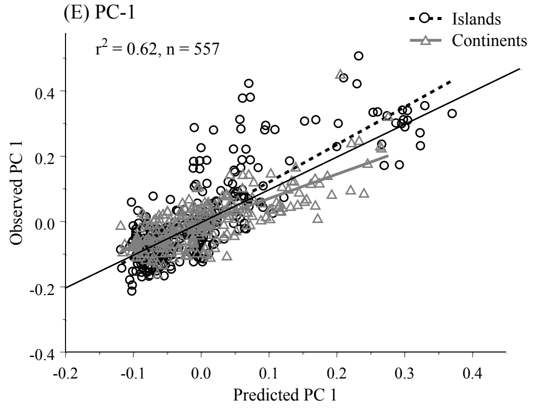
Birds

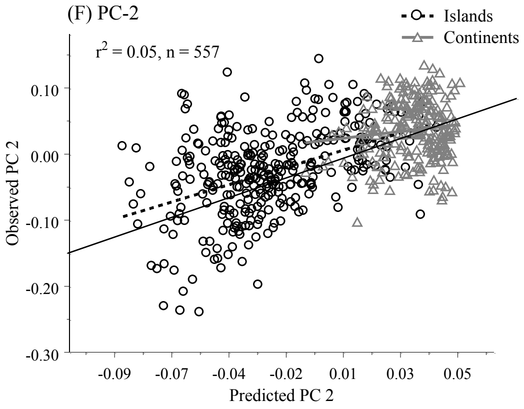

(A) Mean body mass


(B) Body mass variance


(C) Body mass skew


(D) Evenness of the BMFD


(E) PC-1


(F) PC-2

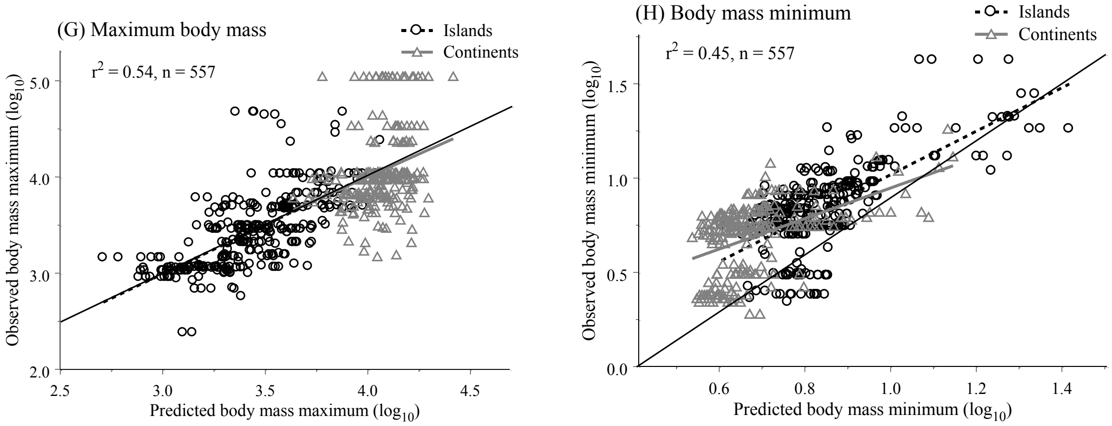
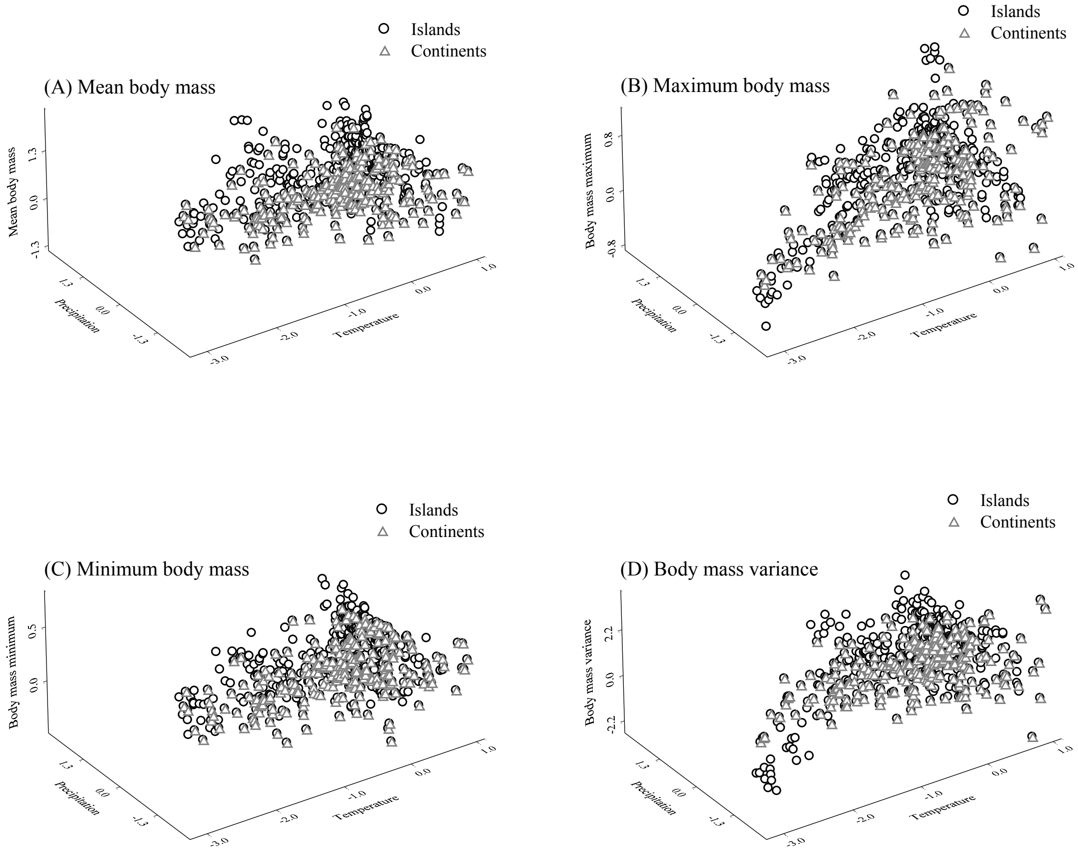


Figure B.1. Observed values as a function of predicted values. (A) mean body size ($\log_2$). (B) body size variance ($\log_2$). (C) body mass skew ($\log_2$). (D) evenness of the body mass frequency distribution. (E) principal component 1. (F) principal component 2. (G) maximum body mass ($\log_{10}$). (H) minimum body mass ($\log_{10}$). The black reference line represents a 1 to 1 ratio. Continental and island assemblages have LOWESS trend lines, tension = 0.80 (N = 557). Predicted patterns were calculated using eq. 1 with the addition of distance to continent added to the regression model. Linear regression line shown separately for each continent.



