

BROAD-SCALE PATTERNS AND DETERMINANTS
OF BETA-DIVERSITY

Meghan Wilde McKnight

A dissertation submitted to the faculty of the University of North Carolina at Chapel Hill in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Curriculum in Ecology.

Chapel Hill
2007

Approved by:

Advisor: Peter S. White

Reader: John Bruno

Reader: Aaron Moody

Reader: Robert K. Peet

Reader: Dean L. Urban

© 2007
Meghan Wilde McKnight
ALL RIGHTS RESERVED

ABSTRACT

MEGHAN WILDE MCKNIGHT: Broad-Scale Patterns and Determinants of Beta-Diversity
(Under the direction of Peter S. White)

Ecologists recognize two components of biodiversity: inventory diversity, the species composition of a single place, and differentiation diversity, more commonly called beta-diversity, which is derived by several different methods from the change in species composition between places. Beta-diversity is determined through a complex array of processes relating to the interaction of species traits and characteristics of the physical landscape over time. Geographic variation in beta-diversity reflects past and present differences in environment, ecological interactions, and biogeographic history, including barriers to dispersal. As beta-diversity quantifies the turnover in species across space, it has important applications to the scaling of diversity, the delineation of biotic regions and conservation planning. Despite the importance of beta-diversity, relatively little is known about diversity's "other component", particularly at broad scales.

In this dissertation, I trace the conceptual evolution of beta-diversity in order to reconcile the different views surrounding it, and examine empirical patterns of terrestrial vertebrate beta-diversity at broad spatial scales in order to gain insight into this important diversity component. I use range data for amphibians, birds, and mammals within the Western Hemisphere to produce the only maps to date of beta-diversity at this scale for multiple classes of terrestrial vertebrates and test for cross-taxon congruence in broad-scale beta-diversity. I also examine the strength and geographic variation of the relationship between beta-diversity and species richness. In a third empirical chapter, I analyze whether beta-diversity of amphibians at a global scale varies systematically across biogeographic realms and biomes.

My results show that vertebrates classes have congruent patterns of beta-diversity across the Western Hemisphere. Further, beta-diversity and richness exhibit disparate patterns for these taxa. I demonstrate, however, that the strength of beta-diversity congruence and the relationship of beta-diversity to species richness vary with spatial extent, geographic location, and between taxa. Amphibian beta-diversity at a global scale also shows complex variation across biogeographic realms and biomes. These findings illustrate the influence of environmental, historical, and taxonomic differences on ecological relationships, and stress the need for stringent tests across multiple taxa and regions.

In memory of
Robert R. Churchill
and
Mingma Norbu Sherpa

ACKNOWLEDGEMENTS

I am grateful to all the members of my committee for their encouragement, confidence, and their help in developing the ideas and methods that underlie this dissertation: John Bruno, Aaron Moody, Bob Peet, Dean Urban, and of course, my advisor Peter White, to whom I am especially indebted. Peter's influence on my work will be obvious to anyone who knows him. Less apparent is that Peter's ability and willingness to play Occam's razor to the complex tangles of ideas and data coming from me, as well as his patient editing, faith in my abilities, and contagious enthusiasm for ecology and conservation have made this set of chapters possible. Dean Urban's incredible knowledge of spatial ecology helped me structure to my own thinking, and spurred me on to tackle big questions. Bob Peet's insight into beta diversity is irreplaceable. His personal observations on the history of beta-diversity and anecdotes of the ecologists pioneering diversity study gave my review chapter a perspective I could not have found elsewhere. I am deeply also grateful to George Powell, whose unfaltering commitment to the conservation of biodiversity has been an inspiration to me; Kevin Gaston, whose work has been a strong influence on my own; and David Olson, whose championing the role of beta-diversity in conservation piqued my interest in this fascinating aspect of diversity.

I thank my co-authors, Peter White, Robert McDonald, John Lamoreux, Bob Ridgely, Wes Sechrest, and Simon Stuart for their invaluable contributions. Robert McDonald was instrumental in developing the algorithm presented in Chapter 3. The insightful comments of several scientists have greatly strengthened the chapters of this dissertation; for their kind help I thank Thomas Brooks, Jack Lennon, Jake Overton, John Terborgh, and an anonymous reviewer (Chapter 3); Kevin Gaston and John Lamoreux (Chapter 4); and John Bruno, Aaron Moody, Bob Peet, Dean Urban, and Peter White

(Chapters 1-6). Dean Urban and Aaron Moody, as well as Jack Weiss of the Curriculum in Ecology, helped me to wade through the muck of statistics used in many of my analyses. I am also grateful to Karen Henry and Denise Kent in the Curriculum in Ecology for their help in administrative matters. The students and faculty of the Curriculum in Ecology and the Plant Ecology Lab provided a stimulating environment in which to learn. In particular, I thank Gabriel Cumming, David Luther, Matthew McKown, and Brooke Wheeler for many stimulating discussions, and also for the moral support and laughter which have sustained me during my graduate studies.

Without the hard work of the many people involved in producing the datasets I used, and who generously made them publicly accessible, the analyses presented in this dissertation would not have been possible. I thank Gerardo Ceballos, Bruce Patterson, Robert Ridgely, Wes Sechrest, Marcelo Tognelli, James Zook, The Nature Conservancy, Conservation International, World Wildlife Fund, and Environment Canada—WILDSPACE for contributions to the compilation of bird and mammal range maps; the Global Amphibian Assessment, IUCN, Conservation International, and NatureServe for developing the amphibian data; and the World Wildlife Fund for developing the Terrestrial Ecoregions of the World GIS data.

I thank the National Science Foundation Graduate Research Fellowship Program, the W.C. Coker Family, the Alma Holland Beers Family, the North Carolina Botanical Garden, and the Graduate School and Curriculum in Ecology at the University of North Carolina at Chapel Hill for the financial support that enabled me to complete my work.

I have been fortunate throughout my education to have had teachers who encouraged learning beyond any standards set by some outside authority and more importantly, who pushed me to always reach further. I wish to express my gratitude to the exceptional teachers who have had a lasting impact on my life: Evelyn McKinnon (Madison Elementary), Sallie Sheldon (Middlebury College), Gerard Courtin (Laurentian University), Dean Urban (Duke University), and Bob Peet and Peter White (UNC Chapel Hill). I have dedicated this dissertation to the memories of two remarkable men

who were my mentors for many years: Bob Churchill (1946 – 2004), Professor of Geography at Middlebury College, who introduced me to the world of GIS and geography, and Mingma Norbu Sherpa (1955 – 2007) of the World Wildlife Fund, who devoted his life to biodiversity conservation of in his own country of Nepal and throughout South Asia.

My family have provided me much support during my graduate studies, as they have throughout my life and for this I am truly grateful to all of them. Though they may not realize it, my parents, Marcy and Scott McKnight, through their creativity and ingenuity have imparted to me tools invaluable to my work. I owe my spatial thinking and ability to work independently to them and to the mountainous landscape of the Granite State in which they raised me. I would especially like to thank my grandfather, William Seymour, for his interest in knowing what it actually is that I study.

Finally, I could not have complete this dissertation without the unwavering support and encouragement of John Lamoreux, who kept me on my feet innumerable times when I was sure I could no longer stand, picked up the pieces whenever things fell apart, and who never for a moment doubted I could do it.

TABLE OF CONTENTS

LIST OF TABLES	xi
LIST OF FIGURES	xii
Chapter	
1. INTRODUCTION AND OUTLINE OF RESEARCH	1
Introduction	1
Outline of Research	5
Description of Data	7
References	10
2. THE OTHER DIVERSITY: THE PAST, PRESENT, AND FUTURE OF DIFFERENTIATION DIVERSITY	14
Abstract	14
Introduction	14
The Evolution of a Concept (and the Confusion that Followed)	15
Whither to?	29
The Two Components of Diversity	33
References	35
3. PUTTING BETA-DIVERSITY ON THE MAP: BROAD-SCALE CONGRUENCE AND COINCIDENCE IN THE EXTREMES	43
Abstract	43
Introduction	44
Results and Discussion	47
Materials and Methods	52

References	58
4. WHAT DO RICHNESS PATTERNS MISS? THE RELATIONSHIP BETWEEN BROAD-SCALE BETA-DIVERSITY AND SPECIES RICHNESS.....	75
Abstract	75
Introduction	76
Materials and Methods	77
Results	79
Discussion	83
References	87
5. GLOBAL VARIATION IN AMPHIBIAN BETA-DIVERSITY	95
Abstract	95
Introduction	96
Methods and Materials	99
Results	104
Discussion	115
References	123
6. CONCLUSIONS: DIVERSITY’S “OTHER COMPONENT”	140
Generalities in Broad-Scale Beta-Diversity	142
Variations in Broad-Scale Beta-Diversity	143
Future Research.....	145
References	148

LIST OF TABLES

Table

3.1. Correlations between beta-diversity ($\beta_{\text{sim-d}}$) and two environmental variables (elevation and number of biome edges within grid cells).	63
3.2. Mean elevation and mean number of biome edges for sets of the highest 2.5% and lowest 2.5% of beta-diversity ($\beta_{\text{sim-d}}$) grid cells.....	64
3.3. Correlations in beta-diversity ($\beta_{\text{sim-d}}$) within the Western Hemisphere, Nearctic realm, and Neotropical realm.....	65
3.4. Correlations in average nearest-neighbor beta-diversity (β_{sim}) within the Western Hemisphere, Nearctic realm, and Neotropical realm	66
5.1. Area, topographic complexity, average species richness for overall biomes, overall biogeographic realms, and the nineteen unique biome/biogeographic realm regions	126
5.2. Coefficients from distance decay regressions for overall biomes, overall biogeographic realms, and the nineteen unique biome/biogeographic realm regressions	127
5.3. Effect of similarity coefficient choice on observed variation in beta-diversity	128
5.4. Bootstrapped 90% confidence intervals for distance decay regression parameters	129

LIST OF FIGURES

Figure

2.1. The number of papers related to differentiation diversity from the years 1960-2000	41
2.2. The relationship between the <i>alpha</i> (α) and <i>beta</i> (β) components of diversity at multiple scales.	42
3.1. Beta-diversity ($\beta_{\text{sim-d}}$) of amphibians, birds, and mammals mapped continuously across the continental Western Hemisphere	67
3.2. Scatterplots showing relationships between beta-diversity ($\beta_{\text{sim-d}}$) and two environmental variables (elevation and number of biome edges within grid cells)	68
3.3. Relationships between beta-diversity ($\beta_{\text{sim-d}}$) of amphibians, birds, and mammals	69
3.4. Geographic variation in beta-diversity ($\beta_{\text{sim-d}}$) congruence of amphibians, birds, and mammals at small spatial extents	70
3.5. Geographic distribution of overlap in amphibian, bird, and mammal high and low beta-diversity ($\beta_{\text{sim-d}}$) areas	71
3.6. Levels of beta-diversity ($\beta_{\text{sim-d}}$) for vertebrate taxa within areas of high and low beta-diversity of amphibians, birds, and mammals	72
3.7. Bird beta-diversity ($\beta_{\text{sim-d}}$) based on both breeding and non-breeding ranges	73
3.8. Average nearest-neighbor beta-diversity of amphibians, birds, and mammals mapped continuously across the continental Western Hemisphere	74
4.1. Spatial coincidence in areas of highest and lowest beta-diversity (β_{sim}) and richness in the Western Hemisphere	89
4.2. Spatial coincidence in areas of highest and lowest beta-diversity (β_{sim}) and richness in the Nearctic Realm	90
4.3. Spatial coincidence in areas of highest and lowest beta-diversity (β_{sim}) and richness in the Neotropical Realm	91
4.4. Contrasting levels of diversity components within areas of highest and lowest beta-diversity (β_{sim}) and richness in the Western Hemisphere.	92
4.5. Contrasting levels of diversity components within areas of highest and lowest beta-diversity (β_{sim}) and richness in the Nearctic realm	93
4.6. Contrasting levels of diversity components within areas of highest and lowest beta-diversity (β_{sim}) and richness in the Neotropical realm	94

5.1. Distance decay regression parameters.....	130
5.2. The nineteen unique biome/biogeographic realm regions.....	131
5.3. Schematic representation of the four comparison categories used to group the results from the distance decay regressions	132
5.4. Rank order of regions within each of the four comparison categories for initial similarity levels and for distance decay rates based on S_{jac} and S_{sim}	133
5.5. Regression coefficients from distance decay regressions for overall biomes and biogeographic realms	134
5.6. Distance decay relationships for overall biomes and biogeographic realms.....	135
5.7. Regression coefficients from distance decay regressions for biomes within each of the six biogeographic realms	136
5.8. Distance decay relationships for biomes within each of the six biogeographic realms	137
5.9. Regression coefficients from distance decay regressions of each of the five biomes within the biogeographic realms in which it occurs	138
5.10. Distance decay relationships for each of the five biomes within the biogeographic realms in which it occurs.	139

CHAPTER 1

Introduction and Outline of Research

Introduction

Ecologists recognize two distinct components of diversity: inventory diversity, the species composition of a single place, and differentiation diversity, more commonly called beta-diversity or species turnover, the change in species composition between places (Whittaker 1977). Beta-diversity is central to many ecological and evolutionary topics, such as the scaling of diversity (Pimm & Gittleman 1992; Blackburn & Gaston 1996; Lennon *et al.* 2001), the delineation of biotic regions or biotic transitions (Williams 1996; Williams *et al.* 1999), and the mechanisms through which regional biotas are formed (Moritz *et al.* 2001; van Rensburg *et al.* 2004; Graham *et al.* 2006). As threats to biodiversity increase, understanding the differentiation component of diversity has new urgency. Conservation strives to preserve all species but, constrained by limited resources and the needs and demands of human societies, it becomes a process of selection of the highest priority areas. Conservation areas essentially sample the Earth's biota, thus care must be taken to their placement. Because beta-diversity quantifies the turnover in species across space, it informs how conservation networks should be configured in order to represent species most efficiently (Pimm & Gittleman 1992; Pressey *et al.* 1993; Margules & Pressey 2000; Groves 2003; Sarkar 2006). For instance, protected areas in regions of high beta-diversity must either be sufficiently large to encompass gradients of species turnover or be within close proximity to other protected areas in order to capture the change in species composition (Nekola & White 2002; Groves 2003; Wiersma & Urban 2005).

Furthermore, because areas of high turnover often have steep environmental gradients or dispersal barriers they are also likely to be sensitive to global change.

Beta-diversity, like species richness, is a manifestation of the spatial distributions of species and consequently is influenced by those ecological processes determining species' ranges, including niche differentiation, competition, and dispersal, as well as the spatial characteristics of the physical environment over which those processes occur, and the history of the biota associated with that region (Nekola & White 1999). Although some of the same processes determine both beta-diversity and species richness, the factors which allow for the co-occurrence of many species in a single location will not necessarily result in high species turnover between that location and another.

Research efforts have not been balanced between diversity's two components; beta-diversity has, until recently, taken a role secondary to species richness (Pimm & Gittleman 1992; Koleff *et al.* 2003a). Fortunately, the last decade has seen a dramatic increase in the number of studies relating to diversity's differentiation component (see Chapter 2). There is much to catch up on. Beta-diversity is a poorly understood phenomenon and we know little about many essential aspects of its nature, particularly at broad spatial scales. My dissertation seeks to improve our understanding of beta-diversity, through three inter-related themes: *What?*, *Where?*, and *Why?* I define these themes in the following paragraphs, after which I describe how they are organized within the chapters of this thesis.

What Is the Differentiation Component of Diversity?

While ecologists generally agree that the differentiation component of diversity describes the change in species composition across space, they do not all agree on the specifics of the concept, or whether the term actually encompasses multiple concepts (Koleff *et al.* 2003a; Vellend 2001; Whittaker *et al.* 2001). This may be in part because ecologists studying species compositional change come from various fields (such as community ecology, macroecology, biogeography, and conservation biology) and from different taxonomic backgrounds. The flow of ideas between fields can at times be limited, which results in variations and divergence in the way the concept of differentiation diversity is thought about and used. There are also discrepancies in approaches within

a single field. The jumble of terminology, concepts, and measurements complicates the understanding of differentiation diversity. At best, the current situation impedes objective comparison and synthesis across studies. At worst, it may actually preclude any comprehensive understanding and generalizations of this important aspect of diversity. The disagreements relate to several issues:

Terminology:

Are beta-diversity, species turnover, between-habitat diversity, and differentiation diversity essentially the same concept or do these terms embody useful differences in meaning?

Scale:

Can the same concept describe the change in species composition observed at different scales, for example, change across a mountainside versus change across a continent?

Dimension:

Are structured change (i.e., turnover along specified gradients of environment or distance) and unstructured change (i.e., the level of the heterogeneity of an entire area) different aspects of a single concept or separate phenomena?

Measurement:

Do both rates of change and static numbers derived from the inventory diversities at two scales quantify the differentiation component of diversity?

Determinants:

Can change due to environmental/niche differences be considered distinct from change due to dispersal limitation and isolation? If so, should they be regarded as separate components of diversity?

Where Is Diversity's Differentiation Component High or Low?

Physical attributes such as steep gradients, topographic complexity, and variation in geologic and environmental history, and species traits such as poor vagility, narrow environmental tolerances and small range size are often associated with high beta-diversity. These associations are often taken as generalities, however, there is little quantitative information on variation in beta-diversity among places or taxa (but see Cody 1986; Harrison *et al.* 1992; Nekola & White 1999; Qian *et al.* 2005). Beta-diversity has been more intensively studied at smaller spatial scales than at larger scales. The paucity of broad-scale studies and comparisons across multiple regions or taxa, coupled with the difficulties in synthesizing across existing studies, has resulted in a lack of tested generalities

regarding broad-scale patterns of beta-diversity and a quantitative map of broad-scale patterns is yet to exist.

There is no better example of the need for more comprehensive study than the latitudinal pattern of beta-diversity, the most studied of broad-scale patterns. Conventional ecological wisdom often holds that the high levels of species richness in the tropics compared to temperate regions is due to higher species turnover, or at least is enhanced by species turnover. While many studies have found that beta-diversity decreases with increasing latitude, others have found the opposite trend or no correlation at all (see Koleff *et al.* 2003b for a review). Differences in taxa studied, location (biogeographic realm), and scale (both grain and extent), as well as variation in methods make it difficult to discern whether there is a general relationship between latitude and beta-diversity (Koleff *et al.* 2003b). The latitudinal pattern of beta-diversity is only one of many patterns in need of attention. In my dissertation I address the following questions relating to potential generalities for beta-diversity pattern: Where is vertebrate beta-diversity high and low? Are areas of high or low beta-diversity concentrated in certain biogeographic realms or biomes? Do taxa exhibit similar overall patterns? Where are these patterns alike and where are they different?

Why Does Diversity's Differentiation Component Occur?

Process is inextricably linked to pattern. As noted above, there are certain species traits and landscape characteristics that are often associated with high beta-diversity. Based on these observations, many ecologists distinguish between two principle causes of species turnover: environmental dissimilarity and geographic distance (Cody 1986; Harrison *et al.* 1992; Simmons & Cowling 1996; Nekola & White 1999). Turnover along environmental gradients is a function of differences among habitats and is largely explained by the competitive sorting of species (Cody 1993; Nekola & White 2002). Dissimilarity of species composition within a habitat type over a geographic distance is explained largely by biogeographic history and dispersal capability (Cody 1993; Nekola & White 2002). Both are influenced by temporal variance in site attributes, species traits linked to specialization, and evolutionary time. Assessing the relative contributions of environment and

distance to turnover is difficult (Cody 1993; Nekola & White 1999), but it has received increasing attention in recent years (e.g., Cody 1986, 1993; Cowling *et al.* 1992; Simmons & Cowling 1996; Nekola & White 1999; Balvanera *et al.* 2002; Condit *et al.* 2002; Duivenvoorden *et al.* 2002, Urban *et al.* 2002; Tuomisto *et al.* 2003; Qian *et al.* 2005).

Most analyses of the determinants of beta-diversity have been conducted at relatively fine grains across small to medium geographic extents and have focused on a single locality (but see Cody 1986; Qian *et al.* 2005). There have been far fewer broad-scale analyses, though that number is increasing as more ecologists begin to explore the nature of beta-diversity. Our current understanding of determinants of beta-diversity mirrors that of pattern – we have little concrete evidence for generalizations about the factors influencing changes in species composition across large scales. Questions regarding the determinants of beta-diversity can only be answered once there is knowledge of broad-scale patterns. Therefore, my analyses of processes represent first approximations based on the patterns I found. For instance, is beta-diversity higher in species-rich areas than in areas with fewer species? Is there greater environmental complexity in regions of rapid species turnover than those where species assemblages are more homogenous? Does the level of beta-diversity exhibited by a taxon vary among regions of differing environments (e.g., is beta-diversity within tropical areas higher than within temperate areas) or between regions with distinct biogeographic histories (e.g., do areas that have undergone extensive glacial cycles and inter-glacial migrations show lower beta-diversity than areas which have experienced greater climatic stability)?

Outline of Research

My thesis explores both the concept of beta-diversity and patterns of this important diversity component at broad spatial scales. I focus on the first theme, *What?* in Chapter 2 by reviewing and synthesizing the existing literature. I examine the second and third themes, *Where?* and *Why?* with empirical data in Chapters 3-5, using the first taxonomically complete distributional data available across large extents for three terrestrial vertebrate classes. The taxonomic scope of these data allow me to compare, for the first time, the beta-diversity patterns of three major taxa at broad scales. The

extent of analysis varies both within and between the chapters, but the grain size (100 km X 100 km) is constant. Beta-diversity at this grain size describes changes in species pools and regional biotic transitions (Williams *et al.* 1999).

In Chapter 2, I trace the history of beta-diversity in order to determine the origins of the various interpretations and uses of the term beta-diversity, and as a means to reconcile alternative definitions.

In Chapter 3, I present the first analysis of cross-taxon congruence in broad-scale beta-diversity, based on the distributions for amphibians, birds, and mammals in the Western Hemisphere. In doing so, I produce the only maps to date of beta-diversity at this scale for multiple classes of terrestrial vertebrates. I test congruence in overall beta-diversity patterns and evaluate whether congruence levels are consistent across multiple spatial extents and among different geographic locations. I further measure the spatial coincidence in areas of highest and lowest beta-diversity between the three groups and test whether the high and low beta-diversity areas differ in elevation range and biome complexity.

In Chapter 4, I investigate the relationship between beta-diversity and species richness. The scope of this study, both in terms of geographic extent and number of taxa, exceeds that of any previous analysis of the relationship between the two diversity components. I examine this relationship for amphibians, birds, and mammals within the Western Hemisphere. I then determine whether the relationships observed for each taxa vary between the Nearctic and Neotropical biogeographic realms.

In Chapter 5, I provide a unique perspective on global patterns of beta-diversity. I test whether beta-diversity varies systematically by biome or biogeographic realm. Using biomes as coarse surrogates for distinct environments and biogeographic realms as surrogates for unique biogeographic histories, I examine whether a particular environment exhibits a similar level of beta-diversity regardless of differences in biogeographic history. These analyses are restricted to amphibian beta-diversity patterns to allow for the global extent of analysis.

In Chapter 6, I synthesize my findings across these chapters and make recommendations for future research directions.

Description of Data

The analyses in Chapters 3-5 use two types of data compiled across 100 km x 100 km grid cells: species lists, derived from range maps for three terrestrial vertebrate classes, and site attributes, obtained from a global hierarchical ecological and biogeographic classification of terrestrial ecoregions and digital elevation models. These data were chosen because they are freely available and they have been used in many high-profile studies (Rodrigues *et al.* 2004; Ceballos *et al.* 2005; Orme *et al.* 2005; Ceballos & Ehrlich 2006; Grenyer *et al.* 2006; Orme *et al.* 2006). There are few biodiversity datasets that could be subject to the level of scrutiny these data have faced, and to date there has been no criticism of them published.

Species Distributional Data

Digital range maps representing the global distributions of 5,817 amphibian species (IUCN *et al.* 2004), and the Western Hemisphere distributions of 3,882 breeding bird species (Ridgely *et al.* 2005), and 1,611 mammal species (Patterson *et al.* 2005) compose the data analyzed in these chapters. The bird and mammal data were compiled by a consortium of conservation organizations led by NatureServe to provide conservation planners a digital library of bird and mammal distributions. These maps were produced using published sources representing thousands of individual references and field observations and were corrected based on expert review (see www.natureserve.org for a complete description of data compilation, review process, and a full list of sources). The amphibian data were a product of the Global Amphibian Assessment (GAA), a global baseline database of amphibian distributions, abundances, population trends, threats, and conservation status developed by IUCN-The World Conservation Union, Conservation International, and NatureServe. The GAA data were compiled and peer reviewed through a collaborative process involving over 520 herpetologists and 13 expert workshops from 2001-2004 (see www.globalamphibians.org for more detailed information and sources).

The sources used to develop the digital range data depicted a species' extent of occurrence based on observational data. These extent of occurrence maps follow the standard IUCN approach of being

minimum convex polygons encompassing collection localities or confirmed sightings. They “predict” species' ranges only in so far as they interpolate between known points (disregarding grossly unsuitable habitat); they do not extrapolate or model beyond these points in an effort to represent probable range (IUCN 2006). In practice, this means that a cloud forest species known only from a narrow altitudinal band across several mountains is mapped only for those mountains within that band of elevation, thus valleys and peaks in between are excluded. Note that the cloud forest itself is not mapped for the species, but rather the range of known points. This minimizes concerns about data circularity that often arise when groups of species are mapped based on presumed habitat affiliations, which in turn are tested against species' ranges.

The presence/absence of each species was recorded in 100 km x 100 km equal area grid cells, roughly equivalent to 1° x 1° at the equator (Behrmann projection, WGS84 datum). A species was considered present if any portion of its range (exclusive of polygons coded as introduced, migratory, or vagrant) occurred within the continental land area of the grid cell. Because all locations with the boundaries of the mapped ranges were recorded as “presences”, false presences are more likely to occur than false absences, thus an underestimation of compositional change is more probable than an overestimation. Such an effect, as well as effects due to potential inaccuracies of the range maps, are minimized by the large grain size I have chosen for my analyses.

These data allowed me to conduct an examination of whether broad generalities in beta-diversity exist across multiple taxa. Although these groups are all vertebrates and each has internal variation in life history characteristics, they nonetheless differ in interesting ways that may influence beta-diversity patterns, such as broad environmental tolerances, seasonal migration patterns, vagility, thermal-regulatory systems, body size and range size distributions, speciation patterns, and responses to glaciation.

Site Attributes

The biogeographic realm and biome delineation from Olson *et al.* (2001) “Terrestrial Ecoregions of the World” were used as a coarse surrogate for areas with unique biogeographic histories and

regions of distinct environments. Each grid cell was assigned to the realm and biome covering the majority of the cell (see individual chapters for assignment rules). The area of each biome found within a grid cell was also recorded.

The biogeographic realm delineation of Olson *et al.* (2001) follows Udvardy (1975) and Pielou (1979), adjusted to match ecoregion boundaries. These eight realms (Antarctic, Afrotropic, Australasia, Indomalaya, Nearctic, Neotropic, Oceania, and Palearctic), roughly continental in scale, represent regions with distinct geologic histories (e.g., tectonic movement and degree and duration of isolation from, and connection with, other regions) in which the biota have experienced largely separate evolutionary histories from other regions and have developed distinctive characteristics (e.g., radiations or degree of endemism). The biomes of Olson *et al.* (2001) describe areas of the world having similar environmental conditions, habitat structure, and ecological dynamics, and were defined primarily on the basis of broad vegetation types (e.g., UNESCO 1969; deLaubenfels 1975; Schmidhüsen 1976). The 14 biomes thus reflect large-scale environmental patterns (e.g., warm-cold, wet-dry): Tropical and Subtropical Moist Broadleaf Forests; Tropical and Subtropical Dry Broadleaf Forests; Tropical and Subtropical Coniferous Forests; Temperate Broadleaf and Mixed Forests, Temperate Conifer Forests; Boreal Forests; Tropical and Subtropical Moist Savannas and Grasslands; Temperate Savannas and Grasslands; Flooded Savannas and Grasslands; Montane Grasslands and Shrublands; Tundra; Mediterranean Forests, Woodlands, and Scrub; Deserts and Xeric Scrub; and Mangroves.

To provide an index of differences in environmental heterogeneity among grid cells, mean grid cell elevation and the range and standard deviation of elevation found within each grid cell were computed using a digital elevation model (DEM) of approximately 1 km X 1 km resolution (The Global 30 Arc Second Elevation Data Set, <http://www1.gsi.go.jp/geowww/globalmap-gsi/gtopo30/gtopo30.html>).

References

- Balvanera, P., Lott, E., Segura, G., Siebe, C. & Islas, A. (2002) Patterns of beta-diversity in a Mexican tropical dry forest. *Journal of Vegetation Science* 13, 145-158.
- Blackburn, T.M. & Gaston, K.J. (1996) The distribution of bird species in the New World: patterns in species turnover. *Oikos* 77, 146-152.
- Ceballos, G., Ehrlich, P.R., Soberon, J., Salazar, I. & Fay, J.P. (2005) Global mammal conservation: What must we manage? *Science* 309, 603-607.
- Ceballos, G. & Ehrlich, P.R. (2006) Global mammal distributions, biodiversity hotspots, and conservation. *Proceedings of the National Academy of Sciences, USA* 103, 19374-19379.
- Cody, M.L. (1986) Diversity, rarity, and conservation in Mediterranean-climate ecosystems. *Conservation biology: the science of scarcity and diversity* (ed. by M.E. Soulé), pp. 122-152. Sinauer Associates, Sunderland, MA.
- Cody, M.L. (1993) Bird diversity components within and between habitats in Australia. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 147-158. University of Chicago Press, Chicago, IL.
- Condit, R., Pitman, N., Leigh, E.G. Jr., Chave, J., Terborgh, J., Foster, R.B., Núñez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. & Hubbell, S.P. (2002) Beta-diversity in tropical forest trees. *Science* 295, 666-669.
- Cowling, R.M., Holmes, P.M. & Rebelo, A.G. (1992) Plant diversity and endemism. *The ecology of the fynbos: nutrients, fire and diversity* (ed. by R.M. Cowling), pp. 62-112. Oxford University Press, Cape Town.
- deLaubenfels, D.J. (1975) *Mapping the world's vegetation: regionalization of formations and flora*. Syracuse University Press, Syracuse, NY.
- Duivenvoorden, J.F., Svenning, J.C. & Wright, S.J. (2002) Beta diversity in tropical forests. *Science* 295, 636-637.
- Graham, C.H., Moritz, C. & Williams, S.E. (2006) Habitat history improves prediction of biodiversity in rainforest fauna. *Proceedings of the National Academy of Sciences, USA* 103, 632-636.
- Grenyer, R., Orme, C.D.L., Jackson, S.F., Thomas, G.H., Davies, R.G., Davies, T.J., Jones, K.E., Olson, V.A., Ridgely, R.S., Rasmussen, P.C., Ding, T.S., Bennett, P.M., Blackburn, T.M., Gaston, K.J., Gittleman, J.L. & Owens, I.P.F. (2006) Global distribution and conservation of rare and threatened vertebrates. *Nature* 444, 93-96.
- Groves, C.R. (2003) *Drafting a conservation blueprint*. Island Press, Washington, D.C.
- Harrison, S., Ross, S.J. & Lawton, J.H. (1992) Beta-diversity on geographic gradients in Britain. *Journal of Animal Ecology* 61, 151-158.
- IUCN (Standards and Petitions Working Group) (2006) *Guidelines for using the IUCN Red List categories and criteria. Version 6.2*. Prepared by the Standards and Petitions Working Group of

- the IUCN SSC Biodiversity Assessments Sub-Committee in December 2006. IUCN, Cambridge, UK.
- IUCN, Conservation International & NatureServe (2004) *Global amphibian assessment*. IUCN/Conservation International/NatureServe, Washington, D.C. and Arlington, VA.
- Koleff, P., Gaston, K.J. & Lennon, J.J. (2003a) Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* 72, 367-382.
- Koleff, P., Lennon, J.J. & Gaston, K.J. (2003b) Are there latitudinal gradients in species turnover? *Global Ecology and Biogeography* 12, 483-498.
- Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70, 966-979.
- Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature* 405, 243-253.
- Moritz, C., Richardson, K.S., Ferrier, S., Monteith, G.B., Stanisci, J., Williams, S.E. & Whiffin, T. (2001) Biogeographical concordance and efficiency of taxon indicators for establishing conservation priority in a tropical rainforest biota. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268, 1875-1881.
- Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* 26, 867-878.
- Nekola, J.C. & White, P.S. (2002) Conservation, the two pillars of ecological explanation, and the paradigm of distance. *Natural Areas Journal* 22, 305-310.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* 51, 933-938.
- Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J. & Owens, I.P.F. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436, 1016-1019.
- Orme, C.D.L., Davies, R.G., Olson, V.A., Thomas, G.H., Ding, T-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Owens, I.P.F., Blackburn, T.M. & Gaston, K.J. (2006) Global patterns of geographic range size in birds. *Public Library of Science, Biology* 4, 1276-1283.
- Patterson, B.D., Ceballos, G., Sechrest, W., Tognelli, M.F., Brooks, T., Luna, L., Ortega, P., Salazar, I. & Young, B.E. (2005) *Digital distribution maps of the mammals of the Western Hemisphere*. NatureServe, Arlington, VA.
- Pielou, E.C. (1979) *Biogeography*. John Wiley and Sons, New York, NY.
- Pimm, S.L. & Gittleman, J.L. (1992) Biological diversity – Where is it? *Science* 255, 940.

- Pressey, R.L., Humphries, C.J., Margules, C.R., Vane-Wright, R.I. & Williams, P.H. (1993) Beyond opportunism: key principles for systematic reserve selection. *Trends in Ecology and Evolution* 8, 124-128.
- Qian, H., Ricklefs, R.E. & White, P.S. (2005) Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters* 8, 15-22.
- Ridgely, R.S., Allnutt, T.F., Brooks, T., McNicol, D.K., Mehlman, D.W., Young, B.E. & Zook, J.R. (2005) *Digital distribution maps of the birds of the Western Hemisphere*. NatureServe, Arlington, VA.
- Rodrigues, A.S.L., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D.C., da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J. & Yan, X. (2004) Effectiveness of the global protected area network in representing species diversity. *Nature*, 428, 640-643.
- Sarkar, S. (2006) Ecological diversity and biodiversity as concepts for conservation planning: comments on Ricotta. *Acta Biotheoretica* 54, 133-140.
- Schmidthüsen, J. (1976) *Atlas zur biogeographie*. Bibliographisches Institut, Mannheim, Germany.
- Simmons, M.T. & Cowling, R.M. (1996) Why is the Cape Peninsula so rich in plant species? An analysis of the independent diversity components. *Biodiversity and Conservation* 5, 551-573.
- Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003) Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299, 241-244.
- Udvardy, M.D.F. (1975) *A classification of the biogeographical provinces of the world*. International Union of Conservation of Nature and Natural Resources, Morges, Switzerland, IUCN Occasional Paper no. 18.
- [UNESCO] United Nations Educational, Scientific and Cultural Organization (1969) *A framework for a classification of world vegetation*. UNESCO, Paris, UNESCO SC/WS/269.
- Urban, D., Goslee, S., Pierce, K. & Lookingbill, T. (2002) Extending community ecology to landscapes. *Ecoscience* 9, 200-212.
- van Rensburg, B.J., Koleff, P., Gaston, K.J. & Chown, S.L. (2004) Spatial congruence of ecological transition at the regional scale in South Africa. *Journal of Biogeography* 31, 843-854.
- Vellend, M. (2001) Do commonly used indices of β -diversity measure species turnover? *Journal of Vegetation Science* 12, 545-552.
- Whittaker, R.H. (1977) Evolution of species diversity in land communities. *Evolutionary Biology* 10, 1-67.
- Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* 28, 453-470.

- Wiersma, Y.E. & Urban, D.L. (2005) Beta diversity and nature reserve system design in the Yukon, Canada. *Conservation Biology* 19, 1262-1272.
- Williams, P.H. (1996) Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. *Proceedings of the Royal Society of London Series B-Biological Sciences* 263, 579-588.
- Williams, P.H., de Klerk, H.M. & Crowe, T.M. (1999) Interpreting biogeographical boundaries among Afrotropical birds: Spatial patterns in richness gradients and species replacement. *Journal of Biogeography* 26, 459-474.

CHAPTER 2

The Other Diversity: The Past, Present, and Future of Differentiation Diversity

Abstract

I trace the conceptual history of beta-diversity from its origins in community ecology to its many applications today. I show the historical development of a differentiation component of diversity, and argue it represents a single phenomenon of species compositional change, regardless of scale or mechanism. I demonstrate that this unifying concept ties together the various divisions previous authors have made. I recommended beta-diversity continue to be applied to this phenomenon, because of its widespread use and historic roots. I then show that there are two fundamentally different ways to quantify beta-diversity, each with several alternative mathematical formulations.

Introduction

When Robert Whittaker coined the term *beta-diversity* in 1960 to describe the differentiation component of diversity, he couldn't have imagined the myriad terms and approaches that have since developed for this concept. Although differentiation diversity has received less attention than the inventory diversity, in the past decade and a half the number of studies has increased dramatically. These studies use numerous terms to describe differentiation diversity, including beta-diversity, between-habitat diversity, and species turnover. Unfortunately, the nomenclature of differentiation diversity is not straightforward. Often different authors apply the same term to disparate ideas or, conversely, describe the same idea using different terms. Moreover, there is disagreement as to whether there are multiple concepts of differentiation diversity. The confusion produced by the

number of terms and measures complicates comparisons and generalizations among studies (Vellend 2001; Koleff *et al.* 2003a).

In this review I trace the evolution of differentiation diversity to explore the origins of these problems and provide a means to reconcile the terminology and interpretations of diversity's differentiation component. I will focus this review on the conceptual issues embedded within differentiation diversity, reviewing mathematical expressions only in terms of the conceptual issues (for a full treatment of alternative mathematical expressions, see Wilson & Shmida 1984; Koleff *et al.* 2003a). Although many of the terms and measures of differentiation diversity can be applied to compositional change over both space and time, I limit this review to differentiation diversity as applied to spatial change. In addition, for reasons of clarity, I use the term *differentiation diversity* to refer to the general phenomenon of change in species composition across space, in order to reserve the term *beta-diversity* for certain measures that describe the phenomenon.

The Evolution of a Concept (and the Confusion that Followed)

“It seems typical of diversity measurement that one phrase will not do if half a dozen can suffice!” – Anne Magurran (1988, pg. 35)

Short histories of differentiation diversity have previously been presented but have failed to give complete accounts of the origins and relationships of the tangle of terms and concepts applied to the differentiation or turnover component of diversity (Vellend 2001; Veech *et al.* 2002). My review focuses on the first two decades of differentiation diversity study because this period shows the origin of the multiple definitions and approaches subsequently used.

1960-1970

Although the concept of community differentiation, often approached through similarity measures, was well established in ecology prior to 1960, Whittaker was the first to phrase differentiation as a measure of species diversity (Whittaker 1956, 1960). Whittaker first defined *beta-diversity* as the “extent of change of community composition, or degree of community differentiation, in relation to a complex-gradient of environment, or a pattern of environments” (Whittaker 1960, pg.

320). *Beta-diversity* (β) was one of “three aspects, or levels” of species diversity; the other two being as *alpha-diversity* (α), the diversity at a sample point, and *gamma-diversity* (γ), the diversity of a number of samples combined and a “resultant” of both *alpha-diversity* and *beta-diversity* of the samples (Whittaker 1960, pg. 320). *Gamma-diversity*, as originally defined, therefore represents pooled samples as opposed to an estimate of total diversity a larger grain size.

Whittaker (1960) provided two measures for *beta-diversity*. The “simplest measurement” was defined as $\beta = \gamma / \bar{\alpha}$, specifying *gamma* as “resulting from a number of individual samples from a community pattern or coenocline” (Whittaker 1960, pg. 321). The second approach, to be used when “a particular gradient is in question,” was based on his earlier (1956) measure of ‘half-changes’ (Whittaker 1960, pg. 321). He defined ‘half-changes’ as “the distance along an environmental gradient necessary to reduce sample similarity to one-half that of the zero distance” (Whittaker 1960, pg. 322) and was calculated as $\beta = (\log a - \log z) / \log 2$, where a is the sample similarity for samples of 0 distance and z is the similarity between the first and last samples as extrapolated from a straight line (Whittaker 1960). In a later paper, Whittaker recognized the limitations of this measure in “sets of samples having multidirectional relationships to one another,” but again stated that it can be used to measure *beta-diversity* along a particular coenocline (Whittaker 1972, pg. 232).

Thus, even the first description of *beta-diversity* presented multiple ideas and measures! Unfortunately, this description of diversity components was restricted to just a few pages imbedded in a long monograph on the vegetation of the Siskiyou Mountains. Whittaker would refer to *beta-diversity* in several papers over the next decade, including the 1965 paper in *Science* (Whittaker 1965) in which he first presented the concept of beta-diversity to a wide scientific audience. However, it wasn’t until 1972 that he published an entire work devoted to his diversity components and their measurements (Whittaker 1972). Perhaps due to this, there was a considerable lag before the term *beta-diversity* became commonly used.

Several papers published by Robert MacArthur and colleagues in the mid 1960s also divided diversity into components. MacArthur (1964) observed that an area can support bird diversity in three ways: vertically, horizontally, and temporally. Ignoring temporal changes, he showed that total diversity = vertical diversity + horizontal diversity, where diversity was calculated using H' , or the Shannon index. A measure of species diversity derived from information theory, $H' = - \sum p_i \ln p_i$, where p_i is the proportion of individuals found in the i th species (Magurran 1988). Total diversity in this study was calculated at a relatively small scale - that of an area large enough to support 20-25 pairs of breeding birds (MacArthur 1964). None of these components referred explicitly to the concept of *differentiation* diversity. However, in his 1965 review of diversity patterns MacArthur distinguished between *within-habitat* and *between-habitat diversity (BHD)*, defining the latter as the difference in diversity between two sites (MacArthur 1965). Akin to Whittaker's *beta-diversity*, *BHD* was originally conceived for areas within a limited geographic area (Whittaker 1960, 1977; MacArthur 1965; Cody 1970). MacArthur (1965) presented two measurements of *BHD*, one for when species are equally common and one for when they are not. To measure the difference between two samples with equally common species, MacArthur first asked the question: "What multiple is the total fauna of the average of the simple censuses?" (MacArthur 1965, pg. 514). He answered this by dividing the total number of species from the combined samples by the average number of species in both samples. MacArthur did not mention that this measurement is the same as Whittaker's "simplest measure" of *beta-diversity*: $\gamma/\bar{\alpha}$ and does not refer to Whittaker's diversity components at all until later in the paper. Thus, MacArthur's total fauna, like Whittaker's *gamma*, represents pooled samples.

When species are not equally common, MacArthur proposed using information theory (H') to convert the samples into an "equivalent number of equally common species" (MacArthur 1965, pg. 514). MacArthur (1964) had previously shown that $e^{H'}$ is equal to the number of equally common species that would give the same value of diversity as measured by H' . MacArthur calculated *BHD* between samples with unequally common species as: $e^{(H'_T - \bar{H}'_w)}$, where H'_T is the diversity of both

samples combined and \bar{H}'_w is the average diversity of the samples (MacArthur 1965). This gives results comparable to dividing the total number of species by the average number of species of the samples, or $\gamma/\bar{\alpha}$, for equally common species or presence-absence data. It is at the end of this description that MacArthur cites Whittaker (1960) for “other measures of difference,” although no particular metric is given (MacArthur 1965, pg. 515). Why MacArthur did not relate his components more directly to Whittaker’s is unclear, as he was obviously aware of Whittaker’s work. In fact, when describing the influence of habitat structure on *within-habitat diversity*, MacArthur stated that “Whittaker recognizes the distinction between within- and between-habitat diversities and calls them alpha and beta respectively” (MacArthur 1965, pg. 517) and towards the end of the paper wrote that Whittaker “recognized the importance of total diversity and called it gamma diversity” (MacArthur 1965, pg. 528). It is important to note that in these early ecological writings, *alpha* and *within-habitat* represented the number of species in an arbitrary plot size rather than an estimate of the “true” richness of a habitat.

MacArthur *et al.* published another paper on *between-habitat diversity* in 1966. Here, they used $H'_T - \bar{H}'_w$, not $e^{(H'_T - \bar{H}'_w)}$, for the measure of *BHD*, with the consequence that this definition of *BHD* does not equal Whittaker’s $\gamma/\bar{\alpha}$ (MacArthur *et al.* 1966). In 1972, however, MacArthur returned to a measurement of *BHD* which was “essentially” $e^{(H'_T - \bar{H}'_w)}$ (MacArthur 1972, pg. 190). Neither of these works make any reference to Whittaker’s diversity components (MacArthur *et al.* 1966; MacArthur 1972). It is not clear which measure MacArthur felt best represented *between-habitat diversity*. MacArthur died in 1972; one can only imagine how the trajectory of diversity studies would have been different had he lived longer.

Whittaker and MacArthur were clearly converging on the same idea, that of recognizing and quantifying differentiation diversity. But while both men were interested in the relationship between compositional change and environmental change (for MacArthur environment was habitat structure), their different approaches to investigating this relationship reflects their individual backgrounds. The

importance of gradients as an organizing concept formed the core idea of Whittaker's career (R. Peet, *pers. comm.*), and he arrived at his components by observing changes in vegetation composition across environmental gradients. MacArthur's components, on the other hand, came from studying species-area curves and the relationship between bird diversity and vegetation structure (MacArthur 1964, 1965). Whittaker was interested in how compositional similarity decreased as environmental distance increased, and his samples were carefully arranged along a specified environmental gradient. He did not consider the dissimilarity between all pairs of samples at all increments of environmental distance (although he later would); rather, he calculated the *rate* of change between the first and last samples over a transect of continuously increasing environmental distance (Whittaker 1960). MacArthur, conversely, did not examine change along a gradient associated with a particular climatic or geological variable. He was interested in change in bird diversity as it related to a gradient of habitat structural diversity, and therefore plotted bird *BHD* against the *BHD* of foliage structure. Though their methods differed, both Whittaker and MacArthur attributed differentiation diversity to the habitat diversification of species (MacArthur 1965; Whittaker 1970).

The differentiation diversity studies of Whittaker and MacArthur during this time were predominately concerned with the relationship between species compositional change and habitat change at relatively small scales, where the change in species was a function of habitat preferences. However, in 1970 the scope of differentiation diversity, both in scale and determinants, was broadened by Martin Cody, a co-author from MacArthur *et al.* (1966). Like MacArthur, Cody was concerned with the relationship between change in bird diversity and change in habitat structural diversity (calculated with the measure of MacArthur *et al.* 1966). Cody distinguished between two types of compositional change: that between different habitats of close proximity and that between similar habitats that were geographically separated, where the former occurred at a smaller scale than the later (Cody 1970). This distinction would shape much of the future work on determinants of differentiation diversity. Cody also introduced a new term to refer to differentiation diversity,

turnover, which he defined as *between-habitat diversity*. Consistent with the near independence of the MacArthur school, the paper made no reference to Whittaker's diversity components (Cody 1970).

Towards the end of the decade, two mathematical ecologists, Richard Levins and E.C. Pielou, also described methods to partition diversity. However, neither related their components to those of Whittaker or MacArthur. This may be a reflection of their purpose for diversity partitioning, as a means to measure niche dimensions rather than change in species composition across space *per se*. Levins presented a new method to approaching niche dimensionality by calculating total *Drosophila* diversity as the sum of within-collection diversity and between-collection diversity (between collections differing in space or time), calling the components 'niche components' (Levins 1968). This description was only a paragraph within a section discussing niche dimensionality and unfortunately does not give a detailed account of the approach, although Levins did write in the preface, "Many of the ideas presented here were developed in the course of collaboration or association with Robert MacArthur and Richard C. Lewontin, to both of whom I am greatly indebted," (Levins 1968, pg. v). Pielou presented two types of diversity components. The first demonstrated that diversity measured as H' can be viewed as hierarchical components, for instance, by calculating total diversity as the sum of generic diversity plus average species diversity within genera (Pielou 1969). The second partitioned diversity into components as a way of calculating niche breadth and niche overlap (Pielou 1972). Neither Whittaker's nor MacArthur's components were mentioned in any of these works and, except for a brief appearance in the mid 1970s, these works did not become well incorporated into diversity studies.

1970-1980

Ten years after the introduction of the idea of differentiation diversity there was still no unified conceptual model, nor standard terminology, relating to the concept. Whittaker's components and terminology, however, reached a wider audience with his 1972 review and synthesis paper, *Evolution and measurement of species diversity*. This was the first time Whittaker described *alpha*-, *beta*-, and *gamma*-diversity in a work devoted to measures of diversity, and he discussed his components and

their measurements in much greater detail than in his previous publications. In addition to his two original measures of *beta-diversity*, Whittaker provided alternatives that allowed the incorporation of abundance data and included MacArthur *et al.*'s (1966) measurement, with the comment that it is affected by the logarithmic scale (Whittaker 1972). Whittaker also noted that compositional change occurs at different scales, perhaps as a response to the work of MacArthur and Cody. He stated that measurements of *beta* can be used for other “levels of community differentiation”, citing MacArthur (1969) and Cody (1970) for examples of geographic differentiation and Pielou (1966) for an example of intra-community differentiation (Whittaker 1972, pg. 235).

Cody (1975) further expanded the distinction of types of differentiation diversity by scale. Although he didn't cite Whittaker by name, Cody called the diversity of a single habitat *alpha-diversity* and the rate of species turnover between habitats *beta-diversity*. He also used *gamma-diversity*, but defined it as species turnover between similar habitats in different biogeographic areas, rather than the inventory diversity of the combined samples as Whittaker had described (Cody 1975). Consistent with his earlier work, Cody's *gamma-diversity* occurred at a larger scale than *beta-diversity* (Cody 1975). To illustrate this, Cody divided a species-area curve into *alpha*, *beta*, and *gamma* components, stating that the slope of the curve between 10^0 and 10^3 or 10^4 square miles was a measure of *beta-diversity* and the slope of the curve above 10^3 or 10^4 square miles measured *gamma-diversity* (Cody 1975). This paper also introduced a new measure of *beta-diversity* based on the gain and loss of species along a gradient, where at any point on the gradient *beta-diversity* was the first derivative of the species accumulation curve (the curve midway between the species gain curve and species loss curve) (Cody 1975). Using this method, *beta-diversity* could be described both for a single point along the gradient and as a function for the entire gradient (Cody 1975). A similar method based on the change in species importance values along a gradient, derived largely from ongoing efforts of Whittaker and colleagues (R. Peet, *pers. comm.*), was proposed in the same year (Bratton 1975). These methods allow for the rate of species turnover to vary along a gradient (Routledge 1977; Peet 1978; Cody 1986, 1993; Wilson & Mohler 1983; Oksanen & Tonteri 1995).

Whittaker (1977) elaborated on the scales of differentiation diversity as well, by applying his two diversity components across seven levels (Whittaker 1977). He described four inventory diversities: *point* (internal alpha, “for a small or microhabitat sample within a community regarded as homogenous”), *alpha* (within-habitat diversity, “for a sample representing a community regarded as homogenous”), *gamma* (landscape, “for a landscape or set of samples including more than one kind of community”), and *epsilon* (regional, “for a broader geographic area including differing landscapes”). Three differentiation diversities linked the 4 inventories: *pattern* (internal beta, “change between parts of an intracommunity pattern”), *beta* (between-habitat, “change along an environmental gradient or among different communities of a landscape”), and *delta* (geographic, “change along climatic gradients or between geographic areas”) (Whittaker 1977, pg. 5). Although Whittaker introduced several new terms in doing so, he did acknowledge the potential complications of the growing number of terms within the literature as whole. He concluded, however, that, “such difference in use [of terms] seems not to matter when the concepts are defined in a given paper” (Whittaker 1977, pg. 5). These classifications of types differentiation diversity, based on the idea that at each scale compositional change results from distinct processes, were the beginnings of an evolution of ideas regarding the mechanisms through which change occurs.

The first review of existing differentiation diversity measures did not appear until 1977. Routledge (1977) was also the first to mathematically relate the discrete habitat measures of Whittaker (1960) and MacArthur (1965), both to each other and to Pielou’s 1972 measure of niche breadth and niche overlap. This review dismissed Whittaker’s (1960) half-change measure as unsatisfactory because it assumed an exponential decay in similarity. Although the measures of Cody (1975) and Bratton (1975) overcame the assumption of continuous change along a gradient, they too were deemed unsatisfactory by Routledge’s criteria as they depended on parameterization of the gradient. To accommodate continuous gradients Routledge gave a modified version of Whittaker’s $\gamma/\bar{\alpha}$ and presented a new measure of species turnover based on the number of

overlapping species: $p = s^2/(2r + s)$, where s is the total number of species and r is the number of species with overlapping ranges (Routledge 1977).

Not all the work concerned with diversity components in the 1970s, however, became part of this growing school of thought. Allan (1975) reviewed three methods of partitioning diversity into additive components. The niche breadth approach, based on the work of Levins (1968), Colwell and Futuyma (1971) and Pielou (1972), calculated the total niche breadth of a species in terms of microhabitat and site niche breadth. The second approach was a reworking of Pielou's (1967, 1969) measure of hierarchical diversity into microhabitat, site, and species components. The final method applied Lewontin's (1972) analysis of diversity of blood groups among different human races to species diversity (calculated with H'): total species diversity = between site diversity + between microhabitat diversity + within microhabitat diversity (Allan 1975), analogous to *beta* + *pattern* + *point* diversities *sensu* Whittaker. Lewontin's approach is strikingly similar to MacArthur *et al.* (1966), but unfortunately Lewontin's original paper doesn't present the derivation of his methods (Lewontin 1972). Allan cited MacArthur's work to support the value of the additive approach (and in particular Lewontin's method), but the citation is not until the last sentence of the paper and he did not present MacArthur *et al.*'s 1966 measurement of *between-habitat diversity*. This was the only reference of MacArthur's work, and Whittaker was not referred to at all. Alatalo and Alatalo (1977) presented another additive model for diversity components measured over multiple dimensions (i.e., multi-dimensional resource space, habitat vs. time vs. vertical zonation). Similar to previous additive partitioning methods, their model was primarily concerned with niche dimensions. Alatalo and Alatalo (1977) did not relate their components to either Whittaker's *beta-diversity* or MacArthur's *between-habitat diversity*, nor was any component explicitly referred to as differentiation diversity.

Neither Alatalo and Alatalo (1977) nor Allan (1975) became well cited in subsequent literature relating to differentiation diversity until Lande (1996) retrieved the concept of additive partitioning from near-oblivion. The failure of additive partitioning to become established in diversity studies may have occurred, as hypothesized by Veech *et al.* (2002), because the authors did not relate their

components to Whittaker's terminology (but see Holland & Jain 1981). However, as noted above, the terminology of differentiation diversity was still evolving through the 1970s. Perhaps more importantly, neither Allan (1975) nor Alatalo and Alatalo (1977) framed their methods primarily in terms of differentiation at all (although the former makes brief mention of this use), but instead laid heavy emphasis on niche dimensions. Furthermore, although Whittaker and others noted the use of differentiation diversity over several scales (Cody 1975; Whittaker 1977), most of the work on differentiation diversity in the 1970s was focused either on specific gradients or at a single scale, which was not conducive to additive partitioning. The few studies that did use additive partitioning, conversely, were not concerned with gradients and were focused on systems acting over small geographic scales (such as ants or vernal pools) (e.g., Holland & Jain 198; Lynch 1981).

By the end of the 1970s, two decades after Whittaker introduced *beta-diversity*, some cohesion in the concept of differentiation diversity had occurred. This concept was most frequently described as *beta-diversity*, which in turn was defined as *species turnover* and *between-habitat diversity*. These terms had become part of the general ecological currency, most frequently associated with the names of Whittaker and MacArthur. *Beta-diversity* was usually, but not always, measured along a gradient.

1980-1990

Whittaker died in 1980, but his influence remained strong in studies of differentiation diversity. Although the number of studies focusing on differentiation diversity remained small during the 1980s, there were several notable contributions by Whittaker's close collaborators and students. These works were primarily concerned with quantitative analyses in community ecology and formed the basis for many ordination techniques used today. For example, the process of scaling ordination axes in units of constant species turnover developed by Hill (1979) during his sabbatical at Cornell allowed gradient length to be used as a measure of differentiation diversity (Hill & Gauch 1980). Rescaling gradients and ordination axes in units of differentiation diversity and using gradient length as a measure of *beta-diversity* soon became commonplace in community ecology (e.g., R. Peet, 1978). Another method for rescaling gradients in units of *beta-diversity* was described by Wilson and

Mohler (1983), in which they presented the *gleason*, a new unit for *beta-diversity* equal to the “amount of compositional turnover which would occur if all changes were concentrated into a single species whose abundance changed 100%” (Wilson & Mohler 1983, pg. 131). The *gleason* did not catch on, but another measure of differentiation diversity for use with presence-absence data along gradients introduced by Wilson and Shmida (1984), *beta turnover*, had more success. This paper also presented a review of existing measures of *beta-diversity* for presence-absence data along gradients and judged them on four criteria: conformity with the notion of community turnover, additivity, independence from alpha diversity, and independence from sample size (Wilson & Shmida 1984). They concluded that their new measure and Whittaker’s $\gamma / \bar{\alpha} - 1$ performed best.

Although most studies of differentiation diversity continued to focus on quantifying pattern, a few studies sought to identify determinants of diversity. Shmida and Wilson (1985), for instance, described four biological determinants of diversity. They concluded that whereas *alpha-diversity* is determined primarily by niche relations and mass effects, *beta-diversity* is principally determined by habitat diversity and mass effects. The fourth determinant, ecological equivalency, affected diversity at a much larger scale than *alpha*- or *beta*- (Shmida & Wilson 1985). In contrast, Cody (1986) no longer defined *beta-diversity* and *gamma-diversity* at different scales. Thus Cody’s *gamma-diversity* (turnover between sites of similar habitats with increasing distance) could occur at the same scale as *beta-diversity*, and was a function of distance and isolation rather than difference in habitat (Cody 1986). This was the first recognition that different processes could be active at the same scale and dispersal limitation was not restricted to large scales. Cody also related diversity components to types of rarity: species in communities with high *alpha-diversity* may have low densities, species in communities with high *beta-diversity* may show high habitat specificity, and those in communities with high *gamma-diversity* are likely to have geographically restricted ranges (Cody 1986).

1990-2000 and Beyond

The number of differentiation diversity studies increased rapidly through the 1990s (Figure 2.1), further perpetuating the confusion of terms and concepts that was well-established by the end of the 1980s. For example, some authors reserved the term *beta-diversity* for turnover only along a specified environmental gradient, some applied *beta-diversity* to species turnover between different habitat types, even if not along a gradient, and still others used *beta-diversity* even more generally, referring to differences in species composition between any two or more sites. Similarly, *gamma-diversity* was used by some authors to refer to turnover between sites of similar habitat but separated by distance, but by others as regional inventory diversity. *Beta-diversity* has been defined as the slope of the species-area curve (Cody 1975; Caswell & Cohen 1993; Rosenzweig 1995; Ricotta *et al.* 2002), as the ratio of regional to local richness (Whittaker 1960), and since Lande (1996) related additive partitioning to the now standard *alpha*-, *beta*-, and *gamma*- diversity components, the difference of regional and local richness (Veech *et al.* 2002). Many authors using this last definition have argued that $\beta = \gamma - \bar{\alpha}$ is preferable to Whittaker's $\beta = \gamma / \bar{\alpha}$ formula because *beta-diversity* defined as the average amount of diversity not found in a single sample is measured in the same units as *alpha*- and *gamma*- (Lande 1996; Loreau 2000; Veech *et al.* 2002). However, while additive partitioning was originally derived using information theory indices of diversity, it is now applied to a range of diversity measures, including species richness and Simpson's index, the consequences of which are frequently overlooked. As previously described, the logarithmic nature of H' means that subtracting is essentially dividing, whereas with non-logarithmic diversity measures such as species richness, additive partitioning is indeed subtracting.