(A) Mean body mass

(B) Maximum body mass

(C) Minimum body mass

(D) Body mass variance

Figure B.2. Effect of temperature and precipitation on bird assemblage structure. The axes represent residuals after statistically controlling for island area and distant to continent. (A) mean body size ($\log_2$). (B) body mass maximum ($\log_{10}$). (C) body mass minimum ($\log_{10}$). (D) body mass variance ($\log_2$). N = 557.

REFERENCES FOR AVIAN BODY WEIGHT DATA

Clement, P., Harris, A. and Davis, J. (1993) *Finches and Sparrows: an Identification Guide*. A & C Black Ltd., London.

del Hoyo, J., Elliott, A. and Sargatal, J. (Eds.) (1992) *Handbook of the birds of the world. Vol. 1. Ostrich to Ducks*. Lynx Edicions, Barcelona.

del Hoyo, J., Elliott, A. and Sargatal, J. (Eds.) (1994) *Handbook of the birds of the world. Vol. 2. New World Vultures to Guineafowl*. Lynx Edicions, Barcelona.

del Hoyo, J., Elliott, A. and Sargatal, J. (Eds.) (1996) *Handbook of the birds of the world. Vol. 3. Hoatzin to Auks*. Lynx Edicions, Barcelona.

del Hoyo, J., Elliott, A. and Sargatal, J. (Eds.) (1997) *Handbook of the birds of the world. Vol. 4. Sandgrouse to Cuckoos*. Lynx Edicions, Barcelona.

del Hoyo, J., Elliott, A. and Sargatal, J. (Eds.) (1999) *Handbook of the birds of the world. Vol. 5. Barn-owls to Hummingbirds*. Lynx Edicions, Barcelona.

del Hoyo, J., Elliott, A. and Sargatal, J. (Eds.) (2001) *Handbook of the birds of the world. Vol. 6. Mousebirds to Hornbills*. Lynx Edicions, Barcelona.

del Hoyo, J., Elliott, A. and Sargatal, J. (Eds.) (2002) *Handbook of the birds of the world. Vol. 7. Jacamars to Woodpeckers*. Lynx Edicions, Barcelona.

del Hoyo, J., Elliott, A. and Christie, D. (Eds.) (2003) *Handbook of the birds of the world. Vol. 8. Broadbills to Tapaculos*. Lynx Edicions, Barcelona.

del Hoyo, J., Elliott, A. and Christie, D. (Eds.) (2003) *Handbook of the birds of the world. Vol. 9. Cotingas to Pipits and Wagtails*. Lynx Edicions, Barcelona.

del Hoyo, J., Elliott, A. and Christie, D. (Eds.) (2005) *Handbook of the birds of the world. Vol. 10. Cuckoo-shrikes to Thrushes*. Lynx Edicions, Barcelona.

del Hoyo, J., Elliott, A. and Christie, D. (Eds.) (2006) *Handbook of the birds of the world. Vol. 11. Old World Flycatchers to Old World Warblers*. Lynx Edicions, Barcelona.

del Hoyo, J., Elliott, A. and Christie, D. (Eds.) (2007) *Handbook of the birds of the world. Vol. 12. Picathartes to Tits and Chickadees*. Lynx Edicions, Barcelona.

Dunning, J. B. Jr. (1993) CRC *Handbook of Avian Body Masses*. CRC Press, Boca Raton, Florida.

Dunning, J. B. Jr. (2007) *CRC Handbook of Avian Body Masses, Second Edition*. CRC Press, Boca Raton, Florida.

Forshaw, J. M. (2006) *Parrots of the World*. Princeton University Press, NJ.

Jackson, J. A., Bock, W. J. and Olendorf, D. (eds.) (2003) *Grzimek's Animal Life Encyclopedia*, Vols. 8-11: Birds. The Gale Group, Inc., Farmington Hills, MI.

Ramirez, L., Diniz-Filho, J. A. F. and Hawkins, B. A. (2008) Partitioning phylogenetic and adaptive components of the geographical body-size pattern of New World birds. Global Ecology and Biogeography, 17: 100-110.

AvianWeb, The: http://avianweb.com/

Birdcare.com.au: http://birdcare.com.au/

Cornell Lab of Ornithology: http://www.birds.cornell.edu/AllAboutBirds/BirdGuide/

Earthlife Web, The: http://www.earthlife.net/

Oiseaux.net: http://www.oiseaux.net/

C. Chapter 3 Appendix: Supplementary material

Tables

Table C.1. A set of related models proposed to account for geographic variation in species richness. SR = species richness, T= temperature, P = precipitation, I = density of individuals.

Model	Relationship	Problems
Correlative (Currie 1991; Francis & Currie 2003; Hillebrand 2004; Field *et al.* 2009)	↑Area → ↑SR ←↑ T, P	No mechanism involved
Preston (Preston 1962b, a)	↑Area → ↑I → ↑ SR ← ↓ m	The variation in the number of individuals does not account for the variation in the number of species; the relationship between species richness and the number of individuals of the rarest species has not been tested
Energy richness (Hutchinson 1959; Wright 1983)	↑T, P → ↑NPP → ↑I → ↑SR	The variation in resource availability does not account for the variation in the number of individuals. The causal path is not supported (Currie *et al.* 2004; Borregaard & Rahbek 2010; McGlynn *et al.* 2010)
Metabolic theory (Allen *et al.* 2002)	↑T → ↑(I energy use) → ↓I / SR→ ↑SR	The predictions derived from the model are not supported (Hayward *et al.* ; Clarke 2006; Algar *et al.* 2007; Carbone *et al.* 2007; Hawkins *et al.* 2007)
Preston-rarity	↑Area → ↑I → ↑SR ← ↓m ← ↓T*P	----

Table C.2. Summary statistics and the difference (in orders of magnitude) for species richness (SR), density of individuals (I), and the number of individuals of the rarest species (m) among the 11 Barva sites and 196 Gentry sites. Note that the number of individuals of the rarest species (in 0.1 ha) can be less than one. To capture at least two individuals, the area would need to increase by an appropriate value.

Barva

Variable	Mean	Max.	Min.	STDEV	Diff. (orders of magnitude)
SR	88.00	149.00	29.00	38.00	0.71
I	537.00	654.00	425.00	67.00	0.19
m	3.00E-03	2.00E-02	4.00E-05	8.00E-03	2.60
ϕ	0.31	0.48	0.17	0.10	NA

Gentry

Variable	Mean	Max.	Min.	STDEV	Diff. (orders of magnitude)
SR	82.00	226.00	5.00	54.00	1.60
I	281.00	672.00	43.00	104.00	1.20
m	0.04	5.29	7.00E-06	0.38	5.9
ϕ	0.46	0.83	0.07	0.16	NA

Figures

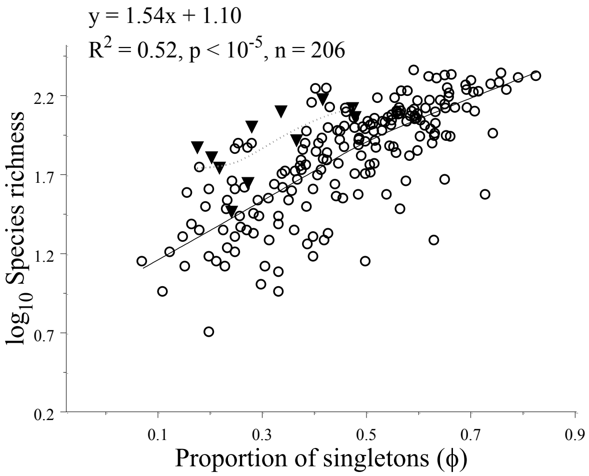


Figure C.1. The number of species as a function of proportion of singletons (world sites of Gentry, open circles and Barva sites inverted triangles). LOWESS line shown with a tension of 0.80.

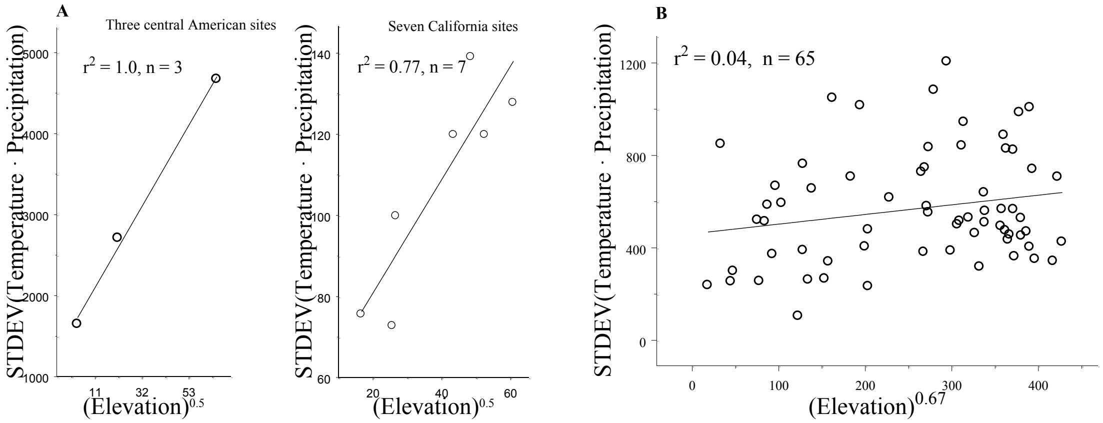


Figure C.2. Standard deviation of the annual variability of temperature (K) precipitation (mm) interaction as a function of elevation (ft), (A) three Central America weather stations, seven western California weather stations (California). (B) 85 Central Asian weather stations (Williams & Konovalov 2008) . Linear regression lines shown. I limited myanalysis to sites below 8600 feet. This was done because the maximum elevation along the Barva transect is 8550 feet.

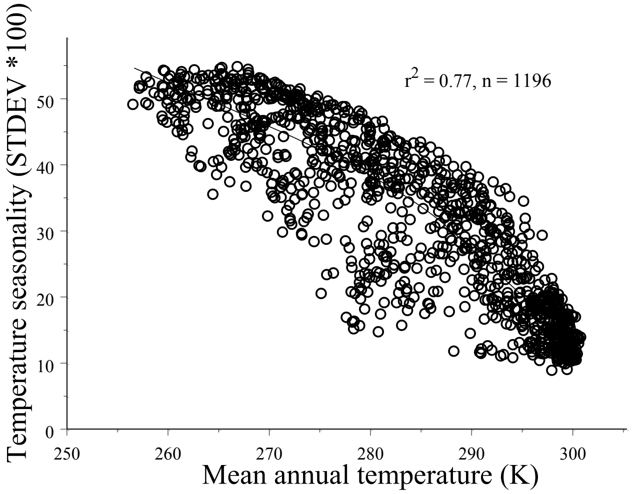


Figure C.3. Temperature seasonality (standard deviation mulitplied by 100) as a function of mean annaul temperature (K) across North and South America. Data from (Hijmans *et al.* 2005). LOWESS line shown with a tension of 0.80.