A wide variety of methods have been developed to quantify compositional change. Wilson & Shmida's 1984 comparison of *beta-diversity* measures compared only six. A more recent review included 24 measures of *beta-diversity*, revealing just how prolific ecologists have been in inventing new measures (Koleff *et al.* 2003a) Moreover, this review was limited to pair-wise comparisons

based on presence-absence data and did not include metrics for abundance data or those measuring differentiation diversity across a gradient. Koleff *et al.* (2003a) considered these measures in terms of species gains and losses, which allows for identification of the sources of differences in species composition and thus provides a standard for comparison. They distinguished between two fundamental types of measures, “broad sense” measures that incorporate “differences in composition attributable to species richness gradients” and “narrow sense” measures that “focus on compositional differences in dependent of such gradients” (Koleff *et al.* 2003a). The measures were tested for several properties, including symmetry, homogeneity, additivity, and sensitivity to underlying richness gradients. Eight measures were judged to adequately reflect species gains and losses and, although the authors noted that no single measure is appropriate in all cases, one metric was recommended as performing best overall (Koleff *et al.* 2003a). This metric, β_{sim} , is calculated as $\min(b,c)/(a + \min(b,c))$, where a = species shared, b = species gained, c = species lost (Lennon *et al.* 2001). Derived from Simpson’s asymmetric index, $a/(a + \min(b,c))$ (Simpson 1943), β_{sim} is not affected by local species richness gradients and therefore provides a measure of beta-diversity that isolates change due to species replacement from differences in species richness (Lennon *et al.* 2001; Koleff *et al.* 2003a).

Research regarding the mechanisms driving differentiation diversity has seen more consensus, with an evolving emphasis on distinguishing between the effects of environment and distance on compositional change. For example, building on his previous work, Cody (1993) distinguished between *beta-diversity*, a function of the “difference in habitats, their areal extent, and their contiguity”, and *gamma-diversity*, a function of “site separation and of the intervening barriers to species dispersal” (Cody 1993, page 147). Similarly, Nekola and White (2002) proposed two conceptual models to explain species distributions, and hence differentiation diversity: the niche difference model, a function of the “physical environment and niche characteristics”, and the model of spatial and temporal constraint, a function of “the spatial arrangements and histories of organisms and habitats” (Nekola & White 2002, pg 305). Accordingly, there has been increased work on

determining the relative contributions of environment and distance to species compositional change (Cowling *et al.* 1992; Simmons & Cowling 1996; Nekola & White 1999; Condit *et al.* 2002; Duivenvoorden *et al.* 2002; Urban *et al.* 2002; Tuomisto *et al.* 2003) and the effects of species traits related to dispersal (Harrison *et al.* 1992; Oliver *et al.* 1998; Ferrier *et al.* 1999; MacNally *et al.* 2002). However, these studies have generally not considered the change in influences over multiple scales (but see Perelman *et al.* 2001; Rey Benayas & Scheiner 2002).

The scope of inquiry has broadened concurrently with the increasing number of studies. For example, differentiation diversity analyses have moved well beyond small-scale patterns, with growing interest in large-scale and global patterns, particularly regarding latitudinal gradients (Willig & Sandlin 1991; Blackburn & Gaston 1996; Mourelle & Ezcurra 1997; Willig & Gannon 1997; Williams *et al.* 1999; Clarke & Lidgard 2000; Koleff & Gaston 2001; Stevens & Willig 2002; Koleff *et al.* 2003b). The taxonomic breadth of studies has also widened, and now includes analyses on macroorganisms (Horner-Devine *et al.* 2004; Green *et al.* 2004) and studies in both the freshwater (Heino *et al.* 2003; Genner *et al.* 2004; Stendera & Johnson 2005) and marine realms (Clarke & Lidgard 2000; Mumby 2001). There has been increased effort to assess the scale dependency of differentiation diversity and its relationship with local and regional richness (Loreau 2000; Lennon *et al.* 2001; Arita & Rodríguez 2002; Gering & Crist 2002; Koleff & Gaston 2002; Heino *et al.* 2003) and to measure the relative contribution of differentiation diversity to total diversity across multiple scales (Wagner *et al.* 2000; Gering *et al.* 2003; Summerville *et al.* 2003). Theoretical research has also increased, such as the development of neutral models and methods of statistical testing, including examination of the effects of sample size and species abundance distributions on measures of differentiation diversity (Bell 2001; Hubbell 2001; Chave & Leigh 2002; Condit *et al.* 2002; Plotkin & Muller-Landau 2002; Summerville *et al.* 2003). In addition to niche relations and space-dispersal interactions as explanations of differentiation diversity, Hubbell (2001) shows that a neutral model produces exponential distance decay, thereby establishing a third category of causal explanation.

The emergence of the field of conservation biology has given a new perspective on differentiation diversity. The importance of patterns of species compositional change for determining the optimal spacing of protected areas in order to efficiently represent species had been widely recognized since the SLOSS (Single Large Or Several Small) debate of the 70s and 80s (e.g., Simberloff & Abele 1976), but there was little discussion of differentiation diversity by name in relation to conservation until the 1990s (but see Cody 1986). Patterns of differentiation diversity are often used to identify areas of high differentiation diversity and biogeographic transition zones, or to identify units for conservation planning (Meirelles *et al.* 1999; Williams *et al.* 1999; Williams-Linera 2002). However, the application of differentiation diversity to set conservation priorities among sites is still primarily indirect, for instance through site selection algorithms and conservation surrogates methods (e.g., umbrella species, indicator species) that are largely driven by differentiation diversity patterns (Margules & Pressey 2000; Groves 2003). As attention to ensuring the long-term persistence of biodiversity increases, the development of techniques to directly incorporate differentiation diversity patterns into prioritization methods are gaining support (Fairbanks *et al.* 2001).

Whither to?

“Perhaps the word ‘diversity’ like many of the words in the early vocabulary of ecologists should be eliminated from our vocabularies as doing more harm than good” – Robert MacArthur (1972, pg. 197)

Even in the early years of its development, the concept of the differentiation component of diversity was described using a variety of approaches, terminologies, and methods. First applied to change along gradients at relatively small spatial scales, the geographic scope of the concept quickly broadened. Today, community ecologists, biogeographers, conservation biologists, landscape ecologists, and macroecologists study the patterns and determinants of differentiation diversity of a variety of organisms at many spatial scales, systems, and locations. While many have noted the difficulties that the plethora of terms and measurements produces (Vellend 2001; Whittaker *et al.* 2001; Koleff *et al.* 2003a), few have attempted to rectify the problem (but see Vellend 2001). The confusion of terms and concepts continues to impede objective comparisons between studies, and

therefore complicates generalizing patterns and determinants of differentiation diversity across different regions or taxa (Whittaker *et al.* 2001; Koleff *et al.* 2003a). In the only direct attempt to clarify the terminology, Vellend (2001) proposed that the term *beta-diversity* be restricted to mathematical relationships between *alpha* and *gamma* diversity (where *gamma* is larger scale or regional diversity) and be used only when information on gradients is either not needed or not available, and that the phrase *species turnover* should be reserved for the rate or degree of change in species composition along a specific gradient, be it environmental or geographic (Vellend 2001). This use, however, disassociates *beta* from its oldest and most commonly used definition. While Whittaker did apply *beta-diversity* to both of these representations of differentiation diversity, others argue that change along gradients was Whittaker's primary focus of *beta* (R. Peet, *pers. comm.*). The question that lay at the root of the confusion is whether differentiation diversity is one unifying phenomenon of change in species composition through space, or whether there are multiple concepts based on differences in either scale and process or in measurement. To answer the first, it is necessary to take a closer look at process and scale and the interaction between them. For the second, I discuss whether alternative measures of differentiation diversity, such as a rate of change along a gradient versus a static measure of heterogeneity, warrant the establishment of separate concepts. Lastly, I make recommendations for the terminology of differentiation diversity.

Scale and Process

Differentiation diversity is determined through a complex array of processes that reflect the interaction of species traits (i.e., vagility, environmental tolerances, resource use, and reproductive strategies) and characteristics of the physical environment (i.e., environmental dissimilarity, physical distance, and isolation) over ecological and evolutionary time. Previous authors have attempted to distinguish between the effects of environment and geographic separation in determining differentiation diversity. For example, Cody's separation of *beta* (change associated with environmental differences) and *gamma* (change due to geographic separation) diversity components (Cody 1986, 1993) or the two pillars of ecological explanation for species distribution (niche

difference vs. spatial and temporal constraint) described by Nekola and White (2002). Such dichotomies are useful conceptual models, but in reality, there is interaction between environment and geographic distance any scale. For instance, niche characteristics will not only interact with the physical environment, but also may interact with the spatial arrangement of habitats, such as when an unfavorable habitat acts as a barrier to species movement between two proximate areas of the same habitat (that is, niche characteristics can explain why the species is unable to cross the barrier). Similarly, while dispersal limitation is suggested as an explanation for differentiation diversity at large scales, niche characteristics also determine species distributions along climatic gradients. Dividing differentiation diversity on the basis of underlying processes is also problematical because it begs such questions as whether the *beta* used to describe change along a climatic gradient on a single mountainside is also used for change along a broad climatic gradient that extends across an entire continent.

Classifying scales of differentiation diversity is also unsatisfactory. The argument to separate differentiation diversity measured at different scales assumes that there is a set of related mechanisms associated with change in species composition at those scales. This assumption, however, is not a valid for several reasons. As described above, compositional change at a single scale may result through multiple processes, such as niche differentiation along an environmental gradient and geographic isolation. Moreover, while there may be some scales at which certain processes dominate, most processes vary in the spatial and temporal scales over which they act and over which they are manifested (Levin 1992; Ricklefs & Schluter 1993). Thus, while processes such as the competitive sorting of species and dispersal limitation may predominate at smaller spatial and temporal scales, the effects of niche differentiation and dispersal are also apparent at large scales. Species' range edges reflect these processes acting over both evolutionary and ecological time, as demonstrated by the expansion and contraction of ranges in response to contemporary climate change. Similarly, speciation and biogeographic processes may dominate at large scales, but they also influence differentiation diversity at smaller scales because they determine which species co-exist at these

scales, and consequently effect the outcome of competition. Scale, described by the grain and extent of analysis, is the observational window through which we observe diversity (Wiens 1989; Palmer & White 1994). For any particular taxon and place, the pattern of differentiation diversity and the strength of different processes influencing it will vary with scale. Indeed, while taxonomic groups (e.g., birds vs. plants) are broadly different in how they encounter both environmental gradients and spatial complexity, there is also considerable variation in niche width and dispersal ability within these groups. Thus, it is problematic to assume in an a priori sense that there are dominant process or scales that by which concepts of differentiation diversity can be divided. These issues also support the simplification of the concepts and measurements such that the existence of dominant processes or scales is an inference from the data rather than an initial assumption.

Whittaker alluded to the interaction of scale and process when he applied the concept his *alpha* and *beta* components of diversity across seven levels, writing, “It should be evident that these concepts intergrade, since they are defined along a continuum of increasing scale. The reader may judge later when the usefulness of the concepts justifies distinguishing seven levels of species diversity,” (Whittaker 1977, pg. 5). I have described in the preceding paragraphs some are ecological reasons prohibiting such a classification of diversity levels, and I have documented in my historical review the conceptual complications such a division can create. Thus, this reader judges that diversity consists of just two components that can be measured at any scale: inventory diversity (*alpha*), encompassing species lists from contiguous areas, and differentiation diversity (*beta*), describing all change in species composition across space, whether along a gradient or not. The *beta* component is the link between *alpha* components at two scales, such as Whittaker described for his seven levels and shown in Figure 2.2 (Whittaker 1977; Loreau 2000; Arita & Rodríguez 2002; Gering & Crist 2002; Gering *et al.* 2003).

Measurement

A single measure of *beta* for an entire region and *beta* measured along a gradient are not irreconcilable ideas, but are nested aspects of the same phenomenon. *Beta* derived from the *alpha*

components at two scales expresses the change that occurs over all gradients and directions. Because it describes the discrepancy between *alpha* components, it is a component in the true sense of the word – it is the part of total diversity that occurs because species are not found everywhere. It informs us of the contribution of change to diversity at larger scales. However, it does not convey the multidimensional nature of differentiation diversity because actual rates or degrees of change in species composition vary along different gradients or in different directions.

To understand the spatial dimensions of *beta*, we must use methods that examine the degree of change across space, for instance, over gradients of specific environmental variables, complex environmental gradients, or gradients of physical distance, which encompass both differences in environment and limitations to movement. Measuring *beta* over spatial gradients is essential to elucidating the mechanisms driving compositional change. However, some metrics of *beta* do not intrinsically separate species replacement from richness gradients. For studies focusing on the replacement of species across space, a metric that does not consider differences in richness as change, such as β_{sim} , is most appropriate. Metrics like Jaccard's or Sorenson's indices are suitable when estimates of overall similarity between samples is preferred.

Just as no single metric can describe the various aspects of inventory diversity (e.g., richness, dominance, and evenness), different methods reveal different aspects of differentiation diversity. For example, calculating the rate of change in samples across an environmental gradient is useful to examine community differentiation in response to environment, but a nested sampling configuration and *alpha*-based measures are more appropriate to evaluate the contribution of the two diversity components to total diversity. Likewise, distance-decay regressions provide information regarding the effect of physical distance on similarity.

The Two Components of Diversity

I have argued that there are two components of diversity regardless of scale or mechanism, but the various terms must still be reconciled. Although the terms *inventory* and *differentiation* are perhaps more intuitive than *alpha* and *beta* as descriptors of diversity, they are unwieldy and not

widely used. Furthermore, as the Greek letters α and β have been associated with diversity components since Whittaker's first description and it would be difficult to divorce the terms from the conceptual components, the terms *alpha* and *beta* are here treated synonymously for the inventory and differentiation components of diversity regardless of process, scale, or measurement. Because these two terms encompass their respective components at any scale, separate terms for change related to a particular process or scale, such as *gamma-diversity* or *delta-diversity*, are superfluous.

The concept of *beta* represents a single phenomenon, the spatial differentiation of species composition. This phenomenon can be represented by two different approaches. First, it can be described as the extent to which *alpha* measured at a smaller scale is exceeded by *alpha* at a larger scale, or the overall level of heterogeneity. Second, it can be measured as the degree of change over gradients of environmental or physical distance (e.g., the distance decay of similarity). Both approaches derive from the same underlying phenomenon. The unity of the concept advocates maintaining *beta*, or *beta-diversity*, for both.

References

- Alatalo, R. & Alatalo, R. (1977) Components of diversity: multivariate analysis with interaction. *Ecology* 58, 900-906.
- Allan, J.D. (1975) Components of diversity. *Oecologia* 18, 359-367.
- Arita, H.T. & Rodríguez, P. (2002) Geographic range, turnover rate and the scaling of species diversity. *Ecography* 25, 541-550.
- Bell, G. (2001) Neutral macroecology. *Science* 293, 2413-2418.
- Blackburn, T.M. & Gaston, K.J. (1996) The distribution of bird species in the New World: patterns in species turnover. *Oikos* 77, 146-152.
- Bratton, S.P. (1975) A comparison of the beta diversity functions of the overstory and herbaceous understory of a deciduous forest. *Bulletin of the Torrey Botanical Club* 102, 55-60.
- Caswell, H. & Cohen, J.E. (1993) Local and regional regulation of species-area relations: a patch-occupancy model. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 99-107. University of Chicago Press, Chicago, IL.
- Chave, J. & Leigh, E.G. (2002) A spatially explicit neutral model of beta-diversity in tropical forests. *Theoretical Population Biology* 62, 153-168.
- Clarke, A. & Lidgard, S. (2000) Spatial patterns of diversity in the sea: bryozoan species richness in the North Atlantic. *Journal of Animal Ecology* 69, 799-814.
- Cody, M.L. (1970) Chilean bird distribution. *Ecology* 51, 455-464.
- Cody, M.L. (1975) Towards a theory of continental species diversities: bird distributions over Mediterranean habitat gradients. *Ecology and evolution of communities* (ed. by M.L. Cody and J.M. Diamond), pp. 214-257. Harvard University Press, Cambridge, MA.
- Cody, M.L. (1986) Diversity, rarity, and conservation in Mediterranean-climate ecosystems. *Conservation biology: the science of scarcity and diversity* (ed. by M.E. Soulé), pp. 122-152. Sinauer Associates, Sunderland, MA.
- Cody, M.L. (1993) Bird diversity components within and between habitats in Australia. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 147-158. University of Chicago Press, Chicago, IL.
- Colwell, R.K. & Futuyma, D.J. (1971) On the measurement of niche breadth and overlap. *Ecology* 52, 567-576.
- Condit, R., Pitman, N., Leigh, E.G. Jr., Chave, J., Terborgh, J., Foster, R.B., Núñez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. & Hubbell, S.P. (2002) Beta-diversity in tropical forest trees. *Science* 295, 666-669.

- Cowling, R.M., Holmes, P.M. & Rebelo, A.G. (1992) Plant diversity and endemism. *The ecology of the fynbos: nutrients, fire and diversity* (ed. by R.M.Cowling), pp. 62-112. Oxford University Press, Cape Town.
- Duivenvoorden, J.F., Svenning, J.C. & Wright, S.J. (2002) Beta diversity in tropical forests. *Science* 295, 636-637.
- Fairbanks, D.H.K., Reyers, B. & van Jaarsveld, A.S. (2001) Species and environment representation: selecting reserves for the retention of avian diversity in KwaZulu-Natal, South Africa. *Biological Conservation* 98, 365-379.
- Ferrier, S., Gray, M.R., Cassis, G.A. & Wilkie, L. (1999) Spatial turnover in species composition of ground-dwelling arthropods, vertebrates and vascular plants in north-east New South Wales: implications for selection of forest reserves. *The other 99%: the conservation and biodiversity of invertebrates* (ed. by W. Ponder and D. Lunney), pp. 68-76. Royal Zoological Society of New South Wales, Sydney.
- Genner, M.J., Taylor, M.I., Cleary, D.F.R., Hawkins, S.J., Knight, M.E. & Turner, G.F. (2004) Beta diversity of rock-restricted cichlid fishes in Lake Malawi: importance of environmental and spatial factors. *Ecography* 27, 601-610.
- Gering, J.C. & Crist, T.O. (2002) The alpha-beta-regional relationship: providing new insights into local-regional patterns of species richness and scale dependence of diversity components. *Ecology Letters* 5, 433-444.
- Gering, J.C., Crist, T.O. & Veech, J.A. (2003) Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. *Conservation Biology* 17, 488-499.
- Green, J.L., Holmes, A.J., Westoby, M., Oliver, I., Briscoe, D., Dangerfield, M., Gillings, M., & Beattie, A.J. (2004) Spatial scaling of microbial eukaryotic diversity. *Nature* 432, 747-750.
- Groves, C.R. (2003) *Drafting a conservation blueprint*. Island Press, Washington, D.C.
- Harrison, S., Ross, S.J. & Lawton, J.H. (1992) Beta-diversity on geographic gradients in Britain. *Journal of Animal Ecology* 61, 151-158.
- Heino, J., Muotka, T. & Paavola, R. (2003) Determinants of macroinvertebrate diversity in headwater streams: regional and local influences. *Journal of Animal Ecology* 72, 425-434.
- Hill, M.O. & Gauch, H.G. (1980) Detrended correspondence analysis: an improved technique. *Vegetatio* 42, 47-58.
- Hill, M.O. (1979) DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Cornell University, Ithaca, NY.
- Holland, R.F. & Jain, S.K. (1981) Insular biogeography of vernal pools in the Central Valley of California. *American Naturalist* 117, 24-37.
- Horner-Devine, M.C., Lage, M., Hughes, J.B. & Bohannon, B.J.M. (2004) A taxa-area relationship for bacteria. *Nature* 432, 750-753.

- Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.
- Koleff, P. & Gaston, K.J. (2001) Latitudinal gradients in diversity: real patterns and random models. *Ecography* 24, 341-351.
- Koleff, P. & Gaston, K.J. (2002) The relationships between local and regional species richness and spatial turnover. *Global Ecology and Biogeography* 11, 363-375.
- Koleff, P., Gaston, K.J. & Lennon, J.J. (2003a) Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* 72, 367-382.
- Koleff, P., Lennon, J.J. & Gaston, K.J. (2003b) Are there latitudinal gradients in species turnover? *Global Ecology and Biogeography* 12, 483-498.
- Lande, R. (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76, 5-13.
- Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70, 966-979.
- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology* 73, 1943-1967.
- Levins, R. (1968) *Evolution in changing environments: some theoretical explorations*. Princeton University Press, Princeton, NJ.
- Lewontin, R.C. (1972) The apportionment of human diversity. *Evolutionary Biology* 6, 381-398.
- Loreau, M. (2000) Are communities saturated? On the relationship between alpha, beta and gamma diversity. *Ecology Letters* 3, 73-76.
- Lynch, J.F. (1981) Seasonal, successional, and vertical segregation in a Maryland ant community. *Oikos* 37, 183-198.
- MacArthur, R., Recher, H. & Cody, M. (1966) On the relationship between habitat selection and species diversity. *American Naturalist* 100, 319-332.
- MacArthur, R.H. (1964) Environmental factors affecting bird species diversity. *American Naturalist* 98, 387-397.
- MacArthur, R.H. (1965) Patterns of species diversity. *Biological Reviews* 40, 510-533.
- MacArthur, R.H. (1972) *Geographical ecology: patterns in the distribution of species*. Harper & Row Publishers, New York, NY.
- MacNally, R., Bennett, A.F., Brown, G.W., Lumsden, L.F., Yen, A., Hinkley, S., Lillywhite, P. & Ward, D.A. (2002) How well do ecosystem-based planning units represent different components of biodiversity? *Ecological Applications* 12, 900-912.

- Magurran, A.E. (1988) *Ecological diversity and its measurement*. Princeton University Press, Princeton, NJ.
- Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature* 405, 243-253.
- Meirelles, S.T., Pivello, V.R. & Joly, C.A. (1999) The vegetation of granite rock outcrops in Rio De Janeiro, Brazil, and the need for its protection. *Environmental Conservation* 26, 10-20.
- Mourelle, C. & Ezcurra, E. (1997) Differentiation diversity of Argentine cacti and its relationship to environmental factors. *Journal of Vegetation Science* 8, 547-558.
- Mumby, P.J. (2001) Beta and habitat diversity in marine systems: a new approach to measurement, scaling and interpretation. *Oecologia* 128, 274-280.
- Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* 26, 867-878.
- Nekola, J.C. & White, P.S. (2002) Conservation, the two pillars of ecological explanation, and the paradigm of distance. *Natural Areas Journal* 22, 305-310.
- Oksanen, J. & Tonteri, T. (1995) Rate of compositional turnover along gradients and total gradient length. *Journal of Vegetation Science* 6, 815-824.
- Oliver, I., Beattie, A.J. & York, A. (1998) Spatial fidelity of plant, vertebrate, and invertebrate assemblages in multiple-use forest in eastern Australia. *Conservation Biology* 12, 822-835.
- Palmer, M.W. & White, P.S. (1994) Scale dependence and the species-area relationship. *American Naturalist* 114, 717-740.
- Peet, R.K. (1978) Forest vegetation of the Colorado Front Range: patterns of species diversity. *Vegetatio* 37, 65-78.
- Perelman, S.B., Leon, R.J.C. & Oesterheld, M. (2001) Cross-scale vegetation patterns of flooding Pampa grasslands. *Journal of Ecology* 89, 562-577.
- Pielou, E.C. (1966) Species-diversity and pattern-diversity in the study of ecological succession. *Journal of Theoretical Biology* 10, 370-383.
- Pielou, E.C. (1967) The use of information theory in the study of the diversity of biological populations. *Proceedings of the 5th Berkeley Symposium on Mathematical Statistics and Probability* 4, 163-177.
- Pielou, E.C. (1969) *An introduction to mathematical ecology*. Wiley-Interscience, New York, NY.
- Pielou, E.C. (1972) Niche width and niche overlap: a method for measuring them. *Ecology* 53, 688-692.
- Pimm, S.L., Russell, G.J., Gittleman, J.L. & Brooks, T.M. (1995) The future of biodiversity. *Science* 269, 347-350.

- Plotkin, J.B. & Muller-Landau, H.C. (2002) Sampling the species composition of a landscape. *Ecology* 83, 3344-3356.
- Rey Benayas, J.M. & Scheiner, S.M. (2002) Plant diversity, biogeography and environment in Iberia: patterns and possible causal factors. *Journal of Vegetation Science* 13, 245-258.
- Ricklefs, R.E. & Schluter, D. (1993) *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, IL.
- Ricotta, C., Carranza, M.L. & Avena, G. (2002) Computing beta-diversity from species-area curves. *Basic and Applied Ecology* 3, 15-18.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.
- Routledge, R.D. (1977) On Whittaker's components of diversity. *Ecology* 58, 1120-1127.
- Shmida, A. & Wilson, M.V. (1985) Biological determinants of species-diversity. *Journal of Biogeography* 12, 1-20.
- Simberloff, D.S. & Abele, L.G. (1976) Island biogeography theory and conservation practice. *Science* 191, 285-286.
- Simmons, M.T. & Cowling, R.M. (1996) Why is the Cape Peninsula so rich in plant species? An analysis of the independent diversity components. *Biodiversity and Conservation* 5, 551-573.
- Simpson, G.G. (1943) Mammals and the nature of continents. *American Journal of Science* 241, 1-31.
- Stendera, S.E.S. & Johnson, R.K. (2005) Additive partitioning of aquatic invertebrate species diversity across multiple spatial scales. *Freshwater Biology* 50, 1360-1375.
- Stevens, R.D. & Willig, M.R. (2002) Geographical ecology at the community level: perspectives on the diversity of New World bats. *Ecology* 83, 545-560.
- Summerville, K.S., Boulware, M.J., Veech, J.A. & Crist, T.O. (2003) Spatial variation in species diversity and composition of forest Lepidoptera in eastern deciduous forests of North America. *Conservation Biology* 17, 1045-1057.
- Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003) Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299, 241-244.
- Urban, D., Goslee, S., Pierce, K. & Lookingbill, T. (2002) Extending community ecology to landscapes. *Ecoscience* 9, 200-212.
- Veech, J.A., Summerville, K.S., Crist, T.O. & Gering, J.C. (2002) The additive partitioning of species diversity: recent revival of an old idea. *Oikos* 99, 3-9.
- Vellend, M. (2001) Do commonly used indices of beta-diversity measure species turnover? *Journal of Vegetation Science* 12, 545-552.

- Wagner, H.H., Wildi, O. & Ewald, K.C. (2000) Additive partitioning of plant species diversity in an agricultural mosaic landscape. *Landscape Ecology* 15, 219-227.
- Whittaker, R.H. (1956) Vegetation of the Great Smoky Mountains. *Ecological Monographs* 26, 1-80.
- Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30, 279-338.
- Whittaker, R.H. (1965) Dominance and diversity in land plant communities. *Science* 147, 250-260.
- Whittaker, R.H. (1970) *Communities and ecosystems*. MacMillan, New York, NY.
- Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon* 21, 213-251.
- Whittaker, R.H. (1977) Evolution of species diversity in land communities. *Evolutionary Biology* 10, 1-67.
- Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* 28, 453-470.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology* 3, 385-397.
- Williams, P.H. (1996) Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. *Proceedings of the Royal Society of London Series B-Biological Sciences* 263, 579-588.
- Williams, P.H., de Klerk, H.M. & Crowe, T.M. (1999) Interpreting biogeographical boundaries among Afrotropical birds: Spatial patterns in richness gradients and species replacement. *Journal of Biogeography* 26, 459-474.
- Williams-Linera, G. (2002) Tree species richness complementarity, disturbance and fragmentation in a Mexican tropical montane cloud forest. *Biodiversity and Conservation* 11, 1825-1843.
- Willig, M.R. & Gannon, M.R. (1997) Gradients of species density and turnover in marsupials: a hemispheric perspective. *Journal of Mammalogy* 78, 756-765.
- Willig, M.R. & Sandlin, E.A. (1991) Gradients of species density and species turnover in New World bats: a comparison of quadrat and band methodologies. *Latin American mammalogy: history, biodiversity, and conservation* (ed. by M.A. Mares and D.J. Schmidly), pp. 81-96. University of Oklahoma Press, Norman, OK.
- Wilson, M.V. & Mohler, C.L. (1983) Measuring compositional change along gradients. *Vegetatio* 54, 129-141.
- Wilson, M.V. & Shmida, A. (1984) Measuring beta diversity with presence absence data. *Journal of Ecology* 72, 1055-1064.

Figure 2.1. The number of papers related to differentiation diversity from the years 1960-2000. The total height of the bar represents the number of papers found by a JSTOR citation search on the terms “beta-diversity” OR “between-habitat diversity” (search queried full text and abstracts; performed 6 March 2006). The checkered portion of each bar reflects the number of papers found when the additional term “AND conservation” was included.