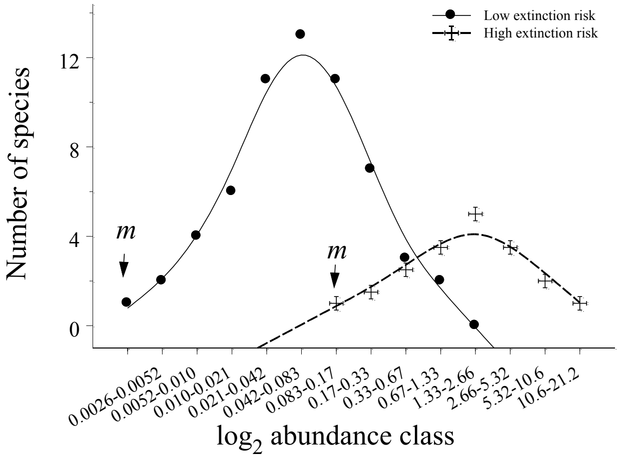


Figure C.4. A hypothetical illustration how Preston's log normal distribution shifts in response to regions that varies in extinction risk (e.g. gradients of temperature and precipitation). I calculated *m* as a function of total number of individuals and species richness. The low extinction site consisted of 500 individuals and 60 species; the high extinction site consisted of 500 individuals and 20 species. See text for description.

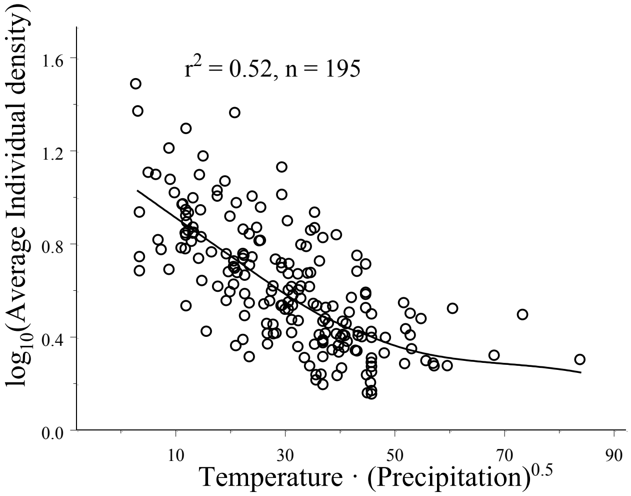


Figure C.5. Average density of individuals per species at Gentry sites as a function of temperature (°C) X precipitation (meters) interaction. The correlation is from a second-degree polynomial fit. Precipitation (meters) was square root transformed. LOWESS line shown with a tension of 0.80.

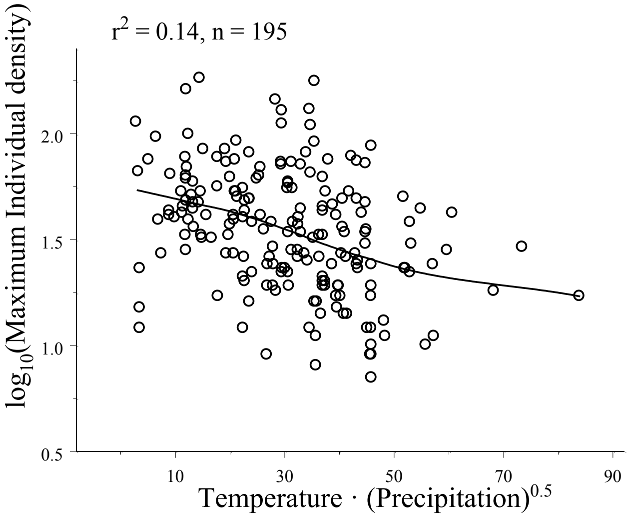


Figure C.6. Maximum density of individuals per species at Gentry sites as a function of temperature (°C) X precipitation (meters) interaction. Precipitation (meters) was square root transformed. LOWESS line shown with a tension of 0.80.

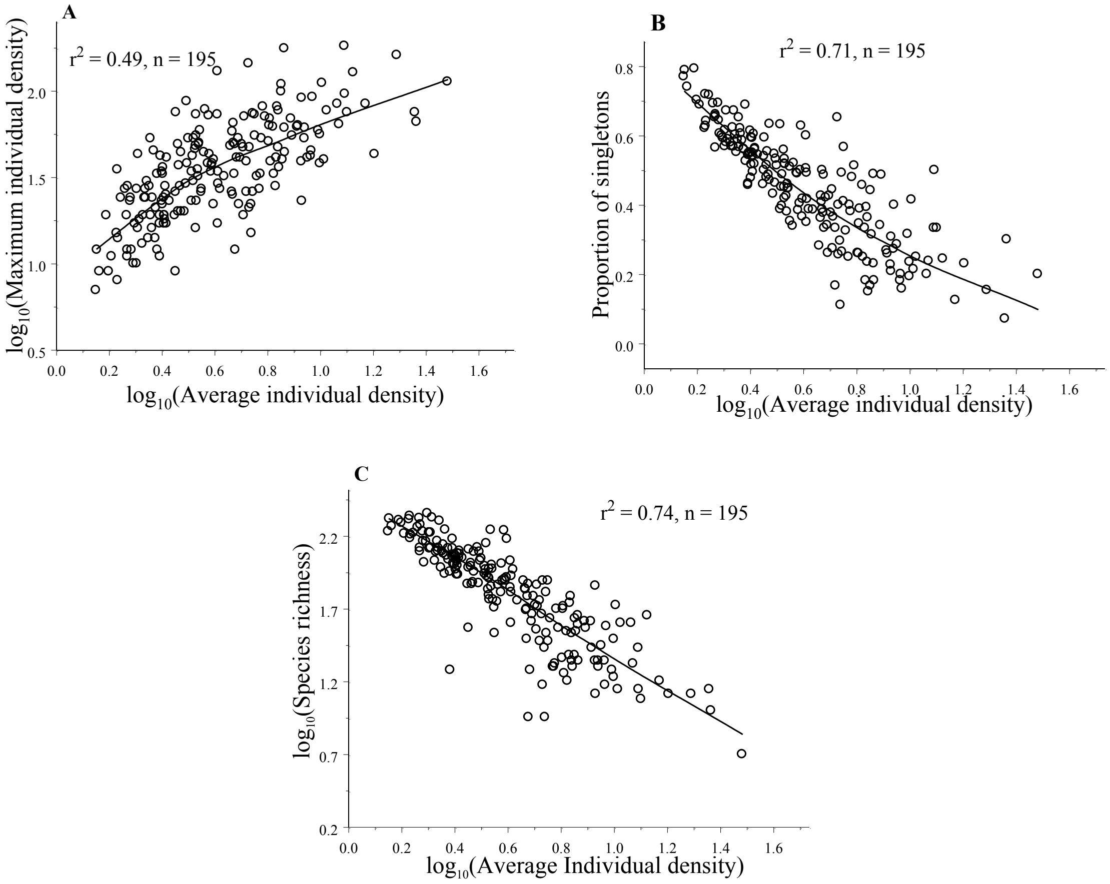


Figure C.7. Average individual density in relation to: (*A*) maximum density of individuals (Gentry sites); (*B*) proportion of singletons; (*C*) species richness. Data from Gentry sites. N = 195. LOWESS lines shown with a tension of 0.80.