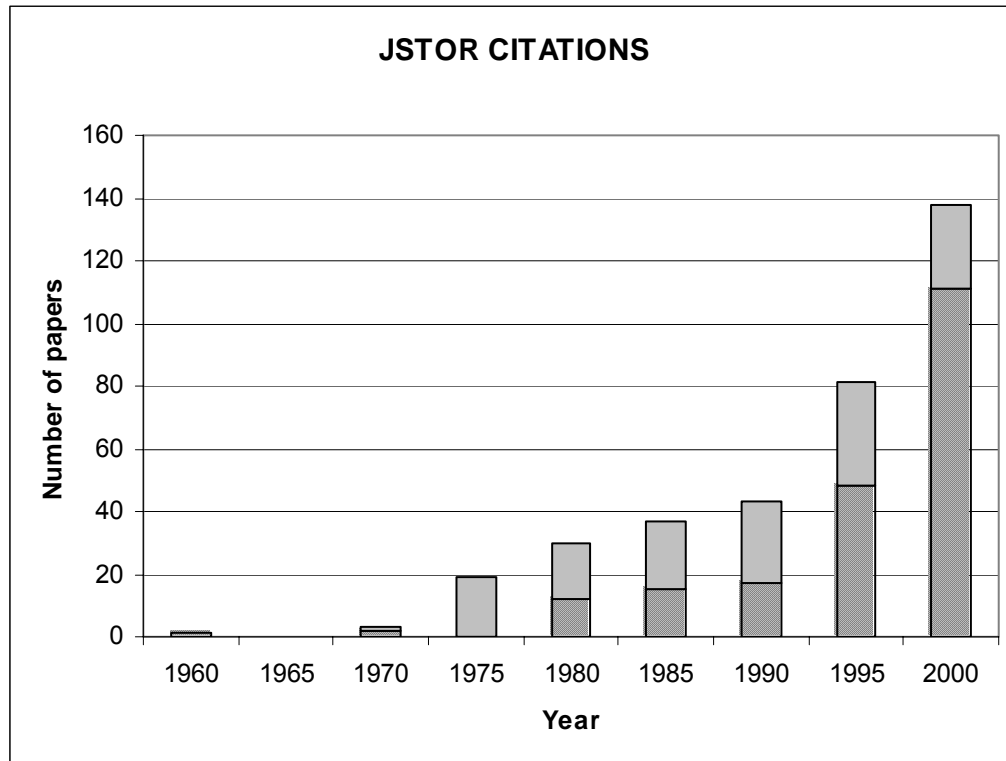
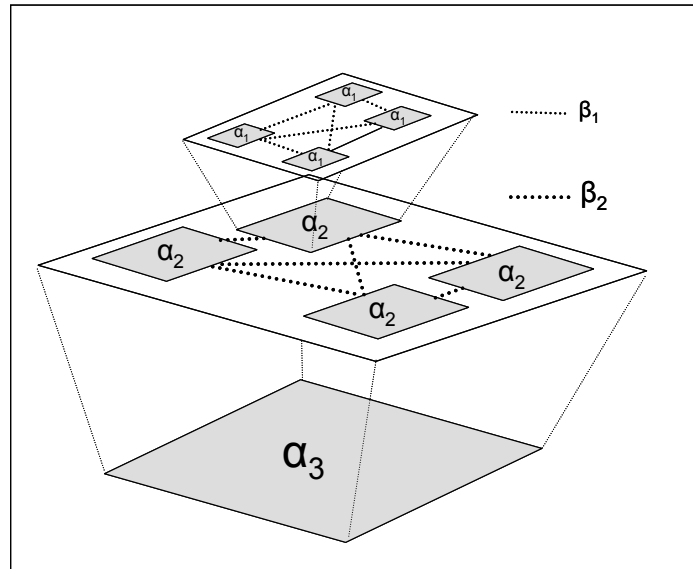


Figure 2.2. The relationship between the *alpha* (α) and *beta* (β) components of diversity at multiple scales.



CHAPTER 3

Putting Beta-Diversity on the Map:

Broad-Scale Congruence and Coincidence in the Extremes¹

Abstract

Beta-diversity, the change in species composition between places, is a critical but poorly understood component of biological diversity. Patterns of beta-diversity provide information central to many ecological and evolutionary questions, as well as to conservation planning. Yet beta-diversity is rarely studied across large extents, and the degree of similarity of patterns among taxa at such scales remains untested. Our study is the first broad-scale analysis of cross-taxon congruence in beta-diversity, and introduces a new method to map beta-diversity continuously across regions. Congruence between amphibian, bird, and mammal beta-diversity in the Western Hemisphere varies with both geographic location and spatial extent. We demonstrate that areas of high beta-diversity for the three taxa largely coincide, but areas of low beta-diversity exhibit little overlap. These findings suggest that similar processes lead to high levels of differentiation in amphibian, bird, and mammal assemblages, while the ecological and biogeographic of factors influencing homogeneity in vertebrate assemblages vary. Knowledge of beta-diversity congruence can help formulate hypotheses about the mechanisms governing regional diversity patterns and should inform conservation, especially as threat from global climate change increases.

¹ Chapter 3 was co-authored with Peter S. White, Robert I. McDonald, John F. Lamoreux, Wes Sechrest, Robert S. Ridgely, and Simon N. Stuart.

Introduction

Beta-diversity, the change in species composition between places, represents the differentiation component of diversity, as opposed to the inventory component which describes the species composition of a single place (Whittaker 1960, 1972; Harrison *et al.* 1992). Although beta-diversity was originally defined as the differentiation of communities along environmental gradients (Whittaker 1960), the concept applies more widely to the phenomenon of species compositional change at any scale, regardless of mechanism (Whittaker 1972; Harrison *et al.* 1992; Condit *et al.* 2002; Koleff *et al.* 2003a; Ferrier *et al.* 2004; Qian *et al.* 2005). Beta-diversity *sensu lato* is determined through a complex array of processes relating to the interaction of species traits (e.g., vagility, niche width) and characteristics of the physical landscape (e.g., environmental dissimilarity, topographic complexity, isolation) over time (Shmida & Wilson 1985; Cody 1986; Harrison *et al.* 1992; Nekola & White 1999, 2002). Geographic variation in beta-diversity, from gradual changes to abrupt transitions, reflects past and present differences in environment, ecological interactions, and biogeographic history, including barriers to dispersal (Cody 1986; Nekola & White 1999, 2002; Gascon *et al.* 2000; Hubbell, 2001; Condit *et al.* 2002; Tuomisto *et al.* 2003; Qian *et al.* 2005; Graham *et al.* 2006).

As beta-diversity quantifies the turnover in species across space, it is central to a wide array of ecological and evolutionary topics, such as the scaling of diversity (Pimm & Gittleman 1992; Blackburn & Gaston 1996; Lennon *et al.* 2001; Drakare *et al.* 2006), the delineation of biotic regions or biotic transitions (Williams 1996; Williams *et al.* 1999), and the mechanisms through which regional biotas are formed (Williams 1996; Williams *et al.* 1999; Moritz *et al.* 2001; Graham *et al.* 2006). Beta-diversity also provides information critical to conservation planning, which strives to represent all biodiversity within practical constraints such as area and cost (Pimm & Gittleman 1992; Pressey *et al.* 1993; Nekola & White 2002; Tuomisto *et al.* 2003; Sakar 2006). While the total number of species, endemic species, or threatened species often contribute to the relative importance of an area (Williams 1998; Reid 1998; Margules & Pressey 2000; Stuart *et al.* 2004; Ricketts *et al.*

2005), it is the rate of species turnover between sites that dictates the optimal spatial arrangement of conservation areas (Pimm & Gittleman 1992; Nekola & White 1999, 2002). Although the principles behind most approaches to systematic planning, such as complementarity, are driven by patterns of beta-diversity (Pressey *et al.* 1993; Ferrier 2002), few methods make explicit use of turnover measures (Fairbanks *et al.* 2001; Ferrier *et al.* 2004). Directly incorporating beta-diversity patterns into priority setting, however, benefits conservation efforts. For example, modeling compositional dissimilarity to develop surrogates for data poor regions can improve biodiversity representation (Ferrier 2002; Ferrier *et al.* 2004; Steinitz *et al.* 2005). Moreover, including turnover estimates in area selection algorithms captures variation in species assemblages, which helps to preserve ecological and evolutionary processes as well as underlying environmental heterogeneity necessary for long-term persistence (Margules & Pressey 2000; Fairbanks *et al.* 2001).

Despite the importance of beta-diversity, relatively little is known about diversity's "other component", particularly at broad scales. This is largely because measures of beta-diversity require knowledge of species identities rather than just species counts. Recent advances in species distributional data have made beta-diversity analyses possible at large extents (Williams 1996; Blackburn & Gaston 1996; Williams *et al.* 1999), but these studies have been limited to one taxon. Cross-taxon congruence in beta-diversity has only been tested at small scales, with variable results (Moritz *et al.* 2001; Tuomisto *et al.* 2003; Su *et al.* 2004; Steinitz *et al.* 2005). Here, we present the first analysis of beta-diversity congruence across large spatial scales, based on distribution data for three groups of terrestrial vertebrates in the continental Western Hemisphere.

Beta-diversity of amphibians ($n = 2,174$) (IUCN *et al.* 2004), breeding birds ($n = 3,882$) (Ridgely *et al.* 2005), and mammals ($n = 1,611$) (Patterson *et al.* 2005) was estimated as a function of the distance decay of similarity – the decrease in compositional similarity with increasing geographic distance between sites (Nekola & White 1999; Condit *et al.* 2002; Tuomisto *et al.* 2003; Qian *et al.* 2005). Although the negative relationship between extent and similarity is a widespread phenomenon, there is considerable geographic variation in the rate at which similarity decays. We modeled distance

decay from each 100 km X 100 km grid cell, and used these models to calculate our measure of beta-diversity, $\beta_{\text{sim-d}}$, as the estimated proportional turnover in species composition at a distance of 100 km (see Materials and Methods). Considering comparisons over a range of distances reduces possible bias in similarity levels from the differences in centroid to centroid distance and shared perimeter length that occur between orthogonal and diagonal neighbors of a rectangular grid. The smoothing that results from the distance decay regressions also limits the influence of artifacts due to small-scale errors in the range map boundary placement.

Our approach makes several improvements to previous distance decay studies (Nekola & White 1999; Condit *et al.* 2002; Tuomisto *et al.* 2003; Qian *et al.* 2005). In contrast to the single rate of change that is typically computed for an entire region, the individual cell based technique accounts for geographic variation in the rate of distance decay and produces a continuous layer of compositional change similar to past grid-based analyses of broad-scale beta-diversity (e.g., Williams 1996; Williams *et al.* 1999; Lennon *et al.* 2001). Furthermore, we modeled distance decay using logistic regression, which has advantages over linear or log-linear ordinary least-square regressions (Condit *et al.* 2002; Tuomisto *et al.* 2003; Qian *et al.* 2005), particularly for proportional data (Ferrier *et al.* 2002). Lastly, following Lennon *et al.* (2001), we measured similarity with a metric shown to be independent of differences in species richness between grid cells in order to isolate change due to species replacement (Koleff *et al.* 2003b) (see Materials and Methods).

We tested congruence in $\beta_{\text{sim-d}}$ of the three taxa using two different approaches. With the first, we measured congruence in overall beta-diversity patterns and examined whether congruence levels were consistent across multiple spatial extents and among different geographic locations. In the second approach, we quantified spatial overlap in the extremes of beta-diversity. We report that the strength of congruence depends on the location and extent at which it is measured, and that overlap in high $\beta_{\text{sim-d}}$ is much greater than in low $\beta_{\text{sim-d}}$. Furthermore, the pairs of taxa varied substantially in level of congruence and degree of overlap.

Results and Discussion

Amphibian, bird, and mammal $\beta_{\text{sim-d}}$ mapped at this scale (Figure 3.1) provide a striking contrast to well-known patterns of broad-scale species richness for these vertebrate groups. Whereas high richness is generally concentrated in the tropics and decreases towards both poles (Baillie *et al.* 2004), $\beta_{\text{sim-d}}$ of all levels is found across a wide range of latitudes. High $\beta_{\text{sim-d}}$ stretches along the mountainous Pacific edge of the continents, while low $\beta_{\text{sim-d}}$ is found within more environmentally uniform portions of northern South America and boreal North America. Accordingly, $\beta_{\text{sim-d}}$ has a positive relationship with both elevation and number of biome boundaries ($\beta_{\text{sim-d}}$ and elevation: Spearman rank $\rho = 0.219\text{--}0.427$, $P < 0.05$ for amphibian $\beta_{\text{sim-d}}$, $P < 0.001$ for taxa; $\beta_{\text{sim-d}}$ and biome edge: $\rho = 0.295\text{--}0.320$, $P < 0.001$ for all; Table 3.1; see Materials and Methods). Although the variables show considerable spread (Figure 3.2), high $\beta_{\text{sim-d}}$ grid cells of all three groups occur at significantly higher elevations and on a greater number of biome edges than expected by chance alone, while low $\beta_{\text{sim-d}}$ grid cells have significantly lower elevations and fewer biome edges than expected by chance (Table 3.2; 10,000 random sets, $P < 0.05$ for elevation in low amphibian $\beta_{\text{sim-d}}$ grid cells, $P < 0.001$ for all others; see Materials and Methods). The weaker significance for elevation in low amphibian $\beta_{\text{sim-d}}$ grid cells is likely due to the wood frog (*Rana sylvatica*) being the only amphibian species to occur throughout much of the boreal region, including high altitude areas such as the Alaska panhandle (Duellman 1999). This amphibian homogeneity differs greatly from the high $\beta_{\text{sim-d}}$ of birds at northern latitudes, which captures the presence of a strong Holarctic element in the avifauna along the arctic coast (Mayr 1946). Such differences in $\beta_{\text{sim-d}}$ reveal the individual biogeographic histories of the taxa and may arise from variation in dispersal ability, particularly in relation to historical factors such as glaciation and faunal interchange (Duellman 1999; Hawkins & Porter 2003). For instance, the elevated mammal $\beta_{\text{sim-d}}$ in South America's southern cone reflects a transition in the region's diverse mammal lineages, notably the radiation of narrow-ranging Hystrignathi rodents (Herskovitz 1972), while the high amphibian $\beta_{\text{sim-d}}$ of the southern Appalachian

Mountains results from the diversification of salamanders within these stable, moist environments (Duellman 1999).

Congruence in Overall β_{sim-d} Patterns

Pair-wise correlations of amphibian, bird, and mammal β_{sim-d} across the Western Hemisphere were positive and significant ($\rho = 0.340\text{--}0.553$, $P < 0.001$ for all; see Materials and Methods), complementing the broad-scale concordance previously reported for the taxa in both richness and endemism (Table 3.3, Figure 3.3) (Lamoreux *et al.* 2006). When measured at the extent of a single biogeographic realm, however, we found that pair-wise congruence was greater within the Neotropics ($\rho = 0.636\text{--}0.695$, $P < 0.001$ for all) than at the hemisphere extent, but within the Nearctic was comparatively weak (amphibians and mammals: $\rho = 0.390$, $P < 0.05$; birds and mammals: $\rho = 0.405$, $P < 0.001$) or even lacking (amphibians and birds: $\rho = 0.032$, *ns*) (Table 3.3, Figure 3.3). The disparity in congruence strength between the realms indicates that congruence measured across large regions can hide incongruities that manifest at reduced spatial extents (Gaston 1996; Prendergast 1997).

To examine congruence at even smaller extents, we used a moving-window algorithm that calculated the correlation in β_{sim-d} between each pair of taxa within a 350 km radius of each grid cell (see Materials and Methods). Composite maps of the resulting correlation coefficients for the pairs revealed considerable geographic variation in congruence (Figure 3.4). Although the majority of correlations were strongly positive, others were weak or strongly negative. The latter were most apparent in the Nearctic realm for correlations with amphibians. Understanding the dependence of diversity relationships on observational scale is of pressing concern for ecology, biogeography, and conservation planning (Pressey *et al.* 1993; Prendergast 1997; Nekola & White 1999; Lennon *et al.* 2001). Our analyses demonstrate that both the geographic location and the spatial extent of analysis affect the level of congruence observed in β_{sim-d} , and emphasize the need for tests across multiple scales and regions in order to make objective comparisons among ecological studies.

Spatial Overlap in High and Low β_{sim-d}

Correlations across all grid cells do not necessarily indicate the level of cross-taxon spatial coincidence in areas of highest or lowest β_{sim-d} – a more useful measure for conservation planning and biogeographic delineation (Prendergast *et al.* 1993; Gaston 1996; van Rensburg *et al.* 2004). Congruence in the extremes of diversity is frequently measured as the degree of overlap in matching percentage sets of two groups (Prendergast *et al.* 1993; Orme *et al.* 2005). We evaluated high and low β_{sim-d} congruence for the pairs of taxa and between all three groups as the proportion of maximum possible overlap (Prendergast *et al.* 1993) in matching percentage sets of the highest 2.5% and lowest 2.5% of each taxon's β_{sim-d} grid cells (see Materials and Methods).

Spatial coincidence in high β_{sim-d} was greatest between amphibians and birds (51.6%). These taxa showed lower, but similar levels of overlap in high β_{sim-d} with mammals (21.5% and 29.2% respectively), and coincidence between all three groups was minimal (15.1%). Grid cells with overlapping high β_{sim-d} primarily occurred in the Northern and Southern Andes (Figure 3.5), consistent with the former as a center of endemism for all three taxa and with the extreme climatic gradient within the latter (Duellman 1999; Baillie *et al.* 2004). A substantial proportion of grid cells were found only in the high β_{sim-d} percentage sets of one taxon. For example, 41.9% of amphibian high β_{sim-d} grid cells were unique, as were 35.4% of bird grid cells and 64.6% of mammal grid cells. The distribution of these grid cells reflects the specific biogeographies of each taxon. Whereas unique grid cells were predominantly located in the Northern Andes for birds and in the Central American highlands for amphibians, unique mammal grid cells were largely outside the tropics (Figure 3.5).

There was comparatively little spatial coincidence in the lowest 2.5% of β_{sim-d} . Low β_{sim-d} of birds and mammals showed the most overlap, at only 11.5%. Coincidence was negligible for the other two pairs of taxa (amphibians and mammals, 5.4%; amphibians and birds, 2.2%), and there was no overlap among all three groups. Accordingly, the majority of grid cells in the low β_{sim-d} percentage sets were restricted to one taxon (83.3–92.5%). These grid cells were located mainly in the boreal and arctic regions of the Nearctic realm for amphibians and mammals, respectively (Figure 3.5).

Conversely, most unique bird grid cells occurred in the Neotropics within several biomes, including a substantial number in the Amazon Basin (Figure 3.5).

The degree of overlap in matching percentage sets, however, does not provide a complete picture of spatial coincidence in the extremes of $\beta_{\text{sim-d}}$. In fact, the majority of highest $\beta_{\text{sim-d}}$ grid cells for all three taxa actually had relatively high levels of $\beta_{\text{sim-d}}$ of the other groups (Figure 3.6), indicating that areas of high beta-diversity largely coincide. On average more than two-thirds of grid cells in the highest 2.5% of one taxon's $\beta_{\text{sim-d}}$ grid cells were also in the highest 10% of $\beta_{\text{sim-d}}$ for the other taxa ($70.0 \pm 8.7\%$, range = 61.5–81.7%). This was not true for low $\beta_{\text{sim-d}}$. Low $\beta_{\text{sim-d}}$ grid cell sets exhibited greater variation in $\beta_{\text{sim-d}}$ values for the other taxa than did the high $\beta_{\text{sim-d}}$ sets. Moreover, less than one quarter of the lowest 2.5% of one taxon's $\beta_{\text{sim-d}}$ grid cells were in the lowest 10% of $\beta_{\text{sim-d}}$ for the other taxa ($21.9 \pm 14.6\%$, range = 2.9–40.6%), further evidence that areas of low $\beta_{\text{sim-d}}$ are spatially distinct (Figure 3.6).

Conclusions

Congruence in beta-diversity of three groups of terrestrial vertebrates is highly dependent on the geographic location and extent of analysis, reflecting taxonomic and regional variation in the influence of large-scale historical processes and environmental factors (Nekola & White 1999; Condit *et al.* 2002; Tuomisto *et al.* 2003; Qian *et al.* 2005; Graham *et al.* 2006). Our results show that although correlations in amphibian, bird, and mammal $\beta_{\text{sim-d}}$ measured at small extents vary in strength throughout the Western Hemisphere, congruence is generally stronger within the Neotropical realm than within the Nearctic. This difference may be part of a broader asymmetry in biodiversity patterns between the northern and southern hemispheres (Chown *et al.* 2004; Orme 2006). The weak pairwise correlations within the Nearctic realm, as well as the minimal overlap in both high and low $\beta_{\text{sim-d}}$, could result from differing responses of amphibians, birds, and mammals to the realm's climatic and geologic history (Duellman 1999; Hawkins & Porter 2003). In contrast, the comparatively strong $\beta_{\text{sim-d}}$ congruence in the Neotropics is indicative of common patterns of speciation and extinction histories. This is particularly apparent within the Neotropical mountains

where the substantial overlap in high $\beta_{\text{sim-d}}$ among the three groups underscores the importance of this region in generating diversity. Variation in $\beta_{\text{sim-d}}$ congruence also has implications for conservation, because the efficacy of conservation surrogates and efforts to model overall biodiversity distribution depend on taxa having concordant beta-diversity patterns (Ferrier 2002). Our results largely support these approaches, but it is important to recognize limitations that may arise from differing congruence levels among biogeographic realms.

Regions of rapid species turnover require increased attention to the placement and size of conservation areas in order to protect biodiversity. Spatial coincidence in areas of high $\beta_{\text{sim-d}}$ is therefore encouraging as successful conservation strategies in these places may be resource intensive. Conservation planning, of course, must occur across hierarchical scales in order to ensure adequate representation (Pressey *et al.* 1993; Margules & Pressey 2000). Broad-scale analyses of $\beta_{\text{sim-d}}$ highlight regions where protected areas should be closely spaced to effectively conserve biodiversity, however, the optimal configuration for conservation networks will depend on finer scale beta-diversity patterns (Kattan *et al.* 2006). Mapping broad-scale $\beta_{\text{sim-d}}$ can also identify areas where species face increasing threat to persistence. For example, because $\beta_{\text{sim-d}}$ is high where species' ranges are particularly susceptible to climatic variability such as steep environmental gradients and centers of endemism (Hannah *et al.* 2002; Bush 2002; Pounds *et al.* 2006), or at biome transitions where range shifts are most noticeable (Hannah *et al.* 2002; Bush 2002), we suggest that areas of high $\beta_{\text{sim-d}}$ are likely to be especially vulnerable to climate change.

The unique biogeography of the Western Hemisphere – the great variation in the effects of Pleistocene glaciation, the complex of mountain chains along much of the western coast, and the relative isolation of the continents – has played a major role in shaping the distribution and evolution of biodiversity. More work is needed to determine if our findings will extend to other parts of the world with different geologic and biogeographic histories. Is congruence always stronger in the southern hemisphere than the northern? Are topography and biome transitions associated with high broad-scale beta-diversity across the globe? These questions, and others regarding the relative

contributions of historical factors and current ecological interactions in determining beta-diversity patterns, are an important area for future inquiry.

Our results describe patterns of species turnover at a 100 x 100 km resolution. As comprehensive finer resolution data become available, further analyses will confirm whether the levels of beta-diversity and congruence we found are consistent at smaller grain sizes. Future research is also needed to ascertain the degree to which our results can be generalized to other taxa, especially more distantly related groups or those that show large variation in dispersal ability. For instance, taxa with poor dispersal and low rates of gene flow are apt to exhibit higher beta-diversity than those groups that have high dispersal and high rates of gene flow. However, we believe that some of our findings, such as the strong relationship between topography and beta-diversity, will prove true for most taxa.

Materials and Methods

Data

Analyses were based on range data for extant species of amphibians ($n = 2,174$), breeding birds ($n = 3,882$), and mammals ($n = 1,611$) in the Western Hemisphere (IUCN *et al.* 2004; Ridgely *et al.* 2005; Patterson *et al.* 2005). The number of species in these groups is not static as new species, especially of amphibians, continue to be discovered (Collins & Halliday 2005). However, the areas from which species are most often described tend to be the same and will likely accentuate the patterns we present (Watson 2005). The maps used for this study are available as digital vector files (ArcView format) at <http://www.natureserve.org>, along with a detailed description of the production process and a complete list of sources. Maps for 630 amphibian species with an IUCN Red List category of Data Deficient (DD) (<http://www.redlist.org>) were excluded from analyses because of the unreliability of their range maps. The exclusion of these species did not substantially affect our results (correlation between amphibian $\beta_{\text{sim-d}}$ using all mapped species and amphibian $\beta_{\text{sim-d}}$ excluding DD species; $\rho = 0.993$, $ess = 158.6$, $P < 0.001$). We confined our analyses to terrestrial breeding birds and we provide a map of bird $\beta_{\text{sim-d}}$ based on both breeding and non-breeding ranges of all terrestrial birds

($n = 3,890$) for comparison. $\beta_{\text{sim-d}}$ of all birds (Figure 3.7) was highly correlated with $\beta_{\text{sim-d}}$ of breeding birds (Figure 3.1) ($\rho = 0.954$, $\text{ess} = 249.12$, $P < 0.001$).

We recorded the presence/absence of each species in 100 km X 100 km equal-area grid cells, roughly equivalent to $1^\circ \times 1^\circ$ at the equator (Behrmann projection, WGS84 datum); a species was considered present if any portion of its range (exclusive of polygons coded as introduced, migratory, or vagrant) occurred within the continental land area of the grid cell. Grid cells on the perimeter of the continents vary considerably in the amount of land they contain, particularly those along the narrow Isthmus of Panama. To avoid potential effects of species-area relationships or errors from range map boundary placement, only grid cells containing $\geq 40\%$ of continental land were included in the analyses (grid cells: $n = 3,693$ for amphibians; $n = 3,821$ for birds and mammals). Estimates of $\beta_{\text{sim-d}}$ using this cut off were not appreciably different from those based on a more conservative cut off of 75% land area, but allowed for the inclusion of additional species. Grid cells were classified as either Nearctic ($n = 1,744$ for amphibians; $n = 1,862$ for birds and mammals), Neotropical ($n = 1,878$, amphibians; $n = 1,888$, birds and mammals), or transitional between the two biogeographic realms ($n = 71$ for all taxa) (Olson *et al.* 2001). Transitional grid cells were not included in analyses at the realm extent.

Analyses

We used a moving window algorithm to model the distance decay of similarity from each individual grid cell in order to calculate a value of beta-diversity, $\beta_{\text{sim-d}}$, as the estimated proportional turnover at 100 km based on the resulting regression parameters for that grid cell. Considering comparisons between grid cells over a range of distances helps alleviate concerns typical of gridded nearest-neighbor analyses of large-scale species distributions. For example, artifacts may arise from the small-scale errors that can occur in range boundary placement when converting polygon maps into gridded data, as well as from the discrepancy in centroid to centroid distance and shared perimeter length between orthogonal and diagonal neighbors of a rectangular grid.

Similarity (S) between two grid cells was calculated as the complement of β_{sim} (i.e., $S = 1 - \beta_{\text{sim}}$), a dissimilarity metric which isolates change due to species replacement from differences in species richness: $\beta_{\text{sim}} = \min(b,c)/(a + \min(b,c))$, where a is the number of species shared, b is the number of species found only in the second grid cell, and c is the number of species found only in the first grid cell, making $\min(b,c)$ the number of unshared species in the more depauperate grid cell (Lennon *et al.* 2001; Koleff *et al.* 2003b). Therefore, $S = 1 - \beta_{\text{sim}} = a/(a + \min(b,c))$, or the proportion of species in the more depauperate grid cell that also occur in the other grid cell.

Note that $S/1-S$ is a transformation of the ratio of shared species to unshared species in the more depauperate grid cell, or $a/\min(b,c)$. This enables us to model distance decay using a logistic regression defined such that: $\ln(a/\min(b,c)) = I + r \cdot \ln(d)$, where d is the centroid to centroid distance, and I and r are fitted regression coefficients. Logistic regression has several advantages over linear and log-linear ordinary least-square regressions, resulting in a better empirical fit than other techniques (Ferrier *et al.* 2002). First, because observed values of S are not directly log transformed, values of either 0 or 1 do not cause problems for the estimation process. Second, \hat{S} is also bound between 0 and 1. Third, the binomial error distribution used accounts for the greater variance in S at low species numbers.

The distance decay regression at each window was built using between-grid cell comparisons of the focal grid cell to all grid cells within a ≤ 500 km centroid to centroid radius. This arbitrary distance was chosen after experimenting with several other maximum distances (350, 1000, 1500, 2000, and 3000 km) because it provided a sufficient total number of between-grid comparisons (i.e., sample size), spread over a range of distances, to ensure a robust distance decay relationship, but did not result in an over-smoothed beta-diversity surface as occurred with greater maximum distances (as judged by visual comparisons of the maps). The resulting regression coefficients for each grid cell were used to estimate $\beta_{\text{sim-d}}$ as $(1 - \hat{S}_d)$ for $d = 100$ km. $\beta_{\text{sim-d}}$ therefore is the value of β_{sim} at distance of 100km predicted by the distance decay model. Turnover at this distance, which is the minimum distance between adjacent grid cells, is more intuitive than that between distant grid cells for

discussion and graphical representation of beta-diversity as a continuous surface, and makes it easier to compare our results to other broad-scale diversity analyses.

Although the number of grid cells included in a regression model decreased with increased proximity to the coast (including major interior water bodies), graphical examination of scatterplots and the resulting maps showed that coastal effects were negligible for amphibians and mammals and varied geographically for birds. The elevated bird $\beta_{\text{sim-d}}$ on some coastal sections likely has a biological rather than methodological basis (Lennon *et al.* 2001). It is important to remember that $\beta_{\text{sim-d}}$ quantifies change in species composition between 100 km X 100 km grid cells, and therefore does not reflect the level of heterogeneity *within* a grid cell. Furthermore, $\beta_{\text{sim-d}}$ is a measure of proportional species turnover and does not represent the absolute number of species gained or lost between grid cells. Lastly, while the smooth surface that results from modeling the effect of distance on similarity reduces the effect of potential errors in gridded large-scale range data, extremely abrupt transitions may be attenuated. However, the major patterns found for $\beta_{\text{sim-d}}$ were also apparent in maps of average nearest-neighbor beta-diversity (the average dissimilarity (β_{sim}) of a focal grid cell and its orthogonal and diagonal neighbors) (Figure 3.8). Further, a comparison of Table 3.3 with pair-wise correlations of average β_{sim} (Table 3.4) shows that the congruence levels we report are not artifacts of the smoothing process.