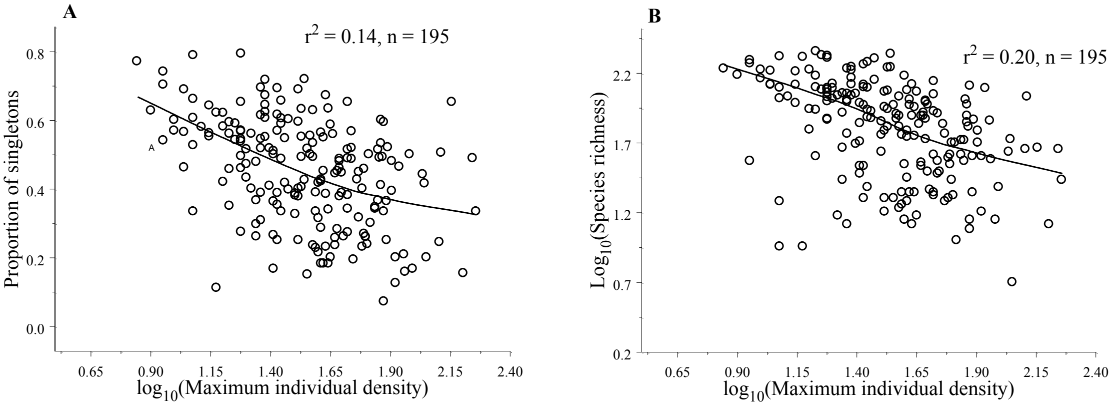


Figure C.8. Maximum individual density in relation to: (*A*) proportion of singletons; (*B*) species richness (*B*). Data from Gentry sites. N = 195. LOWESS lines shown with a tension of 0.80.

D. Chapter 5 Appendix: supplementary material

Tables

Table D.1. An example of how the data was arranged in relation to ten size categories resulting in a sample size of 11,960 size category × grid cell combinations.

size.cat	quadrat	# of species	temperature (C)	precipitation (mm)	continent
1	1	2	15	500	1
1	2	6	11	700	1
1	3	4	13	450	1
1	4	3	23	800	0
1	5	7	28	1100	0
2	1	2	15	500	1
2	2	6	11	700	1
2	3	4	13	450	1
2	4	3	23	800	0
2	5	7	28	1100	0

Table D.2. Statistical summary of the 10 body size categories. The size categories were created using $\log_{3.6}$. This log scale was chosen to create ten size categories.

size category	average mass (kg)	STDV mass	maximum mass (kg)	minimum mass (kg)	total occurrences	total number of species
1	0.0052	0.0013	0.0070	0.0021	9878	114
2	0.0162	0.0052	0.0255	0.0075	32537	377
3	0.0530	0.0192	0.0925	0.0260	21989	488
4	0.1973	0.0651	0.3300	0.0933	8464	238
5	0.6184	0.2517	1.2000	0.3410	9932	227
6	2.3575	0.9370	4.3350	1.2200	10099	129
7	7.2418	2.3276	14.5251	4.4000	10691	75
8	34.7723	14.3456	55.6506	16.3001	5842	26
9	99.5238	28.2250	148.9498	68.5993	2304	12
10	317.4381	123.9821	579.2553	207.5009	1399	8