We tested whether grid cells containing high $\beta_{\text{sim-d}}$ or those with low $\beta_{\text{sim-d}}$ differed significantly in elevation or were found on a greater number of biome edges than could be expected by chance (Manly 1997). To do this, we selected sets of grid cells containing the highest 2.5% and the lowest 2.5% of $\beta_{\text{sim-d}}$ values for each taxon (2.5% = 93 grid cells for amphibians, 96 grid cells for birds and mammals), and calculated the mean elevation and mean number of biome edges for each set. We then compared these values to distributions of values for the mean elevation and mean number of biome edges, respectively, calculated for 10,000 sets of randomly selected grid cells (grid cells per random set: $n = 93$ for amphibians; $n = 96$ for birds and mammals). For each comparison, we computed a one-tailed P -value by counting the number of values in the random distribution greater than or equal to the

value of a high $\beta_{\text{sim-d}}$ set – or less than or equal to the value of a low $\beta_{\text{sim-d}}$ set. Elevation was measured as the mean elevation within a grid cell from a digital elevation model (DEM) of approximately 1 km X 1 km resolution (The Global 30 Arc Second Elevation Data Set, <http://www1.gsi.go.jp/geowww/globalmap-gsi/gtopo30/gtopo30.html>). Following van Rensburg *et al.* (van Rensburg *et al.* 2004), we considered a grid cell to be on a biome edge if a biome (as delineation by Olson *et al.* (2001)) covering $\geq 5\%$ of that grid cell also covered $< 5\%$ of any of the neighboring grid cells. The number of biome edges was then calculated as the number of biomes in that grid cell meeting this definition.

To evaluate the overall relationships between $\beta_{\text{sim-d}}$ and elevation and between $\beta_{\text{sim-d}}$ and number of biome boundaries within a grid cell, we calculated the correlation between $\beta_{\text{sim-d}}$ of the three taxa and each environmental variable. Correlations were calculated with Spearman rank correlation coefficients to accommodate the non-normal distributions of $\beta_{\text{sim-d}}$. Standard significance tests are not appropriate for autocorrelated data because the assumption of independence is violated, therefore we tested for significance using a method developed by Clifford *et al.* (1989) that corrects the sample size of two variables based on the level of the spatial dependency in and between them (Lennon *et al.* 2001). We calculated the “estimated sample size” (*ess*) for each pair of variables using the PASSAGE software package (Rosenberg 2001), and then used the corrected degrees of freedom to test the significance of each correlation.

Pair-wise congruence at the hemisphere and biogeographic realm extents was measured as the correlation in $\beta_{\text{sim-d}}$ values of each pair of taxa, and significance was tested using the method described above. To examine congruence at extents smaller than a biogeographic realm, we calculated the correlation in $\beta_{\text{sim-d}}$ values within a ≤ 350 km radius window (centroid to centroid distance) around each grid cell. We used this window size because it provided a better representation of the geographic variation in $\beta_{\text{sim-d}}$ at small extents than the other window sizes we experimented with (radii of 150, 250, and 450 km). The same overall pattern was also apparent using larger windows but became increasingly muted as the extent widened. Moreover, larger windows had a greater discrepancy in the

number of grid cells occurring within windows around coastal versus inland grid cells, while smaller windows considerably decreased the number of grid cells across which congruence was measured. The ≤ 350 km window was not substantially affected by either of these issues, and differences that did exist in the number of grid cells within coastal and interior windows did not appear to influence the geographical variation in congruence.

Spatial overlap between matching percentage sets of the highest 2.5% and lowest 2.5% of $\beta_{\text{sim-d}}$ grid cells for each pair of taxa and of all three groups was calculated as the maximum overlap possible (Prendergast *et al.* 1993): N_c/N_t , where N_c is the number of grid cells common to the sets and N_t is the total number of grid cells in the smallest set (amphibians have slightly fewer grid cells than birds or mammals).

References

- Baillie, J.E.M., Hilton-Taylor, C. & Stuart, S.N. (2004) *2004 IUCN Red List of threatened species: a global species assessment*. IUCN, Gland, Switzerland.
- Blackburn, T.M. & Gaston, K.J. (1996) The distribution of bird species in the New World: patterns in species turnover. *Oikos* 77, 146-152.
- Bush, M.B. (2002) Distributional change and conservation on the Andean flank: a palaeoecological perspective. *Global Ecology and Biogeography* 11, 463-473.
- Chown, S.L., Sinclair, B.J., Leinaas, H.P. & Gaston, K.J. (2004) Hemispheric asymmetries in biodiversity – a serious matter for ecology. *Public Library of Science, Biology* 2, 1701-1707.
- Clifford, P., Richardson, S. & Hemon, D. (1989) Assessing the significance of the correlation between two spatial processes. *Biometrics* 45, 123-134.
- Cody, M.L. (1986) Diversity, rarity, and conservation in Mediterranean-climate ecosystems. *Conservation biology: the science of scarcity and diversity* (ed. by M.E. Soulé), pp. 122-152. Sinauer Associates, Sunderland, MA.
- Collins, J.P. & Halliday, T. (2005) Forecasting changes in amphibian biodiversity: aiming at a moving target. *Philosophical Transactions of the Royal Society B-Biological Sciences* 360, 309-314.
- Condit, R., Pitman, N., Leigh, E.G. Jr., Chave, J., Terborgh, J., Foster, R.B., Núñez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. & Hubbell, S.P. (2002) Beta-diversity in tropical forest trees. *Science* 295, 666-669.
- Drakare, S., Lennon, J.J. & Hillebrand, H. (2006) The imprint of the geographical, evolutionary and ecological context on species-area relationships. *Ecology Letters* 9, 215-227.
- Duellman, W.E. (1999) *Patterns of distribution of amphibians: a global perspective*. The Johns Hopkins University Press, Baltimore, MD.
- Fairbanks, D.H.K., Reyers, B. & van Jaarsveld, A.S. (2001) Species and environment representation: selecting reserves for the retention of avian diversity in KwaZulu-Natal, South Africa. *Biological Conservation* 98, 365-379.
- Ferrier, S. (2002) Mapping spatial pattern in biodiversity for regional conservation planning: Where to from here? *Systematic Biology* 51, 331-363.
- Ferrier, S., Drielsma, M., Manion, G. & Watson, G. (2002) Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. II. Community-level modelling. *Biodiversity and Conservation* 11, 2309-2338.
- Ferrier, S., Powell, G.V.N., Richardson, K.S., Manion, G., Overton, J.M., Allnutt, T.F., Cameron, S.E., Mantle, K., Burgess, N.D., Faith, D.P., Lamoreux, J.F., Kier, G., Hijmans, R.J., Funk, V.A., Cassis, G.A., Fisher, B.L., Flemons, P., Lees, D., Lovett, J.C. & Rompaey, R.S.A.R. (2004) Mapping more of terrestrial biodiversity for global conservation assessment. *BioScience* 54, 1101-1109.

- Gascon, C., Malcolm, J.R., Patton, J.L., da Silva, M.N.F., Bogart, J.P., Loughheed, S.C., Peres, C.A., Neckel, S. & Boag, P.T. (2000) Riverine barriers and the geographic distribution of Amazonian species. *Proceedings of the National Academy of Sciences, USA* 97, 13672-13677.
- Gaston, K.J. (1996) Biodiversity – Congruence. *Progress in Physical Geography* 20, 105-112.
- Graham, C.H., Moritz, C. & Williams, S.E. (2006) Habitat history improves prediction of biodiversity in rainforest fauna. *Proceedings of the National Academy of Sciences, USA* 103, 632-636.
- Hannah, L., Midgley, G.F. & Millar, D. (2002) Climate change-integrated conservation strategies. *Global Ecology and Biogeography* 11, 485-495.
- Harrison, S., Ross, S.J. & Lawton, J.H. (1992) Beta-diversity on geographic gradients in Britain. *Journal of Animal Ecology* 61, 151-158.
- Hawkins, B.A. & Porter, E.E. (2003) Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. *Global Ecology and Biogeography* 12, 475-481.
- Hershkovitz, P. (1972) The recent mammals of the Neotropical region: a zoogeographic and ecological review. *Evolution, mammals, and southern continents* (ed. by A. Keast, F.C. Erk, and B. Glass), pp. 311-431. State University of New York Press, Albany, New York.
- Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.
- IUCN, Conservation International & NatureServe (2004) *Global amphibian assessment*. IUCN/Conservation International/NatureServe, Washington, D.C. and Arlington, VA.
- Kattan, G.H., Franco, P., Saavedra-Rodríguez, C.A., Valderrama, C., Rojas, V., Osorio, D. & Martínez, J. (2006) Spatial components of bird diversity in the Andes of Colombia: implications for designing a regional reserve system. *Conservation Biology* 20, 1203-1211.
- Koleff, P., Lennon, J.J. & Gaston, K.J. (2003a) Are there latitudinal gradients in species turnover? *Global Ecology and Biogeography* 12, 483-498.
- Koleff, P., Gaston, K.J. & Lennon, J.J. (2003b) Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* 72, 367-382.
- Lamoreux, J.F., Morrison, J.M., Ricketts, T.H., Olson, D.M., Dinerstein, E., McKnight, M.W. & Shugart, H.H. (2006) Global tests of biodiversity concordance and the importance of endemism. *Nature* 440, 212-214.
- Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70, 966-979.
- Manly, B.F.J. (1997) *Randomization, bootstrap and Monte Carlo methods in biology*. Chapman and Hall, London, UK.

- Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature* 405, 243-253.
- Mayr, E. (1946) History of the North American bird fauna. *Wilson Bulletin* 58, 3-41.
- Moritz, C., Richardson, K.S., Ferrier, S., Monteith, G.B., Stanisci, J., Williams, S.E. & Whiffin, T. (2001) Biogeographical concordance and efficiency of taxon indicators for establishing conservation priority in a tropical rainforest biota. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268, 1875-1881.
- Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* 26, 867-878.
- Nekola, J.C. & White, P.S. (2002) Conservation, the two pillars of ecological explanation, and the paradigm of distance. *Natural Areas Journal* 22, 305-310.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* 51, 933-938.
- Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J. & Owens, I.P.F. (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436, 1016-1019.
- Orme, C.D.L., Davies, R.G., Olson, V.A., Thomas, G.H., Ding, T-S., Rasmussen, P.C., Ridgely, R.S., Stattersfield, A.J., Bennett, P.M., Owens, I.P.F., Blackburn, T.M. & Gaston, K.J. (2006) Global patterns of geographic range size in birds. *Public Library of Science, Biology* 4, 1276-1283.
- Patterson, B.D., Ceballos, G., Sechrest, W., Tognelli, M.F., Brooks, T., Luna, L., Ortega, P., Salazar, I. & Young, B.E. (2005) *Digital distribution maps of the mammals of the Western Hemisphere*. NatureServe, Arlington, VA.
- Pimm, S.L. & Gittleman, J.L. (1992) Biological diversity – Where is it? *Science* 255, 940.
- Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J. & Young, B.E. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439, 161-167.
- Prendergast, J.R. (1997) Species richness covariance in higher taxa: empirical tests of the biodiversity indicator concept. *Ecography* 20, 210-216.
- Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. & Gibbons, D.W. (1993) Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365, 335-337.
- Pressey, R.L., Humphries, C.J., Margules, C.R., Vane-Wright, R.I. & Williams, P.H. (1993) Beyond opportunism: key principles for systematic reserve selection. *Trends in Ecology and Evolution* 8, 124-128.

- Qian, H., Ricklefs, R.E. & White, P.S. (2005) Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters* 8, 15-22.
- Reid, W.V. (1998) Biodiversity Hotspots. *Trends in Ecology and Evolution* 13, 275-280.
- Ricketts, T.H., Dinerstein, E., Boucher, T., Brooks, T.M., Butchart, S.H.M., Hoffmann, M., Lamoreux, J.F., Morrison, J., Parr, M., Pilgrim, J.D., Rodrigues, A.S., Sechrest, W., Wallace, G.E., Berlin, K., Bielby, J., Burgess, N.D., Church, D.R., Cox, N., Knox, D., Loucks, C., Luck, G.W., Master, L.L., Moore, R., Naidoo, R., Ridgely, R., Schatz, G.E., Shire, G., Strand, H., Wettengel, W. & Wikramanayake, E. (2005) Pinpointing and preventing imminent extinctions. *Proceedings of the National Academy of Sciences, USA* 102, 18497-18501.
- Ridgely, R.S., Allnutt, T.F., Brooks, T., McNicol, D.K., Mehlman, D.W., Young, B.E. & Zook, J.R. (2005) *Digital distribution maps of the birds of the Western Hemisphere*. NatureServe, Arlington, VA.
- Rosenberg, M.S. (2001) *PASSAGE (Pattern analysis, spatial statistics, and geographic exegesis), Version 1.1.2.3*. Department of Biology, Arizona State University, Tempe, AZ.
- Sarkar, S. (2006) Ecological diversity and biodiversity as concepts for conservation planning: comments on Ricotta. *Acta Biotheoretica* 54, 133-140.
- Shmida, A. & Wilson, M.V. (1985) Biological determinants of species-diversity. *Journal of Biogeography* 12, 1-20.
- Steinitz, O., Heller, J., Tsoar, A., Rotem, D. & Kadmon, R. (2005) Predicting regional patterns of similarity in species composition for conservation planning. *Conservation Biology* 19, 1978-1988.
- Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. & Waller, R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science* 306, 1783-1786.
- Su, J.C., Debinski, D.M., Jakubauskas, M.E. & Kindscher, K. (2004) Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. *Conservation Biology* 18, 167-173.
- Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003) Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299, 241-244.
- van Rensburg, B.J., Koleff, P., Gaston, K.J. & Chown, S.L. (2004) Spatial congruence of ecological transition at the regional scale in South Africa. *Journal of Biogeography* 31, 843-854.
- Watson, D.M. (2005) Diagnosable versus distinct: evaluating species limits in birds. *BioScience* 55, 60-68.
- Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30, 279-338.
- Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon* 21, 213-251.

- Williams, P.H. (1996) Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. *Proceedings of the Royal Society of London Series B-Biological Sciences* 263, 579-588.
- Williams, P.H. (1998) Key sites for conservation: area-selection methods for biodiversity. *Conservation in a changing world* (ed. by G.M. Mace, A. Balmford and J.R. Ginsberg), pp. 211-250. Cambridge University Press, Cambridge, UK.
- Williams, P.H., de Klerk, H.M. & Crowe, T.M. (1999) Interpreting biogeographical boundaries among Afrotropical birds: Spatial patterns in richness gradients and species replacement. *Journal of Biogeography* 26, 459-474.

Table 3.1. Correlations between beta-diversity (β_{sim-d}) and two environmental variables (elevation and number of biome edges within grid cells). Spearman rank correlation coefficients (ρ), number of grid cells (n), and corrected sample size (ess) from each pair-wise comparison are shown.

	Amphibian β_{sim-d}			Bird β_{sim-d}			Mammal β_{sim-d}		
	ρ	n	ess	ρ	n	ess	ρ	n	ess
Mean Elevation (m)	0.219*	3,693	94.96	0.316**	3821	118.16	0.427**	3,821	68.29
Number of Biome Edges	0.307**	3693	261.16	0.320**	3821	281.65	0.295**	3821	130.18

** $P < 0.001$, * $P < 0.05$

Table 3.2. Mean elevation and mean number of biome edges for sets of the highest 2.5% and lowest 2.5% of beta-diversity ($\beta_{\text{sim-d}}$) grid cells. Significance was tested with 10,000 random sets of an equal number of grid cells.

	Low $\beta_{\text{sim-d}}$	High $\beta_{\text{sim-d}}$
Mean elevation (m)		
Amphibians	480.49*	1681.36**
Birds	291.61**	1642.31**
Mammals	198.29**	1543.51**
Biome edge proportion		
Amphibians	0.39**	0.98**
Birds	0.28**	0.95**
Mammals	0.19**	0.97**

** $P < 0.001$, * $P < 0.05$

Table 3.3. Correlations in beta-diversity (β_{sim-d}) within the Western Hemisphere, Nearctic realm, and Neotropical realm. Spearman rank correlation coefficients (ρ), number of grid cells (n), and corrected sample size (ess) from each pair-wise comparison are shown.

	Amphibians and birds			Amphibians and mammals			Birds and mammals		
	ρ	n	ess	ρ	n	ess	ρ	n	ess
Western Hemisphere	0.340**	3,693	224.88	0.499**	3,693	104.68	0.553**	3,821	117.48
Nearctic Realm	0.032	1,744	122.68	0.390*	1,744	43.81	0.405**	1,862	68.94
Neotropical Realm	0.695**	1,878	86.44	0.636**	1,878	51.55	0.662**	1,888	52.44

** $P < 0.001$, * $P < 0.05$

Table 3.4. Correlations in average nearest-neighbor beta-diversity (β_{sim}) within the Western Hemisphere, Nearctic realm, and Neotropical realm. Spearman rank correlation coefficients (ρ), number of grid cells (n), and corrected sample size (ess) from each pair-wise comparison are shown.

	Amphibians and birds			Amphibians and mammals			Birds and mammals		
	ρ	n	ess	ρ	n	ess	ρ	n	ess
Western Hemisphere	0.325**	3,693	218.88	0.484**	3,693	99.49	0.512**	3,821	106.71
Nearctic Realm	0.103	1,744	90.33	0.417*	1,744	32.98	0.370*	1,862	59.01
Neotropical Realm	0.645**	1,878	87.28	0.596**	1,878	48.08	0.627**	1,888	46.19

** $P < 0.001$, * $P < 0.05$

Figure 3.1. Beta-diversity ($\beta_{\text{sim-d}}$) of amphibians, birds, and mammals mapped continuously across the continental Western Hemisphere. $\beta_{\text{sim-d}}$ values for each taxon are divided into 20 quantiles, represented by warm (higher $\beta_{\text{sim-d}}$) to cool colors (lower $\beta_{\text{sim-d}}$). The scale accompanying the color ramp for each taxon shows minimum, 1st quartile, median, 3rd quartile, and maximum values of $\beta_{\text{sim-d}}$. Gray grid cells do not contain amphibian species. (A) Amphibians. (B) Birds. (C) Mammals.

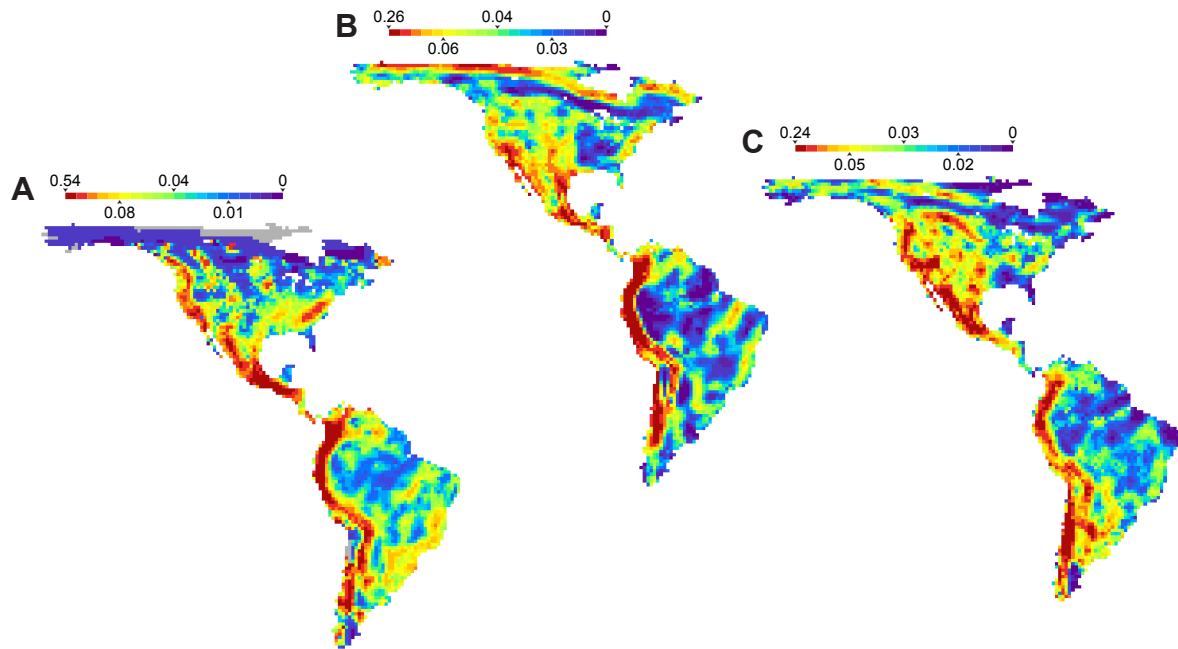


Figure 3.2. Scatterplots showing relationships between beta-diversity ($\beta_{\text{sim-d}}$) and two environmental variables (elevation and number of biome edges within grid cells). For each panel: untransformed (left plots) and transformed (right plots) values of $\beta_{\text{sim-d}}$ (y-axis) against either grid cell elevation (x-axis, upper plots) or number of biome edges within grid cell (x-axis, lower plots). In each plot, the red dots represent the highest 2.5% of $\beta_{\text{sim-d}}$ grid cells, and the purple dots show the lowest 2.5% of $\beta_{\text{sim-d}}$ grid cells. (A) Amphibians. (B) Birds. (C) Mammals.

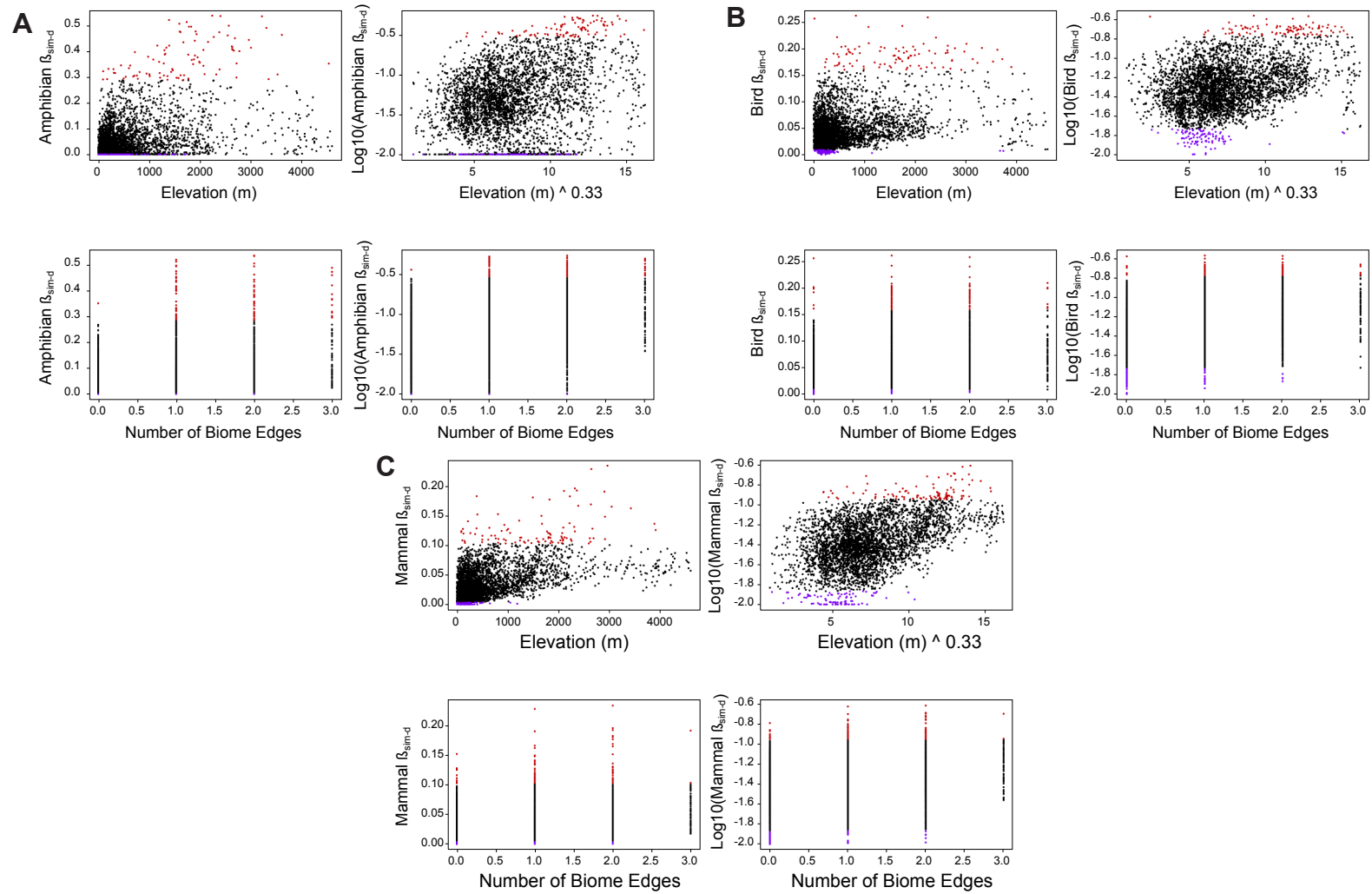


Figure 3.3. Relationships between beta-diversity ($\beta_{\text{sim-d}}$) of amphibians, birds, and mammals. Scatterplots show the relationship between $\beta_{\text{sim-d}}$ for each pair of taxa within the Western Hemisphere (WH, top row), the Nearctic realm (NA, middle row), and the Neotropical realm (NT, bottom row). The axes for each plot are scaled according to the maximum $\beta_{\text{sim-d}}$ value of the two taxa within the extent specified. Note that maximum values for all three taxa are greater in the Neotropics than in the Nearctic, and that amphibians reach much higher rates of assemblage change than either birds or mammals. (A) Amphibians and birds. (B) Amphibians and mammals. (C) Birds and mammals.

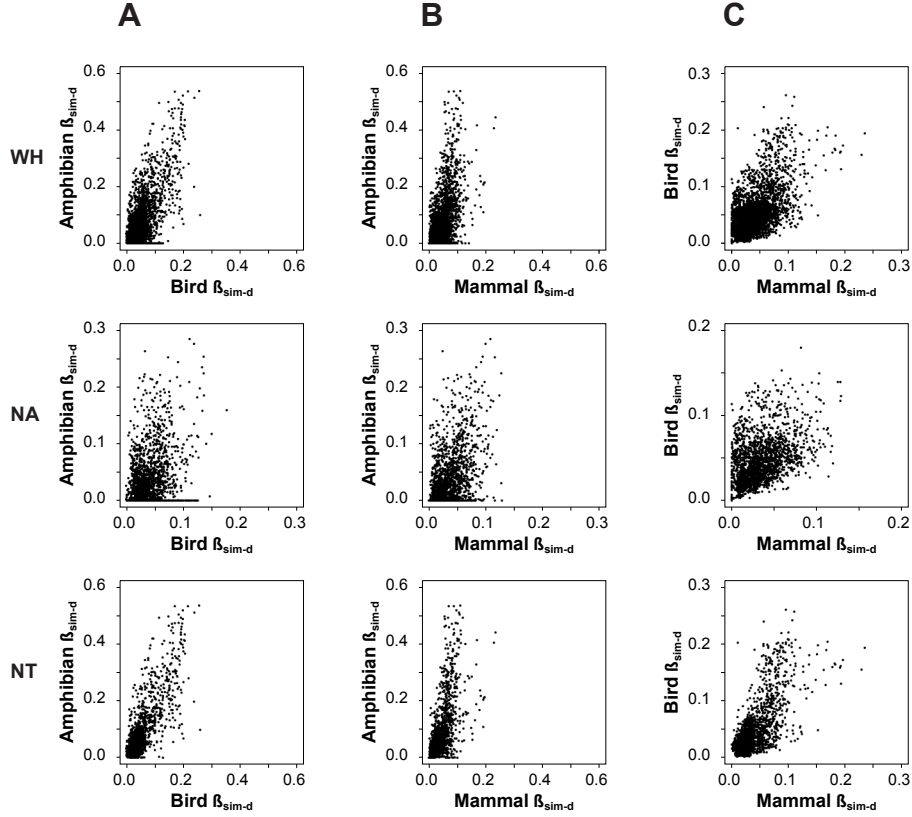


Figure 3.4. Geographic variation in beta-diversity ($\beta_{\text{sim-d}}$) congruence of amphibians, birds, and mammals at small spatial extents. The color of each grid cell in the maps indicates the correlation measured in beta-diversity ($\beta_{\text{sim-d}}$) between pairs of taxa for grid cells within a 350 km radius window. Orange shades represent strong (darkest) to weak (lightest) negative correlations. Purple shades show strong (darkest) to weak (lightest) positive correlations. Gray indicates very weak correlations of either sign or no correlation. Light gray grid cells do not contain amphibian species. Shown to the right of each map are frequency distributions of correlation coefficients for windows located within the entire Western Hemisphere (WH), the Nearctic realm (NA), and the Neotropical realm (NT), which are consistent with the level of congruence measured at these extents. The black line marks the boundary between the two realms. (A) Amphibians and birds. (B) Amphibians and mammals. (C) Birds and mammals.

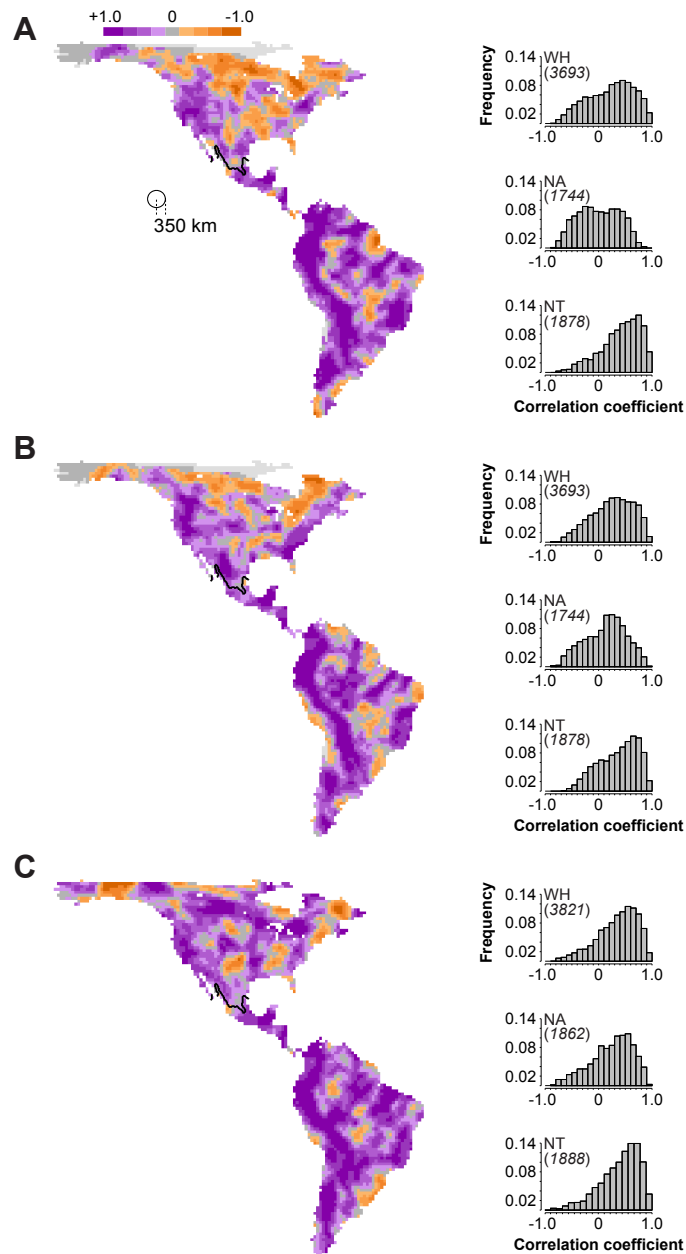


Figure 3.5. Geographic distribution of overlap in amphibian, bird, and mammal high and low beta-diversity ($\beta_{\text{sim-d}}$) areas. Spatial overlap in beta-diversity ($\beta_{\text{sim-d}}$) for percentage sets of each taxon's lowest (left) and highest (right) 2.5% of $\beta_{\text{sim-d}}$ grid cells is shown. Primary colors represent grid cells unique to one taxon (yellow, amphibians; blue, birds; red, mammals), secondary colors indicate overlap between two groups, and white shows overlap of all three groups. The height of the grid cells reflects the number of overlapping groups. Note the greater degree of spatial coincidence in high $\beta_{\text{sim-d}}$ than in low $\beta_{\text{sim-d}}$.

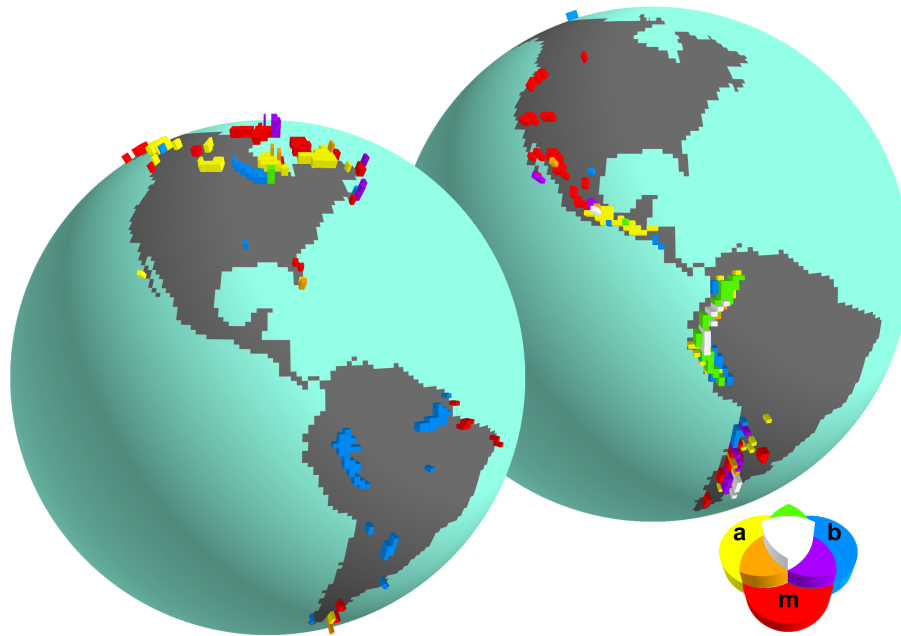


Figure 3.6. Levels of beta-diversity ($\beta_{\text{sim-d}}$) for vertebrate taxa within areas of high and low beta-diversity of amphibians, birds, and mammals. Percentage sets of the highest (A) and lowest (B) 2.5% of beta-diversity ($\beta_{\text{sim-d}}$) grid cells for one taxon contain a range of $\beta_{\text{sim-d}}$ levels for the other taxa (green, amphibians; blue, birds; purple, mammals), as shown by the box plots (median, 1st and 3rd quartiles, and minimum and maximum percentage rank of $\beta_{\text{sim-d}}$). The red dashed line indicates the highest or lowest 10% of $\beta_{\text{sim-d}}$.

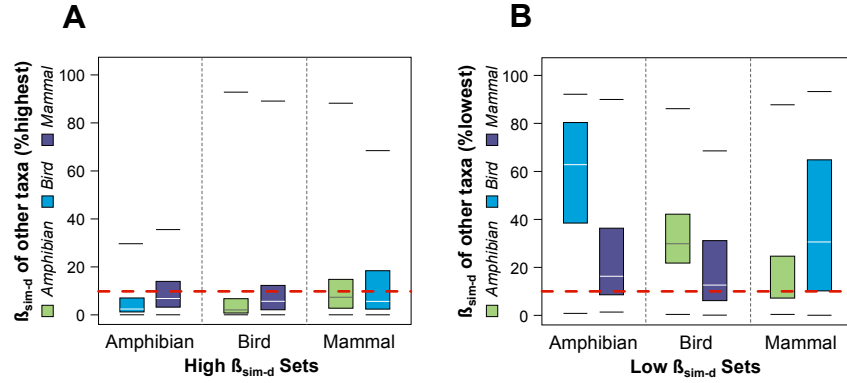


Figure 3.7. Bird beta-diversity ($\beta_{\text{sim-d}}$) based on both breeding and non-breeding ranges. Beta-diversity ($\beta_{\text{sim-d}}$) values are divided into 20 quantiles, represented by warm (higher $\beta_{\text{sim-d}}$) to cool colors (lower $\beta_{\text{sim-d}}$). The scale accompanying the color ramp shows minimum, 1st quartile, median, 3rd quartile, and maximum values of $\beta_{\text{sim-d}}$.

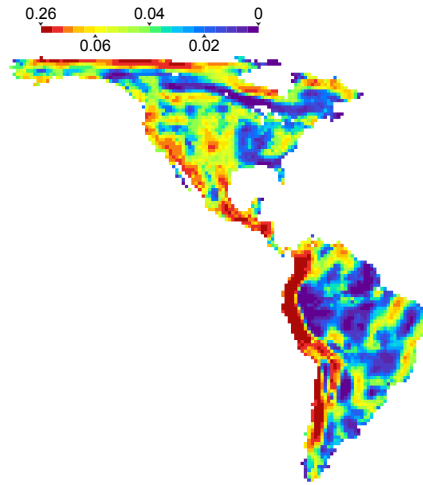
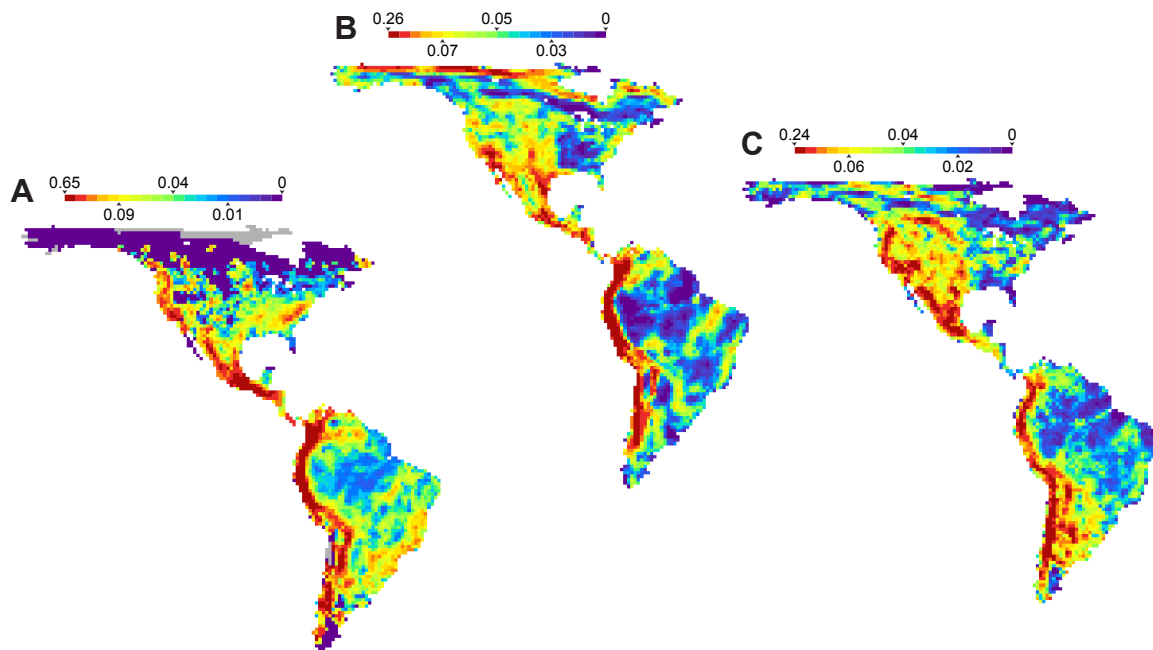


Figure 3.8. Average nearest-neighbor beta-diversity of amphibians, birds, and mammals mapped continuously across the continental Western Hemisphere. Average nearest-neighbor beta-diversity (β_{sim}) values are divided into 20 quantiles, represented by warm (higher β_{sim}) to cool colors (lower β_{sim}). The scale accompanying the color ramp shows minimum, 1st quartile, median, 3rd quartile, and maximum values of β_{sim} . Gray grid cells do not contain amphibian species. (A) Amphibians. (B) Birds. (C) Mammals.



CHAPTER 4

What Do Richness Patterns Miss?

The Relationship Between Broad-Scale Beta-Diversity and Species Richness¹

Abstract

Both species richness and beta-diversity contribute to patterns of biodiversity. However, their relative contributions and the differences between the environmental and geographic patterns of species richness and beta-diversity are not well known. Comparative studies of the two diversity components across multiple regions or taxa are lacking. We examined the relationship between beta-diversity and richness for three terrestrial vertebrate classes, amphibians, birds, and mammals, within the continental Western Hemisphere. For the hemisphere as a whole, we found no meaningful relationship between beta-diversity and richness for any group. However, there was considerable variation in the strength of the correlation and whether the relationship was positive or negative between regions with different biogeographic histories. The degree of coincidence in the high and low extremes of the two diversity measures also varied between taxa and regions. Such variation suggests that environmental, historic, and taxonomic differences influence the relationship observed between beta-diversity and species richness. Our results demonstrate that patterns of beta-diversity contain information that cannot be provided by measures of species richness.

¹ Chapter 4 was co-authored with Peter S. White.

Introduction

Diversity has two components. Inventory diversity, commonly referred to as richness, describes the species composition of a single place whereas differentiation diversity, also called beta-diversity, describes the turnover in species between places (Whittaker 1977). Richness, the simpler of the two components to measure and describe, has been the lens through which diversity patterns have been predominantly seen to the point that most ecologists view diversity patterns and richness patterns as synonymous. However, beta-diversity conveys information beyond that provided by richness. In short, the species richness of different places is not additive due to effects of varying beta-diversity, and this non-additive property means that richness maps cannot be used to assess the total richness at scales larger than the observational scales. Further, beta-diversity also has important applications in that it supports the delineation of biotic regions and the optimal configuration of conservation networks (Pimm & Gittleman 1992; Williams 1996; Nekola & White 1999, 2002; Williams *et al.* 1999; van Rensburg *et al.* 2004; see also Chapters 1 and 3). Broad-scale patterns of richness, particularly latitudinal gradients, have long been recognized and today are relatively well documented (Gaston 2000; Willig *et al.* 2003; Baillie *et al.* 2004). Moreover, there have been advances regarding the mechanisms driving richness at such scales (for review, see Gaston 2000; Hawkins *et al.* 2003). Beta-diversity patterns across large extents, conversely, are not well described (but see Williams 1996; Williams *et al.* 1999; Chapter 2) and the drivers of this component at broad scales have scarcely been examined.

In order to further investigate the mechanisms generating and maintaining diversity patterns across scales we must understand the relationship between beta-diversity and richness. For example, if the two components are congruent, much of what we know about the patterns, mechanisms, and scale dependency of richness may also apply to beta-diversity. But if they are not congruent, diversity becomes more complex as the processes underlying beta-diversity are likely quite different from those underlying richness. While a growing number of studies have examined the relationship between beta-diversity and richness by comparing latitudinal gradients of the two components (see

Koleff *et al.* 2003a and references therein), results have been mixed. Furthermore, few studies have actually quantified the relationship directly. Two analyses of bird diversity in Great Britain found that at relatively fine scales beta-diversity and richness were negatively correlated, but the relationship became weakly positive as grain increased (Lennon *et al.* 2001; Koleff & Gaston 2002). These authors suggested that at even larger scales, the relationship would be strongly positive. However, the studies were conducted in a region of limited spatial extent and one that, in a global context, is relatively species poor. The single study at a larger scale found little evidence of a relationship between beta-diversity and richness across the globe (Williams 1996).

Here, we test the relationship between broad-scale beta-diversity and species richness within the Western Hemisphere for three terrestrial vertebrate classes. We are, therefore, able to compare our results across groups without problems deriving from differences in methods or scales of analyses. As patterns of various diversity measures, and the relationships between them, have been found to vary among regions with different biogeographic histories (Chapter 3; Qian *et al.* 2005), we further test the relationships within the Nearctic and Neotropical biogeographic realms separately. Specifically, we answer the following questions: Are beta-diversity and richness correlated across the Western Hemisphere? Is the relationship consistent between the Nearctic and Neotropical realms? Are the areas of highest richness congruent with those highest in beta-diversity? Similarly, are the areas of lowest richness congruent with those of lowest beta-diversity?

Materials and Methods

We used digital range maps (IUCN *et al.* 2004; Patterson *et al.* 2005; Ridgely *et al.* 2005) to record the presence/absence of extent species of amphibians ($n = 2,174$), breeding birds ($n = 3,882$), and mammals ($n = 1,611$) native to the continental Western Hemisphere in 100 km X 100 km equal-area grid cells (Berhmann projection; WGS84 datum) containing $> 40\%$ of continental land ($n = 3,821$). Grid cells were attributed to the biogeographic realm (Nearctic or Neotropical following Olson *et al.* 2001) that covered $\geq 75\%$ of its area. Only grid cells for which all adjacent neighbors

were in the same realm were used in the realm extent analyses (see Chapters 1 for a description of these datasets).

Beta-diversity (β_{sim}) for each grid cell was calculated as the average dissimilarity between the focal grid cell and its adjacent neighbors (maximum of 8):

$$\beta_{sim} = \frac{1}{n} \sum_{i=1}^n \frac{\min(b_i, c_i)}{a_i + \min(b_i, c_i)} \quad (1)$$

where n is the number of adjacent neighbors and for pairwise comparisons between the focal grid cell and each neighbor, a is the number of species shared, b is the number of species found only in the neighbor, and c is the number of species found only in the focal grid cell (Lennon *et al.* 2001). β_{sim} is the most appropriate measure of beta-diversity for investigating the relationship of beta-diversity and richness because (unlike more commonly used dissimilarity metrics) it computes beta-diversity as the proportion of species of the more depauperate grid cell that occur in only one of the grid cells, thereby isolating change due to species replacement as opposed to change due to local richness gradients (Lennon *et al.* 2001; Koleff *et al.* 2003b). Species richness was measured as the number of species occurring within each grid cell.

We tested the correlation between β_{sim} and richness at three geographic extents: the entire Western Hemisphere, the Nearctic realm, and the Neotropical realm. Correlations were calculated as Pearson correlation coefficients and tested for significance with non-parametric randomization tests (10,000 iterations each) (Manly 1997). To evaluate the degree of coincidence in the extreme areas of the two diversity components at each of the three extents, we used an arbitrary threshold (10%) to define sets of the “highest” and “lowest” grid cells for each diversity measure. We then measured the proportional overlap between sets of the highest grid cells and the lowest grid cells for each diversity component using Jaccard’s similarity coefficient: $S/(R + B - S)$, where S is the number of grid cells shared by both sets, R is the number of grid cells found only in the richness set, and B is the number of grid cells found only in the β_{sim} set. We also examined the distribution of rank values of the other diversity component found within the grid cells of each set.

First, grid cells were ranked in order of highest to lowest richness, highest to lowest beta-diversity, lowest to highest richness, and lowest to highest beta-diversity. From each of these rankings, we selected the grid cells in the highest or lowest 10% of beta-diversity and richness for each taxon. In cases where *too many* grid cells had equal diversity values for an even break at these percentages, we used the next possible percentage threshold. For example, at the extent of the Western Hemisphere the lowest 22% of amphibian β_{sim} grid cells all had the same value, making it impossible to select sets of the lowest 10% of grid cells for each amphibian component. Thus, we compared the lowest 22% of grid cells for each amphibian diversity component across the Western Hemisphere. Similarly, at the extent of the Nearctic realm we compared the lowest 43% of each diversity component for amphibians.

Results

Western Hemisphere

There was no significant correlation between β_{sim} and richness within the Western Hemisphere for either birds ($r = -0.022$, *ns*) or mammals ($r = -0.014$, *ns*), and a weak positive correlation for amphibians ($r = 0.107$, $P < 0.005$). There was little spatial coincidence between the highest β_{sim} and richness areas for either amphibians (4.3%) or mammals (6.3%), and only a slightly greater degree for birds (12.6%). Grid cells containing the highest values for both diversity measures occurred in the Northern Andes for all three taxa, and also in the Central Andes for birds and mammals (Figure 4.1 A–C). The geographic distributions of each diversity component were generally similar for amphibians, birds, and mammals: the highest β_{sim} grid cells were found predominately throughout the Andes and in mountainous regions of Mesoamerica and western North America, while the highest richness grid cells were almost entirely contained within the tropical latitudes of South America (Figure 4.1 A–C).

For amphibians and mammals, the highest β_{sim} grid cells had moderate levels of richness, although for both taxa some of the highest β_{sim} grid cells contained extremely high or low levels of richness (those found in the Northern and Southern Andes, respectively) (Figure 4.1 A, C, Figure 4.4

A, E). Similarly, the highest richness grid cells for amphibians and mammals contained moderate levels of β_{sim} , (Figure 4.4 B, F), even though there were subtle differences between the taxa in the location of these grid cells. The richest amphibian grid cells were concentrated in the Amazon Basin and the Atlantic forests, with a small proportion also occurring on the eastern slopes of the Andes. The richest mammal grid cells, in contrast, were predominantly in Northern and Central Andes with a smaller proportion in the western Amazon Basin, as well as the Guianan Shield (Figure 4.1 A, C). Sets of the highest richness and β_{sim} grid cells for birds contained a much wider range of values for the other component than did the sets for amphibians or mammals (Figure 4.4 A, C, E). For both bird diversity components a large proportion of grid cells were in the Northern and Central Andes, where levels of both richness and β_{sim} were relatively high (Figure 4.1 B). However, the highest bird β_{sim} grid cells were found in areas of lower richness, such as the Southern Andes and the arctic coast. Some of the richest bird grid cells were also located in areas where β_{sim} was low, like the Amazon Basin and Guianan Shield (Figure 4.1 B).

Areas of lowest β_{sim} and richness for amphibians (42.3% for the lowest 22% of grid cells) and mammals (20.4%) showed a higher degree of coincidence than that found for the equivalent highest areas. For birds, however, there was little overlap between the lowest areas of the two diversity components (4.2%). While the lowest richness grid cells for all three taxa primarily occurred outside the tropics, as did the majority of lowest β_{sim} grid cells for amphibians and mammals, a large proportion of lowest bird beta-diversity grid cells occurred *within* tropical latitudes (Figure 4.1 D–F). In fact a large portion of the lowest bird β_{sim} grid cells were in the species-rich Amazon Basin, and the majority of the lowest bird richness grid cells occurred in areas with relatively high levels of β_{sim} , such as the arctic, thus the lowest areas of the two diversity components for birds actually contained relatively high levels of the other component (Figure 4.1 E, Figure 4.4 C, D). In contrast, sets of the lowest mammal β_{sim} and richness grid cells, which were both primarily found in the arctic, contained relatively low levels of the other diversity component (Figure 4.1 F, Figure 4.4 E, F). The lowest 22%

of amphibian β_{sim} and richness grid cells, found mainly within the boreal forests and the arctic, also contained low levels of the other component (Figure 4.1 D, Figure 4.4 A, B).

Nearctic Realm

When we restricted the analysis to grid cells in the Nearctic, beta-diversity and richness were positively correlated for mammals ($r = 0.672$, $P < 0.005$) and amphibians ($r = 0.389$, $P < 0.005$), but showed a weak negative correlation for birds ($r = -0.174$, $P < 0.005$). The degree of spatial coincidence in highest β_{sim} and richness grid cells within the Nearctic for mammals (24.8%) was much greater than at the hemisphere extent. Grid cells with highest values for mammal β_{sim} and richness occurred within the topographically complex arid regions of the Southwestern US and Northern Mexico, where levels are generally high for both components (Figure 4.2 C). For amphibians, in contrast, overlap within the Nearctic (7.5%) was similar to that for the hemisphere extent. Grid cells containing the highest values for both diversity components occurred in the Southern Appalachian Mountains. The richest amphibian grid cells were predominantly found in the Atlantic coastal plain/Mississippi bottomlands in eastern North America, but the highest amphibian β_{sim} grid cells primarily occurred in mountainous regions on the Pacific coast (Figure 4.2 A). Despite the disparity in degree of overlap between amphibians and mammals, the highest grid cells of one diversity component for both taxa contained relatively high levels of the other component, and the lowest grid cells of one component for both taxa had similarly low levels of the other component (Figure 4.5 A, B, E, F). For birds, overlap in sets of the highest β_{sim} and richness grid cells within the Nearctic (1.9%) was lower than for the hemisphere as a whole. The richest bird grid cells in this realm, found mostly in the Pacific Northwest, had moderate levels of β_{sim} (Figure 4.2 B, Figure 4.5 D), and the highest β_{sim} grid cells for birds, which occurred mainly along the arctic coast and Northern Mexico, actually had relatively low richness levels (Figure 4.2 B, Figure 4.5 C).

Coincidence in lowest β_{sim} and richness within the Nearctic realm for mammals (31.2%) and for amphibians (73.4% for the lowest 43% of grid cells) was greater than for the hemisphere extent. Lowest areas for both components for mammals, found primarily in the arctic, and for amphibians,

found in the arctic and boreal regions, generally contained low levels of the other component (Figure 4.2 D, F, Figure 4.5 A, B, E, F). Sets of lowest bird β_{sim} and richness grid cells in the Nearctic showed much less overlap (6.5%). For birds in this realm, the lowest β_{sim} grid cells occurred in the boreal region and Mississippi bottomlands and contained moderate levels of richness (Figure 4.2 D, Figure 4.5 C), while the lowest richness grid cells, which occurred along the arctic coast, had a comparatively wide range of β_{sim} levels (Figure 4.2 D, Figure 4.5 D).

Neotropical Realm

Within the Neotropical realm beta-diversity and richness were negatively correlated for mammals ($r = -0.336$, $P < 0.005$) and amphibians ($r = -0.186$, $P < 0.005$), but were not significantly correlated for birds ($r = -0.024$, ns). There was little overlap in highest β_{sim} and richness grid cells within the Neotropics for either amphibians (4.4%) or mammals (10.5%), as found at the hemisphere extent. For amphibians, sets of the highest β_{sim} and richness grid cells within the Neotropics both had moderate levels of the other component (Figure 4.6 A, B), similar in geographic distribution (Figure 4.3 A) to those found for the hemisphere as a whole. The highest mammal β_{sim} grid cells within the Neotropics contained lower levels of richness (Figure 4.6 E, F) than found at the hemisphere extent – although some highest mammal β_{sim} grid cells occurred in areas with high mammal richness (e.g., Northern Andes), a large proportion were found in relatively species poor areas (e.g., Southern Andes) (Figure 4.3 C). In contrast, the richest mammal grid cells in the Neotropics, many which were found in the Northern Andes and adjacent Amazon Basin, had higher levels of β_{sim} (Figure 4.3 C, Figure 4.6 F) than found at the hemisphere extent. For birds, coincidence in the highest β_{sim} and richness grid cells in the Neotropics (19.3%) was greater than for the hemisphere as a whole. Grid cells with the highest values for both components occurred in the Northern and Central Andes (Figure 4.3 B). Richness levels ranged widely for the highest β_{sim} grid cell sets in this realm, as β_{sim} was also high in the relatively species poor Southern Andes (Figure 4.6 C). The reverse was also true: β_{sim} levels vary widely for the highest richness grid cell sets (Figure 4.6 D). For example, the Amazon Basin and the

Northern Andes both have high bird richness, but β_{sim} is low in the former and high in the latter (Figure 4.3 B).

The lowest β_{sim} and richness grid cells had a substantial degree of spatial coincidence within the Neotropics for amphibians (20.8%). These grid cells were predominantly found within the Southern Cone (Figure 4.3 D). Despite this degree of overlap, however, the lowest amphibian β_{sim} and richness grid cells within the Neotropics contained a wide range of levels of the other diversity component (Figure 4.6 A, B). This contrasts with the low levels found for the hemisphere as a whole. Overlap in lowest β_{sim} and richness areas within the Neotropics for mammals (4.9%) was lower than that found at the hemisphere extent. Coincidence in the lowest β_{sim} and richness grid cells for birds was also low within the Neotropics (2.2-3.0%). The lowest richness grid cells for both birds and mammals within the Neotropics had relatively high β_{sim} levels (Figure 4.6 D, F), and these grid cells were found in the Southern Andes for both taxa, where β_{sim} was high, as well as in the Southern Temperate grasslands, where β_{sim} levels were moderate (Figure 4.3 E, F). Likewise, the lowest β_{sim} grid cell sets for birds and mammals in this realm had relatively high richness levels (Figure 4.6 C, E), as many occurred in species rich regions like the Amazon Basin (Figure 4.3 E, F).

Discussion

The general lack of correlation we found between broad-scale beta-diversity and richness across the Western Hemisphere for these three groups of terrestrial vertebrates is consistent with previous findings regarding the patterns and determinants for the two diversity components individually. Within the Western Hemisphere, richness shows a clear latitudinal gradient - it is highest in the tropics and decreases towards higher latitudes (Baillie *et al.* 2004). In contrast, areas of high and low beta-diversity are characterized by different levels of topographic and environmental complexity, and both occur across a wide range of latitudes (see Chapter 3), and therefore with a range of richness values. Recent studies have documented congruence in broad-scale patterns of both richness and beta-diversity among amphibians, birds, and mammals (Lamoreux *et al.* 2006; Chapter 3).

While richness is generated through multiple factors, researchers have found latitudinal richness gradients to be correlated with contemporary environmental factors such as energy and water availability (Gaston 2000; Hawkins *et al.* 2003). Beta-diversity at large scales is more likely influenced by broad-scale differences in environment, barriers to dispersal and gene flow, and historical patterns of evolution (Nekola & White 2002; Graham *et al.* 2005). These factors can occur at any latitude and within any combination of environmental parameters.

Given the disparate broad-scale patterns of diversity's two components, two striking results stand out. First, we found that although there was little spatial overlap in areas of highest beta-diversity and highest richness, the grid cells which did contain the highest values for both diversity components were almost always located in areas with complex topography. This occurred for all three taxa and at each of the extents for which overlap was measured. Second, the degree of overlap in lowest areas of the diversity components was much greater for amphibians and mammals than for birds, and within the Nearctic realm compared to the Neotropical realm.

What are the mechanisms through which these results may arise? Overlap in both highest richness and highest beta-diversity in mountain areas likely reflects an intersection of mechanisms, rather than a single and consistent underlying factor. While energy is a major factor influencing the high levels of richness in the tropics (Rahbek & Graves 2001; Ruggiero & Kitzberger 2004; Tognelli & Kelt 2004), the greater richness in the Andean Mountains compared to that in Amazonian lowlands likely results from the large number of narrow ranged species occurring there. Recent studies have shown that the richness of these species is strongly related to within-grain habitat heterogeneity, presumably because of increased species turnover *within* a grid cell (Jetz & Rahbek 2002; Ruggiero & Kitzberger 2004). β_{sim} as used in this analysis, however, measures species turnover *between* grid cells which, in an extreme scenario will be low among even rich grid cells with high habitat heterogeneity if these habitats and the species in them occur in most grid cells. Beta-diversity at large scales describes regional turnover in species composition, rather than fine-scale habitat preferences as may be captured by beta-diversity at smaller grain sizes (Williams *et al.* 1999), and reflects differences in

broad-scale environmental tolerances and dispersal barriers. In the Nearctic realm, habitat heterogeneity has been found to be strongly correlated with mammal richness in the energy-rich, southern portion of the realm (Kerr & Packer 1997). A positive relationship between habitat heterogeneity and beta-diversity in the southern Nearctic has also been documented (Arita & Rodríguez 2002), although the scales and methods of these studies were not identical.