Figures

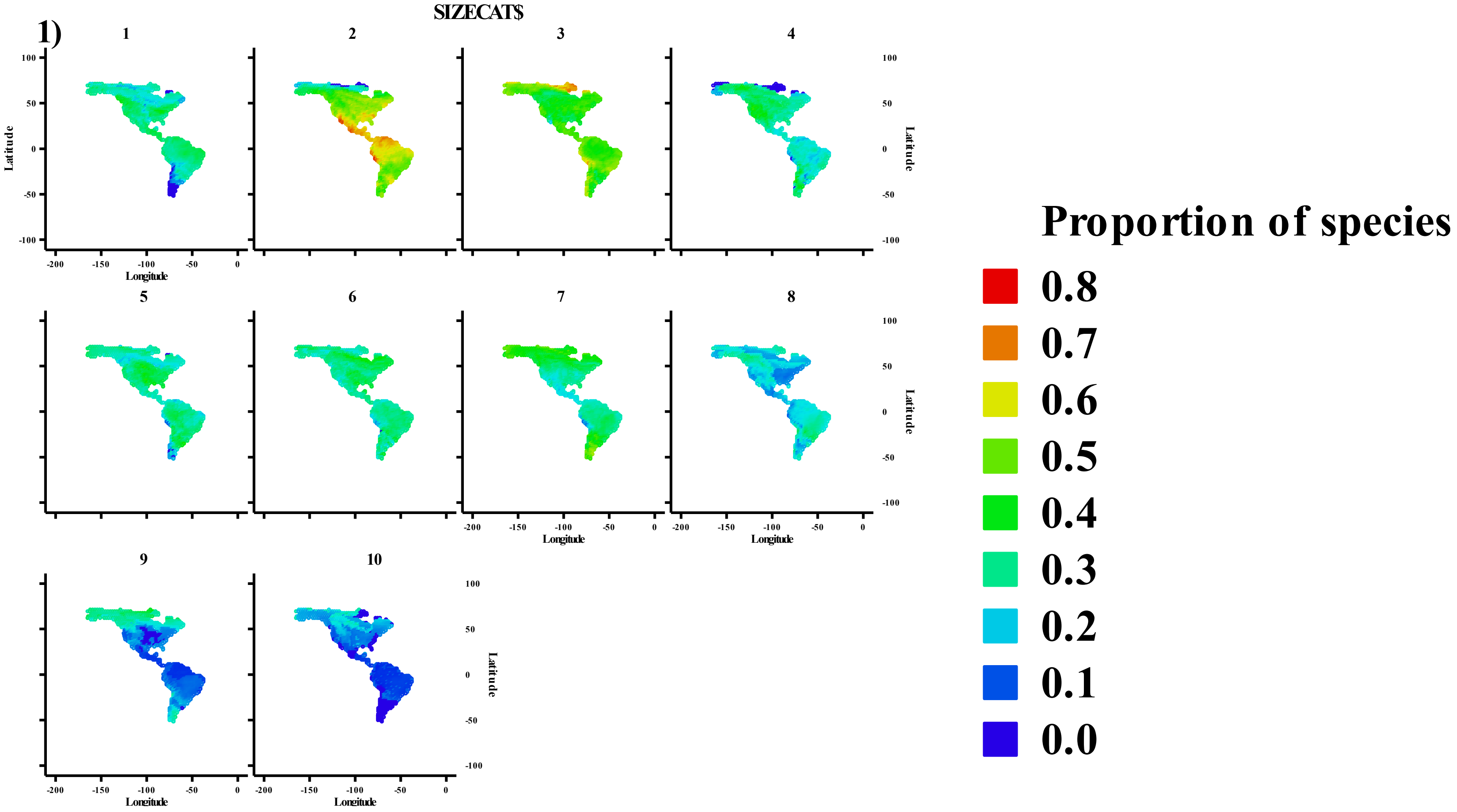


Figure D.1. Proportion (arc-sin) of species observed among the 10 size categories based on $\log_{3.6}$ bins.

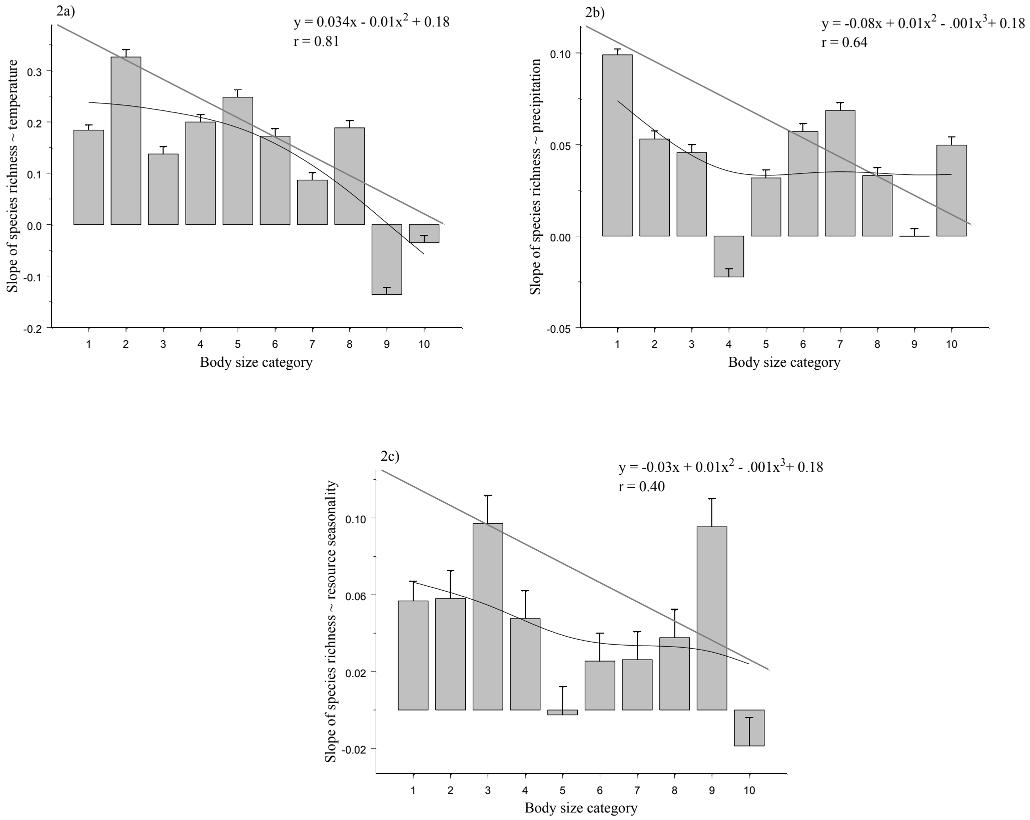


Figure D.2. Slope coefficients of species richness (+/- SE) for the various size categories ($\log_{3.6}$ bins) as a function of the three environmental variables. a) Mean annual temperature; a second-degree polynomial was added to depict the general shape of the coefficients. b) Mean annual precipitation; a third degree polynomial was added to depict the general shape of the coefficients. c) Resource seasonality (maximum NPP – minimum NPP) a third degree polynomial was added to depict the general shape of the coefficients.

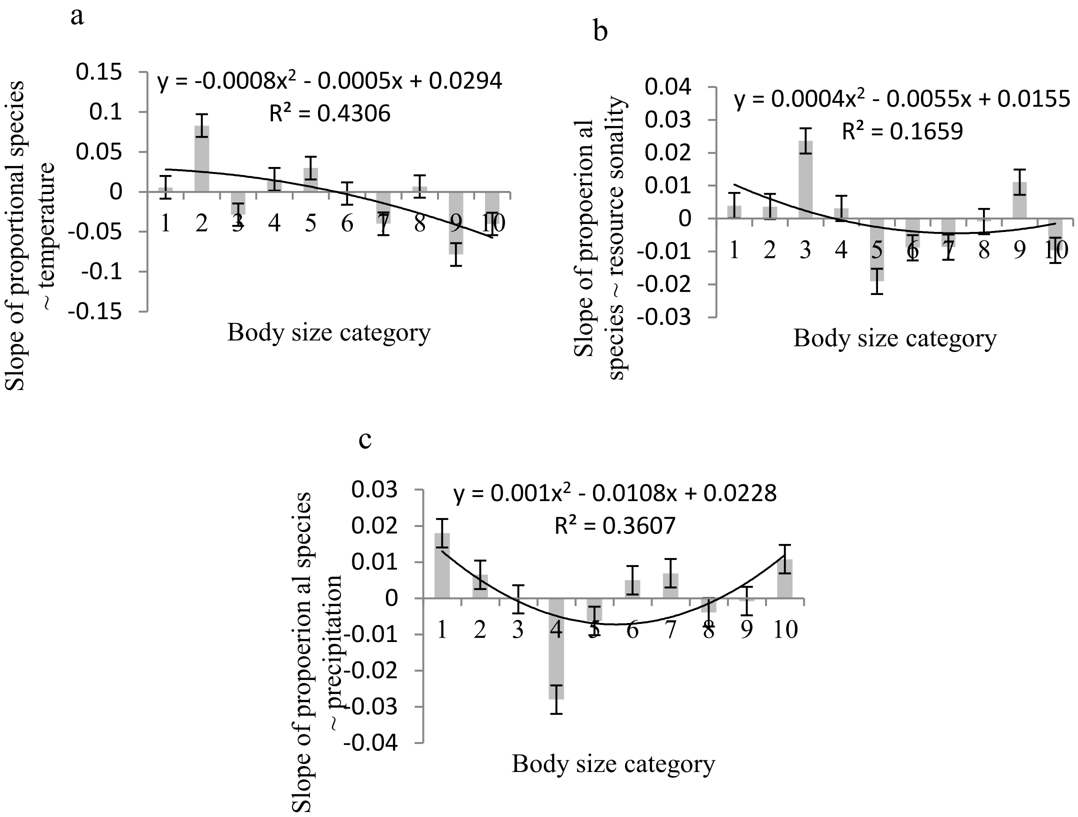


Figure D.3. Slope of proportional species richness (+/- SE) for the various size categories as a function of a) mean annual temperature; b) resource seasonality); c) mean annual precipitation. Slope coefficients were generated from equation 1. Second-degree polynomials were added to depict the general shape of the coefficients.

Equations

Equation D.1. ANCOVA results from equation 1b in methodology. Note that this is will be modified to make it more presentable. Species richness and mean annual precipitation were transformed using a cube-root transformation; resource seasonality was transformed using a square root transformation. Note that temp.mean.K represents mean annual temperature (K), Ucubrt.precmean represents the cube-root of mean annual precipitation (mm), sqrt.max.minus.NPP represents the square root of resource seasonality, SIZE.CAT represents the various size categories treated as a categorical variable.

```
Call: lm(formula = species.plus.5.3power ~ SIZE.CAT + temp.mean.K +
       sqrt.max.minus.min.NPP + U.cubrt.precmean + SIZE.CAT:temp.mean.K +
       SIZE.CAT:U.cubrt.precmean + SIZE.CAT:sqrt.max.minus.min.NPP, data =
       grouped.169.stacked.03, na.action = na.exclude)
                              Value Std. Error   t value  Pr(>|t|)
              (Intercept)  -5.07142   0.26347  -19.24862   0.00000
                SIZE.CAT2  -4.92570   0.37260  -13.21974   0.00000
                SIZE.CAT3   0.61598   0.37260    1.65319   0.09832
                SIZE.CAT4   2.30834   0.37260    6.19519   0.00000
                SIZE.CAT5   3.00283   0.37260    8.05908   0.00000
                SIZE.CAT6   3.60585   0.37260    9.67750   0.00000
                SIZE.CAT7   3.85935   0.37260   10.35784   0.00000
                SIZE.CAT8  -2.25014   0.37260   -6.03899   0.00000
                SIZE.CAT9   2.31455   0.37260    6.21186   0.00000
               SIZE.CAT10   2.95553   0.37260    7.93215   0.00000
              temp.mean.K   0.02224   0.00105   21.21528   0.00000
   sqrt.max.minus.min.NPP   0.00154   0.00044    3.47171   0.00052
         U.cubrt.precmean   0.15786   0.00973   16.21662   0.00000
     SIZE.CAT2temp.mean.K   0.01802   0.00148   12.15558   0.00000
     SIZE.CAT3temp.mean.K  -0.00190   0.00148   -1.27955   0.20073
     SIZE.CAT4temp.mean.K  -0.00838   0.00148   -5.65024   0.00000
     SIZE.CAT5temp.mean.K  -0.01088   0.00148   -7.33630   0.00000
     SIZE.CAT6temp.mean.K  -0.01315   0.00148   -8.86836   0.00000
     SIZE.CAT7temp.mean.K  -0.01249   0.00148   -8.42570   0.00000
     SIZE.CAT8temp.mean.K   0.00805   0.00148    5.42622   0.00000
     SIZE.CAT9temp.mean.K  -0.00644   0.00148   -4.34684   0.00001
    SIZE.CAT10temp.mean.K  -0.00829   0.00148   -5.59212   0.00000
SIZE.CAT2U.cubrt.precmean  -0.07412   0.01377   -5.38381   0.00000
                                     Value Std. Error   t value  Pr(>|t|)
       SIZE.CAT3U.cubrt.precmean  -0.09801   0.01377   -7.11921   0.00000
       SIZE.CAT4U.cubrt.precmean  -0.07698   0.01377   -5.59191   0.00000
       SIZE.CAT5U.cubrt.precmean  -0.15753   0.01377  -11.44226   0.00000
       SIZE.CAT6U.cubrt.precmean  -0.11000   0.01377   -7.99030   0.00000
       SIZE.CAT7U.cubrt.precmean  -0.20077   0.01377  -14.58308   0.00000
       SIZE.CAT8U.cubrt.precmean  -0.07656   0.01377   -5.56089   0.00000
       SIZE.CAT9U.cubrt.precmean  -0.12682   0.01377   -9.21156   0.00000
      SIZE.CAT10U.cubrt.precmean  -0.05404   0.01377   -3.92518   0.00009
 SIZE.CAT2sqrt.max.minus.min.NPP   0.00023   0.00063    0.37197   0.70992
 SIZE.CAT3sqrt.max.minus.min.NPP   0.00199   0.00063    3.18405   0.00146
 SIZE.CAT4sqrt.max.minus.min.NPP   0.00165   0.00063    2.64119   0.00827
```

```
 SIZE.CAT5sqrt.max.minus.min.NPP   0.00375   0.00063    5.98542   0.00000
 SIZE.CAT6sqrt.max.minus.min.NPP   0.00123   0.00063    1.96269   0.04971
 SIZE.CAT7sqrt.max.minus.min.NPP   0.00106   0.00063    1.69319   0.09044
 SIZE.CAT8sqrt.max.minus.min.NPP  -0.00352   0.00063   -5.62608   0.00000
 SIZE.CAT9sqrt.max.minus.min.NPP  -0.00096   0.00063   -1.52852   0.12641
SIZE.CAT10sqrt.max.minus.min.NPP   0.00034   0.00063    0.53841   0.59030
Residual standard error: 0.25456 on 11920 degrees of freedom
Multiple R-Squared: 0.7587
F-statistic: 960.99 on 39 and 11920 degrees of freedom, the p-value is 0
```