The apparent contrast in the degree of overlap in lowest beta-diversity and richness may have a similar explanation. For example, we found substantial overlap in lowest areas of the two diversity components for mammals at high latitudes within the Nearctic realm. In the Neotropical realm, lowest mammal richness also occurred at high latitudes but beta-diversity was lowest within parts of the eastern Amazon Basin. This suggests that whereas richness may be constrained by the low level of ambient energy (Kerr & Packer 1997), low beta-diversity is more likely a reflection of homogenous environments and absence of large barriers to gene flow (Nekola & White 1999). That these processes are found together in the Nearctic, but in different places in the Neotropics reflects the different biogeographic histories of the realms.

Conclusions

The relationship of beta-diversity and richness differs considerably between biogeographic realms, among biomes, and in the degree of coincidence in the high and low extremes of the two diversities, as well between three terrestrial vertebrate classes. Such variation illustrates the influence of environmental, historic, and taxonomic differences on ecological relationships, and stresses the need for stringent tests across multiple taxa and regions. Several findings, however, proved consistent across the three groups. For instance, we found little correlation between β_{sim} and richness at the Western Hemisphere extent. Moreover, the extreme areas of one diversity component contained a wide range of levels of the other. These results indicate that at large spatial scales beta-diversity and richness exhibit disparate patterns and have implications for the mechanisms underlying broad-scale diversity patterns. That not all species rich, tropical areas have rapid species turnover suggests that the role beta-diversity plays producing the high richness of the tropics is not straightforward.

Furthermore, our finding that high levels of the two diversity components co-occur in topographically complex areas both within and outside of the tropics confirms the importance of history and topography in generating diversity.

The patterns and determinants of diversity are, of course, dependent on both the extent and grain of analysis, and our results do not indicate what relationships will be found at other resolutions. However, the scale we have used is consistent with those typically used in analyses of the evolutionary and ecological processes underlying broad-scale diversity patterns or those used for conservation planning across large extents. Our comparison of beta-diversity's relationship with richness across multiple geographic extents and vertebrate classes clearly demonstrates that diversity's differentiation component contains information that cannot be described by species inventories alone.

References

- Arita, H.T. & Rodríguez, P. (2002) Geographic range, turnover rate and the scaling of species diversity. *Ecography* 25, 541-550.
- Baillie, J.E.M., Hilton-Taylor, C. & Stuart, S.N. (2004) *2004 IUCN Red List of threatened species: a global species assessment*. IUCN, Gland, Switzerland.
- Duellman, W.E. (1999) *Patterns of distribution of amphibians: a global perspective*. The Johns Hopkins University Press, Baltimore, MD.
- Gaston, K.J. (1996) Biodiversity – Congruence. *Progress in Physical Geography* 20, 105-112.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature* 405, 220-227.
- Graham, C.H., Moritz, C. & Williams, S.E. (2006) Habitat history improves prediction of biodiversity in rainforest fauna. *Proceedings of the National Academy of Sciences, USA* 103, 632-636.
- 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.
- IUCN, Conservation International & NatureServe (2004) *Global amphibian assessment*. IUCN/Conservation International/NatureServe, Washington, D.C. and Arlington, VA.
- Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science* 297, 1548-1551.
- Kerr, J.T. & Packer, L. (1997) Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature* 385, 252-254.
- Koleff, P. & Gaston, K.J. (2002) The relationships between local and regional species richness and spatial turnover. *Global Ecology and Biogeography* 11, 363-375.
- Koleff, P., Lennon, J.J. & Gaston, K.J. (2003a) Are there latitudinal gradients in species turnover? *Global Ecology and Biogeography* 12, 483-498.
- Koleff, P., Gaston, K.J. & Lennon, J.J. (2003b) Measuring beta diversity for presence-absence data. *Journal of Animal Ecology* 72, 367-382.
- Lamoreux, J.F., Morrison, J.M., Ricketts, T.H., Olson, D.M., Dinerstein, E., McKnight, M.W. & Shugart, H.H. (2006) Global tests of biodiversity concordance and the importance of endemism. *Nature* 440, 212-214.
- Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70, 966-979.
- Manly, B.F.J. (1997) *Randomization, bootstrap and Monte Carlo methods in biology*. Chapman and Hall, London, UK.

- Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* 26, 867-878.
- Nekola, J.C. & White, P.S. (2002) Conservation, the two pillars of ecological explanation, and the paradigm of distance. *Natural Areas Journal* 22, 305-310.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* 51, 933-938.
- Patterson, B.D., Ceballos, G., Sechrest, W., Tognelli, M.F., Brooks, T., Luna, L., Ortega, P., Salazar, I. & Young, B.E. (2005) *Digital distribution maps of the mammals of the Western Hemisphere*. NatureServe, Arlington, VA.
- Pimm, S.L. & Gittleman, J.L. (1992) Biological diversity – Where is it? *Science* 255, 940.
- Qian, H., Ricklefs, R.E. & White, P.S. (2005) Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters* 8, 15-22.
- Rahbek, C. & Graves, G.R. (2001) Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences, USA* 98, 4534-4539.
- Ridgely, R.S., Allnutt, T.F., Brooks, T., McNicol, D.K., Mehlman, D.W., Young, B.E. & Zook, J.R. (2005) *Digital distribution maps of the birds of the Western Hemisphere*. NatureServe, Arlington, VA.
- Ruggiero, A. & Kitzberger, T. (2004) Environmental correlates of mammal species richness in South America: effects of spatial structure, taxonomy and geographic range. *Ecography* 27, 401-416.
- Tognelli, M.F. & Kelt, D.A. (2004) Analysis of determinants of mammalian species richness in South America using spatial autoregressive models. *Ecography* 27, 427-436.
- van Rensburg, B.J., Koleff, P., Gaston, K.J. & Chown, S.L. (2004) Spatial congruence of ecological transition at the regional scale in South Africa. *Journal of Biogeography* 31, 843-854.
- Whittaker, R.H. (1977) Evolution of species diversity in land communities. *Evolutionary Biology* 10, 1-67.
- Williams, P.H. (1996) Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. *Proceedings of the Royal Society of London Series B-Biological Sciences* 263, 579-588.
- Williams, P.H., de Klerk, H.M. & Crowe, T.M. (1999) Interpreting biogeographical boundaries among Afrotropical birds: spatial patterns in richness gradients and species replacement. *Journal of Biogeography* 26, 459-474.
- Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology and Systematics* 34, 273-309.

Figure 4.1. Spatial coincidence in areas of highest and lowest beta-diversity (β_{sim}) and richness in the Western Hemisphere. Coincidence in the highest (A-C) and lowest (D-F) 10% of β_{sim} and richness grid cells within the Western Hemisphere (note that for amphibians, coincidence was measured for the lowest 22% of grid cells). Orange grid cells are the highest or lowest 10% for both diversity components. Grid cells in the highest or lowest 10% of grid cells for only one component appear in shades of green (β_{sim}) or blue (richness). The shade of a grid cell reflects the level of the other diversity component found within it, from the highest quartile (darkest shade) to those in the lowest quartile (lightest shade). (A, D) Amphibians. (B, E) Birds. (C, F) Mammals.

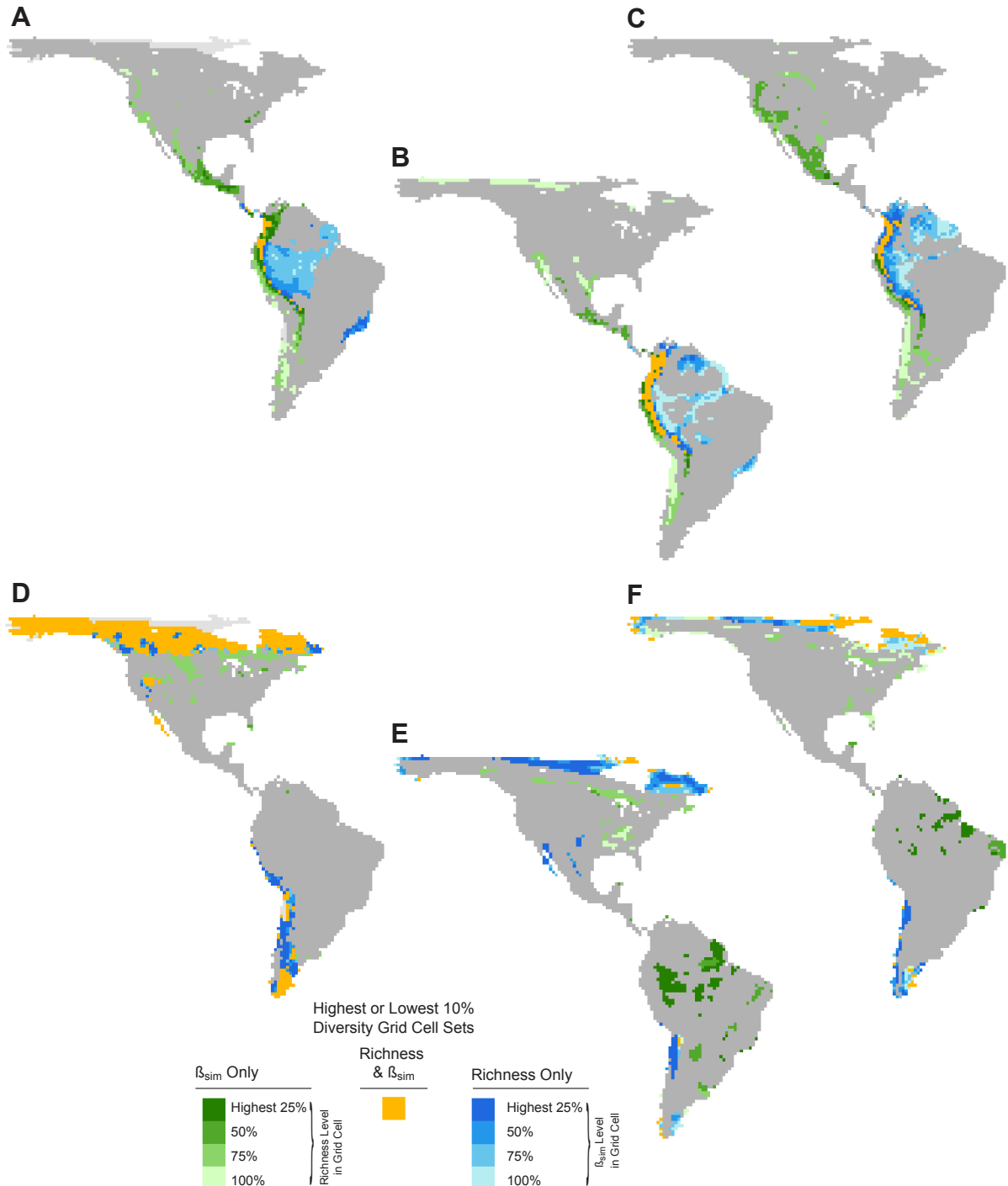


Figure 4.2. Spatial coincidence in areas of highest and lowest beta-diversity (β_{sim}) and richness in the Nearctic realm. Coincidence in the highest (A-C) and lowest (D-F) 10% of β_{sim} and richness grid cells within the Nearctic realm (note that for amphibians, coincidence was measured for the lowest 43% of grid cells). Orange grid cells are the highest or lowest 10% for both diversity components. Grid cells in the highest or lowest 10% of grid cells for only one component appear in shades of green (β_{sim}) or blue (richness). The shade of a grid cell reflects the level of the other diversity component found within it, from the highest quartile (darkest shade) to those in the lowest quartile (lightest shade). (A, D) Amphibians. (B, E) Birds. (C, F) Mammals.

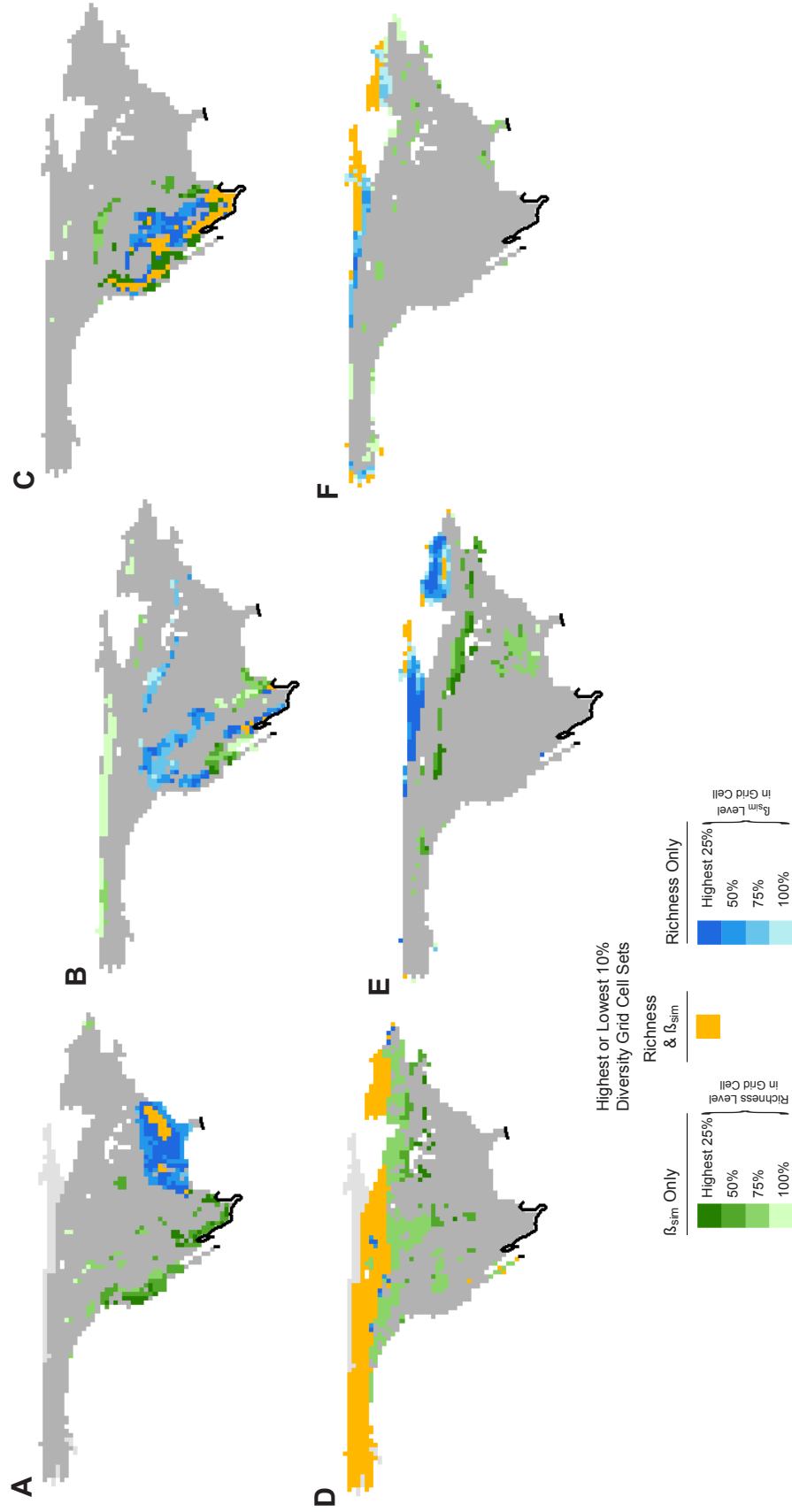


Figure 4.3. Spatial coincidence in areas of highest and lowest beta-diversity (β_{sim}) and richness in the Neotropical realm. Coincidence in the highest (A-C) and lowest (D-F) 10% of β_{sim} and richness grid cells within the Neotropical realm. Orange grid cells are the highest or lowest 10% for both diversity components. Grid cells in the highest or lowest 10% of grid cells for only one component appear in shades of green (β_{sim}) or blue (richness). The shade of a grid cell reflects the level of the other diversity component found within it, from the highest quartile (darkest shade) to those in the lowest quartile (lightest shade). (A, D) Amphibians. (B, E) Birds. (C, F) Mammals.

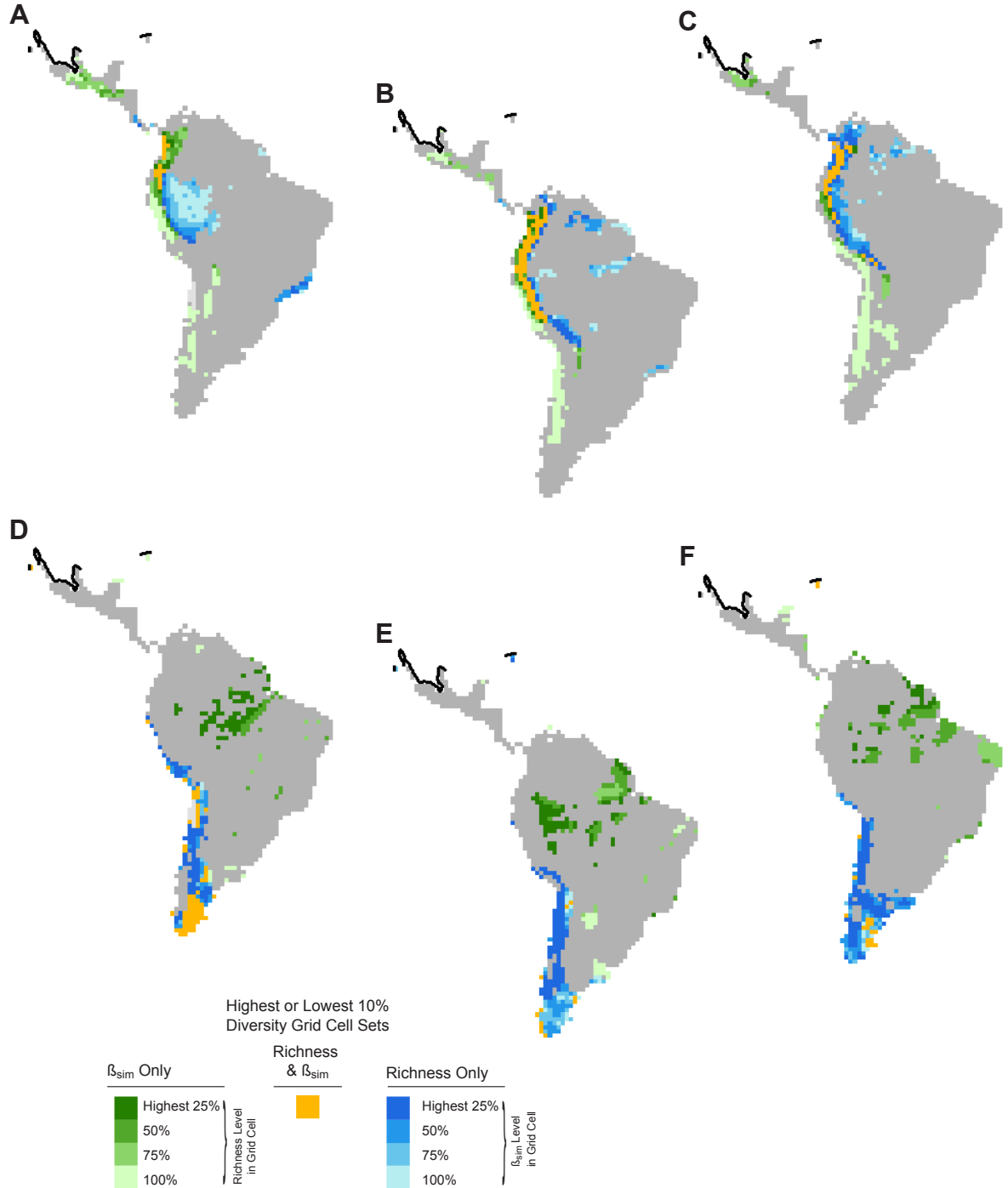


Figure 4.4. Contrasting levels of diversity components within areas of highest and lowest beta-diversity (β_{sim}) and richness in the Western Hemisphere. Areas of the highest and lowest β_{sim} (left panel) and richness (right panel) grid cells contain a wide range of levels of the other diversity component. For each box plot, the x-axis shows sets of the highest or lowest 10% of grid cells selected for the first diversity component (note that the lowest 22% of grid cells were selected for amphibians). The scale of the y-axis, from 1% to 100%, represents the level of the second component for the grid cells in the selected set, for example, a grid cell might be in the highest 5% or highest 75% of all values for the second component (minimum, 1st quartile, median, 3rd quartile, maximum, and outliers are shown). The horizontal dotted lines, indicating the 2.5%, 5%, 10% highest and lowest of all values, serve as a reference to overall levels of the second diversity component. (A, B) Amphibians. (C, D) Birds. (E, F) Mammals.

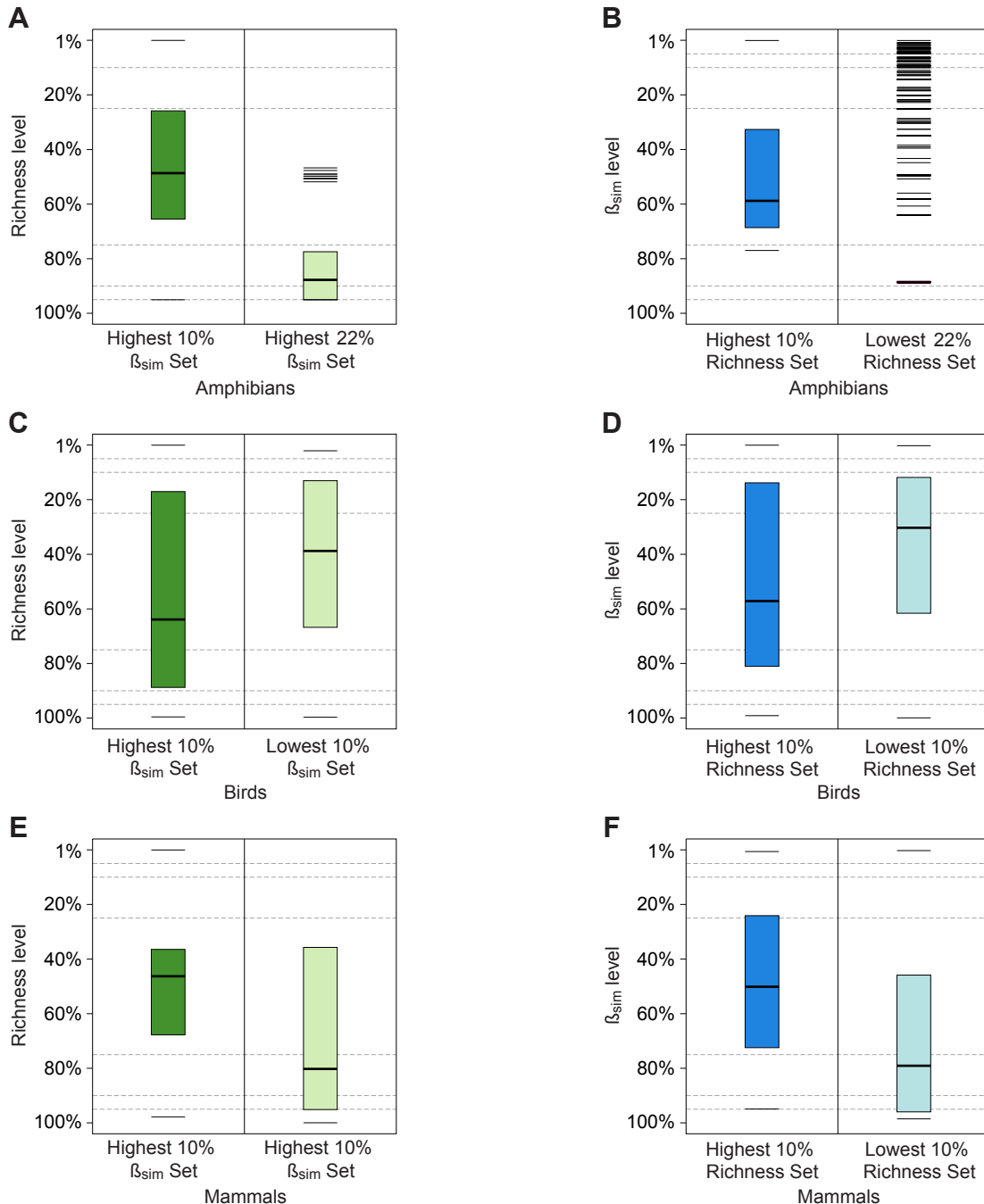


Figure 4.5. Contrasting levels of diversity components within areas of highest and lowest beta-diversity (β_{sim}) and richness in the Nearctic realm. Areas of the highest and lowest β_{sim} (left panel) and richness (right panel) grid cells contain a wide range of levels of the other diversity component. For each box plot, the x-axis shows sets of the highest or lowest 10% of grid cells selected for the first diversity component (note that the lowest 43% of grid cells were selected for amphibians). The scale of the y-axis, from 1% to 100%, represents the level of the second component for the grid cells in the selected set, for example, a grid cell might be in the highest 5% or highest 75% of all values for the second component (minimum, 1st quartile, median, 3rd quartile, maximum, and outliers are shown). The horizontal dotted lines, indicating the 2.5%, 5%, 10% highest and lowest of all values, serve as a reference to overall levels of the second diversity component. (A, B) Amphibians. (C, D) Birds. (E, F) Mammals.

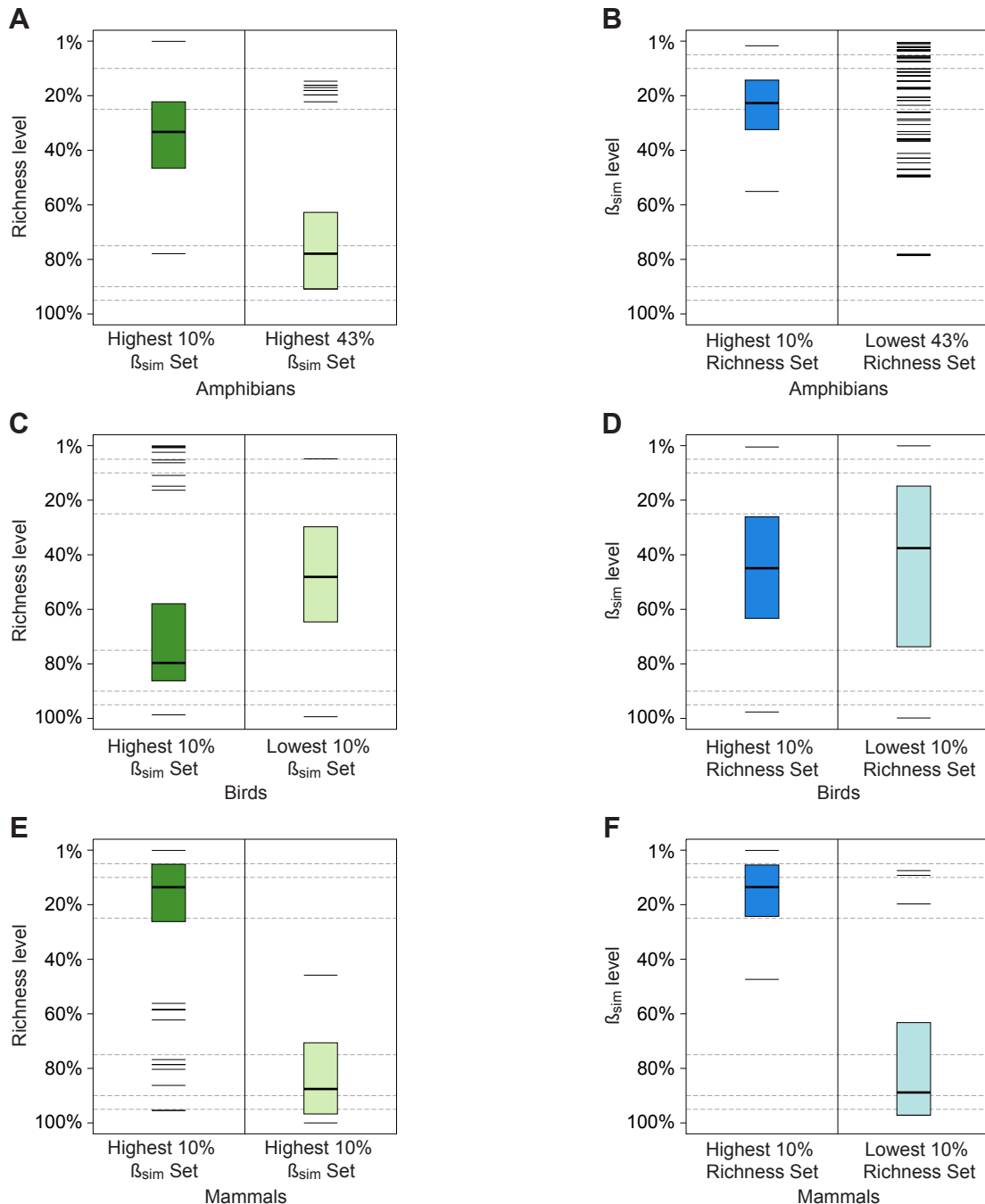
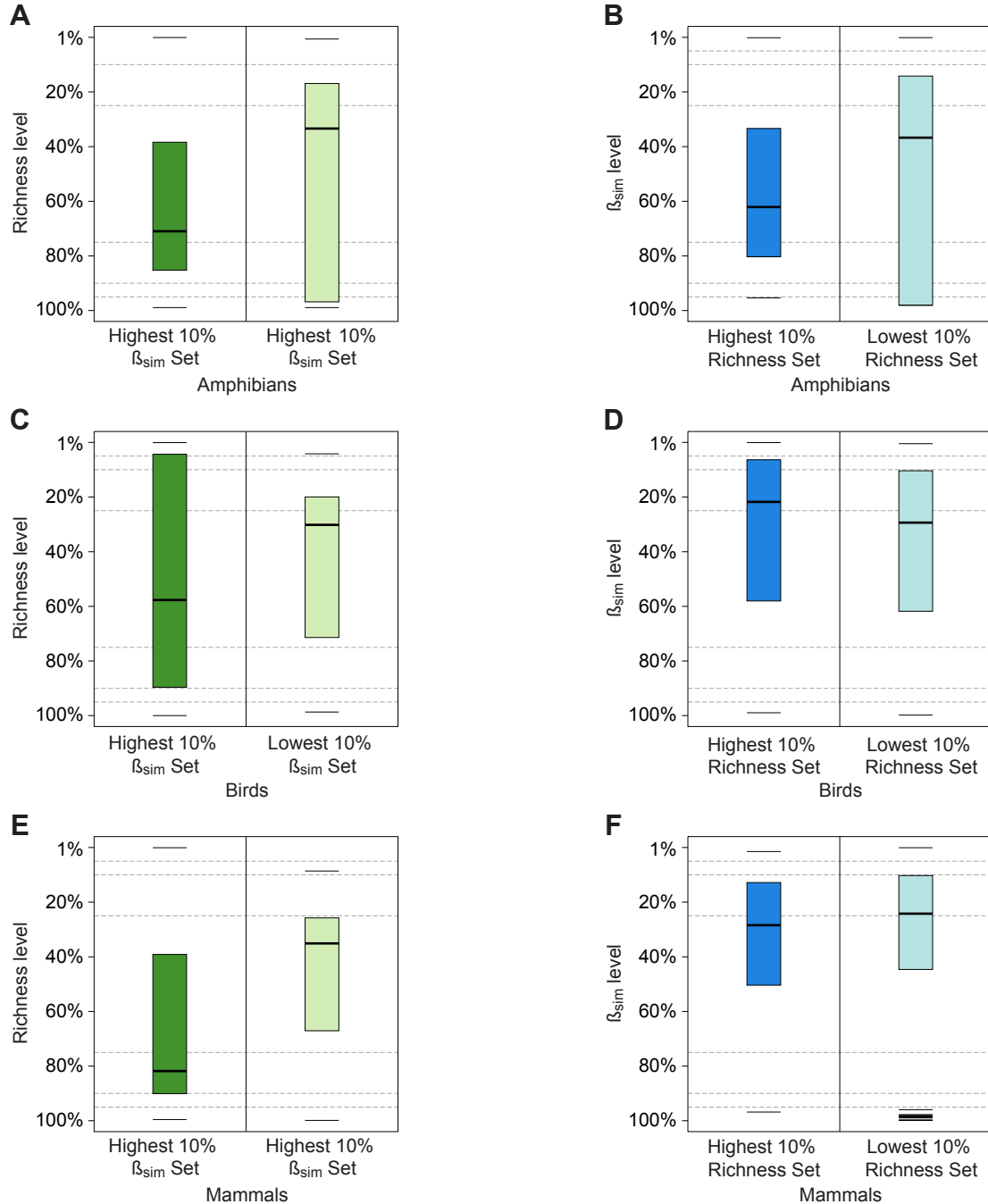


Figure 4.6. Contrasting levels of diversity components within areas of highest and lowest beta-diversity (β_{sim}) and richness in the Neotropical realm. Areas of the highest and lowest β_{sim} (left panel) and richness (right panel) grid cells contain a wide range of levels of the other diversity component. For each box plot, the x-axis shows sets of the highest or lowest 10% of grid cells selected for the first diversity component. The scale of the y-axis, from 1% to 100%, represents the level of the second component for the grid cells in the selected set, for example, a grid cell might be in the highest 5% or highest 75% of all values for the second component (minimum, 1st quartile, median, 3rd quartile, maximum, and outliers are shown). The horizontal dotted lines, indicating the 2.5%, 5%, 10% highest and lowest of all values, serve as a reference to overall levels of the second diversity component. (A, B) Amphibians. (C, D) Birds. (E, F) Mammals.