Equation D.2. Regression results from equation 1a where the relationship between the slope-coefficients and body size category from Figure 5.4 where treated as linear functions. The same transformations were used from Equation D.1. Note that temp.mean.K represents mean annual temperature (K), Ucubrt.precmean represents the cube-root of mean annual precipitation (mm), sqrt.max.minus.NPP represents the square root of resource seasonality, SIZE.CAT represents the various size categories treated as a continous variable.

```
Call: lm(formula = species.plus.5.3power ~ SIZE.CAT + temp.mean.K +
       sqrt.max.minus.min.NPP + U.cubrt.precmean + SIZE.CAT:temp.mean.K +
       SIZE.CAT:U.cubrt.precmean + SIZE.CAT:sqrt.max.minus.min.NPP, data =
       grouped.169.stacked.03, na.action = na.exclude)
                                    Value Std. Error   t value  Pr(>|t|)
                     (Intercept)  -6.19632   0.27422  -22.59607   0.00000
                        SIZE.CAT   0.41338   0.04419    9.35350   0.00000
                     temp.mean.K   0.02572   0.00109   23.57306   0.00000
          sqrt.max.minus.min.NPP   0.00335   0.00046    7.27790   0.00000
                U.cubrt.precmean   0.09611   0.01013    9.48564   0.00000
            SIZE.CAT:temp.mean.K  -0.00128   0.00018   -7.26465   0.00000
       SIZE.CAT:U.cubrt.precmean  -0.00650   0.00163   -3.97790   0.00007
SIZE.CAT:sqrt.max.minus.min.NPP  -0.00023   0.00007   -3.03385   0.00242
Residual standard error: 0.38784 on 11952 degrees of freedom
Multiple R-Squared: 0.43836
F-statistic: 1332.6 on 7 and 11952 degrees of freedom, the p-value is 0
```

Equation D.3. Regression results from equation 2 where the relationship between the slope-coefficients and body size category from Figure 5.4 where treated as polynomial functions. Note that temp.mean.K represents mean annual temperature (K), Ucubrt.precmean represents the cube-root of mean annual precipitation (mm), sqrt.max.minus.NPP represents the square root of resource seasonality, SIZE.CAT represents the various size categories treated as a continous variable. The same transformations were used from Equation D.1.

```
       *** Linear Model ***
Call: lm(formula = species.plus.5.3power ~ SIZE.CAT + temp.mean.K +
       sqrt.max.minus.min.NPP + U.cubrt.precmean + SIZE.CAT:temp.mean.K +
       SIZE.CAT:U.cubrt.precmean + SIZE.CAT:sqrt.max.minus.min.NPP +
       sqrt.max.minus.min.NPP:SIZE.CAT.sqrd + SIZE.CAT.cub:
       sqrt.max.minus.min.NPP + U.cubrt.precmean:SIZE.CAT.sqrd + temp.mean.K:
       SIZE.CAT.sqrd, data = grouped.169.stacked.03, na.action = na.exclude)
                                        Value Std. Error   t value  Pr(>|t|)
                         (Intercept)  -6.19632   0.19706  -31.44413   0.00000
                            SIZE.CAT   0.41338   0.03176   13.01610   0.00000
                         temp.mean.K   0.02607   0.00079   32.86471   0.00000
              sqrt.max.minus.min.NPP  -0.00321   0.00051   -6.27733   0.00000
                    U.cubrt.precmean   0.23062   0.01231   18.73027   0.00000
                SIZE.CAT:temp.mean.K  -0.00145   0.00014  -10.37564   0.00000
           SIZE.CAT:U.cubrt.precmean  -0.07375   0.00510  -14.45706   0.00000
     SIZE.CAT:sqrt.max.minus.min.NPP   0.00579   0.00022   25.79710   0.00000
sqrt.max.minus.min.NPP:SIZE.CAT.sqrd  -0.00134   0.00003  -43.53221   0.00000
 SIZE.CAT.cub:sqrt.max.minus.min.NPP   0.00008   0.00000   52.64762   0.00000
      U.cubrt.precmean:SIZE.CAT.sqrd   0.00611   0.00045   13.54704   0.00000
           temp.mean.K:SIZE.CAT.sqrd   0.00002   0.00001    2.89927   0.00375
Residual standard error: 0.27871 on 11948 degrees of freedom
Multiple R-Squared: 0.71006
F-statistic: 2660.1 on 11 and 11948 degrees of freedom, the p-value is 0
```

Glossary

Assemblage structure: Characteristics of species assemblages that include, but not limited to the number of species, number of individuals, body mass frequency distribution, or the number of species in size classes

BIC: Bayesian Information Criterion. A measure of the goodness of fit of a statistical model. Models with lower BIC values are preferred.

Body mass frequency distribution (BMFD/TSFD): statistical summaries that characterize the size of species in an assemblage; number of species or individuals in defined size classes.

Environmental variables: typically a set of abiotic variables that include, but not limited to temperature, precipitation, land area, and habitat heterogeneity.

Path Analysis: an extension of multiple regressions that allows one to examine more than one dependent variable at a time and allows for variables to be dependent with respect to some variables and independent with respect to others; allows one to test a specific hypothesis (or competing hypotheses) regarding the causal relationship or statistical dependencies among variables

Species assemblage: a term used to describe the collection of species making up any co-occurring community of organisms in a given habitat or defined area

Species richness: The number of distinct species that occur in a defined area.