CHAPTER 5

Global Variation in Amphibian Beta-Diversity

Abstract

I used the two parameters of the distance decay relationship, initial similarity and rate of distance decay, to examine beta-diversity of amphibians across biomes and realms on a gridded map (100 km X 100 km resolution) that covered the terrestrial surface of the globe. This is the first comprehensive description of beta-diversity at this scale for any taxon. I used biomes as a first approximation of environmental conditions and biogeographic realms as a first approximation of independent evolutionary history in order to test whether amphibian beta-diversity varies systematically at the global scale. Broad-scale beta-diversity across biomes and realms is complex, particularly in comparison with species richness. Beta-diversity is neither convergent across biogeographic realms nor predicted by environment (as represented by biomes) within a biogeographic realm, however, some interesting contrasts emerged for certain biomes (e.g., forests vs. grasslands), as well as for certain realms (e.g., Afrotropics vs. Neotropics, Nearctic vs. Palearctic). Grassland biomes showed a higher rate of distance decay than forest biomes within both temperate and tropical regions. Biomes in the Nearctic realm generally had lower levels of initial similarity and faster rates of distance decay relative to their rates within the Palearctic realm. Distance decay rates within Afrotropical moist forests and grasslands were more rapid than distance decay rates within Neotropical moist forests and grasslands. Furthermore, there was a strong positive relationship overall between topographic complexity and initial similarity level, but there was no significant correlation between topographic

complexity and the rate of distance decay. Finally, while initial similarity levels were affected by local differences in richness, distance decay rates were relatively robust to such gradients.

Introduction

Although there are well-known geographic trends in species richness at broad scales for both biodiversity in general (Rosenzweig 1995; Gaston 2000) and for certain groups in particular (Currie & Paquin 1987; Roy *et al.* 1998; Lamoreux *et al.* 2006), the same cannot be said for beta-diversity, the differentiation component of diversity. At a basic level, we know that turnover in species composition occurs along environmental gradients and that turnover is likely to be affected by barriers to dispersal, but we cannot yet make generalizations about beta-diversity across the globe. While previous analyses found that biogeographic history contributed to beta-diversity, these studies were restricted to single biomes (Cody 1975, 1986; Nekola & White 1999; Qian *et al.* 2005). Whether there is systematic variation in beta-diversity with environment or with the differences in evolutionary history from one biogeographic realm to another has yet to be examined. Despite this lack of attention, global variation in beta-diversity has important consequences for conservation, particularly large-scale conservation efforts. Many methods for conservation planning are based on the assumption that beta-diversity patterns are consistent between biomes and realms (Ferrier *et al.* 2004). Understanding patterns of broad-scale beta-diversity would also allow us to develop better models to predict overall biodiversity pattern, and to estimate potential impacts of climatic change and habitat loss on biodiversity distributions.

Studies of beta-diversity across multiple biomes and biogeographic regions have been hindered by the limited availability of appropriate data for analyses at such a large scale (Westoby 1993). The analyses in this chapter were based on species distributional data from the recently completed Global Amphibian Assessment (IUCN *et al.* 2004), which mapped, for the first time, the global ranges of all but 101 of the world's 5,918 described amphibian species. Increased knowledge of broad-scale amphibian beta-diversity has immediate relevance to conservation, because of the crisis currently faced by amphibian biodiversity. Amphibians have a greater proportion of species that are globally

threatened than either mammals or birds, yet far less is known about diversity patterns of amphibian than these other taxa (Stuart *et al.* 2004). Moreover, it is likely that threats to amphibians will increase, as studies have found that recent extinctions of amphibians were related to global warming (Pounds *et al.* 2006) and that the current decline of many extant species is due to enigmatic causes (Stuart *et al.* 2004).

Quantifying Beta-Diversity: Initial Similarity and Distance Decay Rate

The decrease of compositional similarity with increasing geographic distance between samples, or the distance decay of similarity, is a powerful approach to evaluating beta-diversity within a region (Nekola & White 1999; Condit *et al.* 2002). The distance decay relationship is quantified by regressing the similarity of pairs of samples against the geographic distance between them. It provides information on two complementary aspects of beta-diversity: level of *initial similarity* and the *rate* of distance decay. Initial similarity, or similarity at zero distance, is estimated by the intercept of the regression while the distance decay rate, or the degree by which similarity declines over distance, is measured by the regression slope. While many factors influence these two aspects of compositional change, certain processes may be more strongly related to one or the other. For instance, factors such as rarity, range size, distribution of the ranges are more strongly related to initial similarity, while larger scale environmental gradients and barriers to dispersal have a greater effect on the rate of distance decay (Harrison *et al.* 1992; Nekola & White 1999). Previous studies of distance decay have primarily used the slope of the regression to measure beta-diversity (Harrison *et al.* 1992; Qian *et al.* 1998, Nekola & White 1999; Condit *et al.* 2002; Qian *et al.* 2005; McDonald *et al.* 2005), with little consideration of the intercept (but see Harrison *et al.* 1992; Nekola & White 1999). Both aspects, however, are important to understanding the spatial structure of beta-diversity. For example, when the level of initial similarity is constant between regions (equivalent intercepts), it is the relative rates of distance decay within the regions that determine differences in beta-diversity levels. Likewise, if the rate at which similarity decays is constant between regions (equivalent slopes), it is the relative levels of initial similarity that indicate differences in beta-diversity. When both parameters differ, the

relative level of similarity between regions will depend on the degree of difference in each parameter, as well as the distance at which similarity is measured (Figure 5.1).

Questions Addressed

I used the two parameters of the distance decay relationship, initial similarity and rate of distance decay, to examine beta-diversity of amphibians across biomes and realms on a gridded map (100 km X 100 km resolution) that covered the terrestrial surface of the globe. I used biomes as a first approximation of environmental conditions and biogeographic realms as a first approximation of independent evolutionary history (following the biome and realm delineation of Olson *et al.* 2001; see Chapter 1) in order to test whether amphibian beta-diversity varies systematically at the global scale, and whether beta-diversity is convergent in places with similar environments but different biogeographic histories. While my approach is exploratory, there are reasons to expect systematic variation in beta-diversity at the global scale. Among the expectations are these: because range sizes tend to increase toward the poles, beta-diversity would be expected to be lower in cooler (extra-tropical) than warmer (tropical) biomes; because amphibians are limited by dry conditions (and these conditions would slow dispersal), beta-diversity would be expected to be higher in drier (grassland) than wetter (forest) biomes; because topographic complexity may be correlated with environmental variation and with barriers to gene flow and dispersal, beta-diversity would be expected to be positively correlated with topographic complexity; and because longer evolutionary histories and more stable environments increase the opportunity for speciation, beta-diversity would be expected to be higher in areas with longer histories and more stable environments (beta-diversity would therefore be expected to be different in different biogeographic realms and would be expected to be higher in the tropical than in extra-tropical biomes).

Even though these expectations are reasonable, they do not represent all possible influences on beta-diversity and cannot be directly tested. Because there has been little work even at the descriptive level of broad-scale beta-diversity patterns, in this paper I take an exploratory approach to presenting the first comprehensive analysis of systematic variation in beta-diversity at the global scale. I

addressed the following questions regarding biomes: Does beta-diversity vary among biomes, without regard to biogeographic realm, as would be expected if there is strict control by contemporary environment on beta-diversity? Within each realm, does beta-diversity vary among biomes and is the relative rank of biomes consistent across realms? I addressed parallel questions with regard to realms: Does beta-diversity vary among realms, without regard to biome, as would be expected if factors other than broad environmental patterns control distance-decay? Within a biome, does beta-diversity vary among realms and is the relative rank of realms consistent across biomes, as would be expected if evolutionary history played a dominant role? Because topographic complexity may influence differences in beta-diversity among regions, I examined the relationship between topographic complexity and each distance decay parameter. I also examined the effect of local richness gradients on the resulting variation in beta-diversity.

Methods and Materials

Data

I used an objective delineation of 14 terrestrial biomes and 8 biogeographic realms (Olson *et al.* 2001; see Chapter 1 for a description of this dataset) to identify regions broadly uniform in climate and evolutionary history. This dataset was overlaid on a grid of 100 km X 100 km equal-area cells (Berhmann projection; WGS84 datum) covering the globe to select contiguous grid cells with $\geq 95\%$ of area in a unique region (unique combination of biome and realm). In order to examine beta-diversity in the same biome between regions differing in evolutionary history, only those biomes with sufficient number of contiguous grid cells in at least three biogeographic realms were used for the analyses. Because two realms, the Antarctic and Oceania, did not have contiguous grid cell regions with amphibian distributions, the analyses were conducted within six biogeographic realms (Afrotropic, Australasia, Indomalaya, Nearctic, Neotropic, and Palearctic). The following five biomes met this criterion: Tropical Moist Forests (TMF); Temperate Broadleaf Forests (TBF); Tropical Grasslands and Savannas (TRG); Temperate Grasslands and Savannas (TPG); and Deserts and Xeric Scrub (DXS). Within the DXS biome, I further restricted the analyses to warm deserts because cold

deserts contain few amphibian species, and have large extents in which no amphibians occur. TBF in the western and eastern extremes of the Palearctic realm were considered separately because of their potentially divergent biogeographic histories due to the large geographic distance between them. TBF in Australasia and DXS in the Nearctic were exceptions to the contiguity criterion because of the small total number of grid cells for these two regions. In order to have a large enough number of grid cells for the analyses of these regions, groups of grid cells that were separated by one grid cell distance from the larger contiguous region were included: two groups, of two or three grid cells each, for Australasia TBF, and one group of eight grid cells for Nearctic DXS. A total of nineteen regions, each representing a unique combination of biome and realm, were identified within the five biomes and six realms listed above (Table 5.1, Figure 5.2).

Digital range maps for the world's 5,918 described amphibian species (IUCN *et al.* 2004; see Chapter 1 for a description of this dataset) were used to derive species lists for each grid cell. However, species categorized as Data Deficient by the IUCN Red List (Baillie *et al.* 2004) were excluded from the analyses as these species lack sufficient information to accurately describe their distributions (S. Stuart, *pers. comm.*). The average number of amphibian species per grid cell varied between the regions (Table 5.1). I computed an index of topographic complexity for each of the 19 unique biome/realm combinations, as well as for each biome overall (regardless of realm) and for each realm overall (regardless of biome) (Table 5.1). Topographic complexity was calculated as the average within-grid cell standard deviation of elevation from a digital elevation model (DEM) of approximately 1 km X 1 km resolution (<http://www1.gsi.go.jp/geowww/globalmap-gsi/gtopo30/gtopo30.html>).

Analyses

Metrics. The distance between grid cells within each unique region was calculated as the Euclidian distance between grid cell centroids. Because of the differences in extents of the unique regions, only pairs of grid cells separated by $\leq 100,000$ km were used in the analyses (the approximate maximum extent for several extreme regions) to avoid bias due to the differing extents.

Species compositional similarity for all pairs of grid cells separated by $\leq 100,000$ km within each unique region was calculated with two different similarity metrics. The first, Jaccard's coefficient, is commonly used in studies of beta-diversity in general, and in distance decay analyses in particular: $S_{jac} = a/(a + b + c)$, where a is the number of species shared by both grid cells, b is the number of species unique to one grid cells, and c is the number of species unique to the second grid cell. However, because this metric does not differentiate between changes in species composition due to differences in numbers of species versus changes due to species replacement it may be influenced by richness gradients. The second metric, based on Simpson's coefficient, has been shown to measure compositional change independent of change due to richness gradients: $S_{sim} = a/(a + \min(b + c))$ (Simpson 1943; Lennon *et al.* 2001).

Regression Models. For each similarity metric (S_{jac} and S_{sim}), regressions of similarity on distance were performed for the 19 unique biome/realm regions, for the six biogeographic realms overall (regardless of biome), and for the five biomes overall (regardless of realms). Four different data transformations (untransformed data, log10 transformed similarity, log10 transformed distance, and both similarity and distance log10 transformed) were used and compared to find the best fit. Significance of regression coefficients (slope and intercept) was tested using matrix permutations, which retain the spatial structure of the data (1,000 permutations) (Mantel 1967). Because distance decay analyses were restricted to grid cells within a certain distance, after each permutation of the full matrix, only pairs within this distance were retained for the calculation of the regression coefficients. For the overall realm and biome regressions, the matrices for each unique region were permuted separately, and the permuted data rejoined for the regression coefficient calculations.

Comparison Categories. In order to test for significant differences in initial similarity levels and distance decay rates between regions, and to evaluate the degree of systematic variation in these parameters, the results from the distance decay regressions based on each similarity metric were grouped into four categories of comparisons, each addressing one of the research questions outlined above (see Figure 5.3):

[BIOMES], in which the five overall biome regressions were compared in order to answer, “*Does beta-diversity vary among biomes, without regard to biogeographic realm?*”

[BIOMES/Realm], in which the 19 unique biome/realm combination regressions were grouped according to realm, and comparisons across biomes were made separately for each realm (6 realms, 2-4 biomes in each) in order to answer, “*Within each realm, does beta-diversity vary among biomes and is the relative rank of biomes consistent across realms?*”

[REALMS], in which the six overall realm regressions were compared in order to answer, “*Does beta-diversity vary among realms, without regard to biome?*”

[REALMS/Biome], in which the 19 unique biome/realm combination regressions were grouped according to biome, and comparisons were made separately across the realms where each biome occurred (5 biomes, each in 3 or more realms) in order to answer, “*Within a biome, does beta-diversity vary among realms and is the relative rank of realms consistent across biomes?*”

Significance of Differences in Beta-Diversity. I tested the significance of differences in initial similarity levels and distance decay rates between regions within each of the four categories using 90% confidence intervals generated by bootstrapping the intercept and slope coefficients for each regression (1,000 iterations) (Manly 1997; S-PLUS 2005). Parameters for which the 90% confidence intervals did not overlap were concluded to be significantly different. For the [BIOMES/Realm] category, the comparisons between biomes were made separately within each realm. Similarly, for the [REALMS/Biome] category, the comparisons between the realms were made separately for each biome.

Systematic Variation in Beta-Diversity. To evaluate whether biomes and realms exhibited systematic differences in beta-diversity, the regions in each comparison category were ranked for each distance decay parameter, in order of greatest to least influence on higher beta-diversity. Regions were ranked from lowest to highest for initial similarity level (i.e., lowest to highest intercept coefficient), and from fastest to slowest distance decay rate (i.e., highest to lowest absolute value of

the slope coefficient). Thus, the highest-ranking region for initial similarity was that with the *lowest* level of initial similarity, and for distance decay rate was that with the *fastest* rate of decay.

For the [BIOMES/Realm] category, the above procedure was performed for each realm separately. The ranks of biomes within each realm were then compared to the ranks of those biomes within each of the other realms in order to determine whether there were consistent patterns across certain climatic gradients in all the realms. Specifically, whether initial similarity levels and distance decay rates in *warmer* biomes (tropical climates) were consistently higher or lower than in *cooler* biomes (temperate climates); and whether initial similarity levels and distance decay rates in *wetter* biomes (forests) were consistently higher or lower than in *drier* biomes (grasslands).

For the [REALMS/Biome] category, the ranking procedure was done separately for each biome. The ranks of the realms within a biome were compared to the ranks for other biomes, allowing us to examine whether there were consistent differences between certain biogeographic realms across all biomes. Specifically, were initial similarity levels and distance decay rates in biomes (TMF and TRG) within one tropical realm, the Afrotropics, consistently higher or lower than in those biomes within another tropical realm, the Neotropics; and were initial similarity levels and distance decay rates for temperate biomes (TBF and TPG) consistently higher or lower in the Nearctic realm (New World) than in the Palearctic realm (Old World).

Comparison of Similarity Metric (S_{jac} vs. S_{sim}). To determine whether the distance decay relationship is affected by using a similarity metric independent of local richness differences (S_{sim}), correlations were calculated between the intercept coefficients based on S_{jac} and S_{sim} and between the slope coefficients based on the two similarity metrics. Significance of the correlation coefficients was tested using non-parametric randomization tests (10,000 iterations each) (Manly 1997). In order to examine whether systematic variation in beta-diversity changed when richness gradients were removed, the percentage of comparisons that changed in rank order of initial similarity or rank order of distance decay when distance decay regressions were based on S_{sim} compared to when they were based on S_{jac} was computed for each comparison category. The percentage of comparisons having

initial similarity and distance decay rates that were significantly different based on S_{jac} but not significantly different based on S_{sim} , and the percentage of comparisons that were *not* significantly different based on S_{jac} but were significantly different based on S_{sim} , were also computed for each category.

Topographic Complexity. The correlation between the topographic complexity index and each of the regression parameters were calculated to determine whether the differences I found might be related to differences in topographic complexity. Correlations were tested for significance as described above. Because these correlations are based on the coefficients from all the regressions (5 overall biomes, 6 overall realms, and 19 unique biome/realm regions), they may not represent the relationships between topographic complexity and initial similarity or distance decay rate for each particular set of regions for which comparisons in beta-diversity variation are actually made (e.g., across the biomes found in one realm, or across the realms in which one biome occurs). Calculating correlations within each of these sets is not appropriate because of the small number of regions within each group. Therefore, for each of these sets I compared the rank order of regions for the topographic complexity index (where the highest ranking region had the highest level of complexity) with their rank orders for initial similarity and for distance decay rate.

Results

Distance Decay Regressions

The intercepts and slope coefficients were significant for all regressions (Table 5.2). The best fit for all but two regressions was obtained using log transformed distance. For these two exceptions (Palearctic TBF and Palearctic DXS), regressions using other transformations gave only slightly higher R^2 values, therefore regressions on log10 transformed distance were used for all to maintain consistency among comparisons. As the minimum between sample distance in this study is 1 (in units of 100 km), a log10 transformation of distance has the added advantage in that the intercept term represents similarity at the minimum distance measured, thereby eliminating the concern that the intercept, or similarity at zero distance, is not ecologically meaningful. With this transformation,

similarity (J) is predicted as $J = I + S \cdot \log_{10}(d)$, where I and S are the respective intercept and slope parameters and d is distance as units of 100 km. As similarity at a distance of 1 (between adjacent grid cells), I represents the initial level of similarity, and S is the rate of the decay in similarity from this level. Thus, similarity decays linearly with exponentially increasing distance. This contrasts with previous large-scale distance decay analyses of plants, birds, and mammals for which $\log(\text{similarity})$ increased linearly either with untransformed distance or $\log(\text{distance})$ (Nekola & White 1999; McDonald *et al.* 2005).

In general, values of R^2 were lower for distance decay regressions based on S_{sim} than for those based on S_{jac} . Values of R^2 ranged from 0.127 (Palearctic deserts) to 0.650 (Afrotropic TMF) for regressions based on S_{jac} , and from 0.014 (Indomalayan DXS) to 0.574 (Indomalayan TMF) for regressions based on S_{sim} (Table 5.2). These values are comparable to those found in other large-scale distance decay analyses (Nekola & White 1999; Tuomisto *et al.* 2003).

There was no significant correlation between the intercept and slope coefficients based on either similarity metric (S_{jac} : $r = 0.289$, $P = 0.130$; S_{sim} : $r = -0.120$, $P = 0.518$).

Comparison of Similarity Metrics (S_{jac} vs. S_{sim})

Initial similarity level was more affected by similarity metric than was the rate of distance decay, as shown by the strength of correlation between the intercept coefficients based on S_{jac} and S_{sim} compared with the strength of correlation between the slope coefficients based on S_{jac} and S_{sim} . There was a strong, positive correlation between slope coefficients ($r = 0.919$, $P < 0.05$). Intercept coefficients were also positively correlated ($r = 0.652$, $P < 0.05$), but the relationship was not as strong as for the slopes.

The proportion of initial similarity comparisons that were significantly different was generally smaller when initial similarity levels were based on S_{sim} than when initial similarity levels were based on S_{jac} (Table 5.3). This was particularly apparent for the [BIOMES/Realm] category (see Figure 5.3 for a description of the categories). In contrast, a greater proportion of distance decay rate comparisons were significantly different when distance decay rates were based on S_{sim} than when

distance decay rates were based on S_{jac} (Table 5.3). This was especially true for the [REALMS/Biome] category.

The percentage of comparisons changing rank order for initial similarity levels when S_{sim} was used instead of S_{jac} for the [BIOMES/Realm] category was greater than the percentage of comparisons changing rank order for the [REALMS/Biome] category. However, the percentage of realms affected by the biome rank order changes for initial similarity in the [BIOMES/Realm] category was smaller than the percentage of biomes affected by the realm rank order changes in the [REALMS/Biome] category (Table 5.3). There was a similar trend for distance decay rates. The percentage of comparisons changing rank order for distance decay rates when S_{sim} was used instead of S_{jac} was greater for the [BIOMES/Realm] category than for the [REALMS/Biome] category, but the percentage of realms affected by the biome rank order changes for distance decay rates in the [BIOMES/Realm] category was smaller than the percentage of biomes affected by the realm rank order changes in the [REALMS/Biome] category (Table 5.3).

In what is presented below I report the results from analyses based on both of the similarity metrics because the differences between them can inform whether using S_{sim} , which accounts for differences in richness between sites, changes the overall pattern in beta-diversity variation observed. The results from analyses using S_{jac} are also useful for comparison purposes, because most published distance decay analyses do not remove effects of local richness gradients.

Topographic Complexity

There was a negative correlation across all regions between the topographic complexity index and initial similarity based on both S_{jac} ($r = -0.613$; $P < 0.05$) and S_{sim} ($r = -.557$, $P < 0.05$). In contrast, there was no significant correlation between the topographic complexity index and rate of distance decay based on either similarity metric (S_{jac} : $r = -0.129$, $P = 0.511$; S_{sim} : $r = -.300$, $P = 0.110$). Within sets of regions for which distance decay parameters were compared (e.g., across the biomes found in one realm, or across the realms in which one biome occurs), the rank order for the topographic

complexity index was not generally the same as the rank orders of the regions for either initial similarity or distance decay rate (Figure 5.4).

There were a few exceptions where the rank order of regions for the topographic complexity index was either identical or the exact opposite of the rank orders for one or both of the distance decay parameters. Three realms in particular stand out in this regard: Indomalayan, Nearctic, and Neotropics. Biomes within the Indomalayan and the Nearctic realms had identical rank orders for initial similarity and topographic complexity (Figure 5.4). For biomes in the Neotropics, the rank orders for topographic complexity and for initial similarity were identical for S_{jac} , but were opposite for S_{sim} . Biomes in both the Indomalayan and Neotropical realms also had the same rank orders for distance decay rate and topographic complexity, but biomes in the Nearctic realm had opposite rank orders for these two variables.

TMF and TRG were the only biomes for which the rank order of realms for topographic complexity was identical to or opposite of their rank order for initial similarity or distance decay rate (Figure 5.4). For TMF, realms had identical rank orders for topographic complexity and initial similarity based on S_{sim} . For TRG, realms had opposite rank orders for topographic complexity and initial similarity based on S_{sim} , and identical rank orders for topographic complexity and distance decay rate based on S_{jac} . Note, however, that in several of these examples the initial similarity levels and distance decay rates were *not* significantly different between all comparisons (Figure 5.4, see also the results for the [BIOMES/Realm] and [REALMS/Biome] categories detailed below).

[BIOMES]: Does Beta-Diversity Vary Among Biomes, Without Regard to Biogeographic Realm?

Initial similarity levels for the overall biome distance decay regressions were significantly different between most biome comparisons whether based on S_{jac} or S_{sim} (Figure 5.4, Figure 5.5 A), but there were exceptions. Based on S_{jac} , levels of initial similarity were not significantly different between TMF, TRG, and TPG (Table 5.4 A, Figure 5.4, Figure 5.5 A). Based on S_{sim} , initial similarity levels did not differ significantly between TPG and DXS (Table 5.4 B, Figure 5.4, Figure 5.5 A).

Distance decay rates for overall biomes were also significantly different between most biome comparisons for both similarity metrics (Figures 5.4, 5.5 A). Only TMF and TBF did not have significantly different distance decay rates based on S_{jac} (Table 5.4 A, Figure 5.4, Figure 5.5 A). Based on S_{sim} , distance decay rates did not differ significantly between TRG and DXS or between TPG and DXS (Table 5.4 B, Figure 5.4, Figure 5.5 A).

There were slight differences in the rank order of biomes between regressions based on S_{jac} and regressions based on S_{sim} for both initial similarity and for distance decay rates (Figure 5.4). For initial similarity based on both metrics, TRG was ranked in the middle, and DXS was ranked lowest (highest initial similarity). The ranks of the other three biomes, particularly the two temperate biomes (TBF and TPG) were different for each metric. Therefore, there was little pattern in the ranks based on S_{jac} , but based on S_{sim} there was a general wet-warm to dry-cool trend in the rank order of biomes for initial similarity levels (highest ranking to lowest ranking; described in more detail below). For distance decay rates based on both metrics, the two forest biomes were ranked lowest (TBF) and second lowest (TMF). The two grassland biomes (TRG and TPG) and deserts (DXS) were the three highest-ranking biomes based on both S_{sim} and S_{jac} , but the relative order of these biomes differed between the two metrics. Of course, at any given distance the relative difference in similarity between two biomes depends on the relative differences in both initial similarity and distance decay rate (see Figure 5.1). For example, similarity at near distances is lower in TMF than in DXS, but similarity at greater distances is lower in DXS than in TMF (Figure 5.6 A).

Perhaps of greater interest than the actual rank order is whether the relative levels of initial similarity and distance decay rate are consistent across certain climatic contrasts. In this study, I compared forest and grassland biomes to examine the distance decay parameters across a wetter to drier gradient, and tropical and temperate biomes to look at variation across a warmer to cooler gradient.

Forest vs. Grassland Biomes. Differences between wetter biomes (forests) and drier biomes (grasslands) were more pronounced for S_{sim} than for S_{jac} . Initial similarity levels based on S_{jac} were

lower within wetter biomes than drier biomes in temperate environments, but were not statistically different in tropical environments (Table 5.4 A, Figure 5.4, Figure 5.6 A). Distance decay rates based on S_{jac} were lower for wetter biomes than for drier biomes within both tropical and temperate environments. Based on S_{sim} , levels of initial similarity were lower for wetter biomes (forest) than for drier biomes (grasslands) within both tropical and temperate environments. Distance decay rates based on S_{sim} were more rapid for drier biomes than for wetter biomes within both tropical and temperate environments (Table 5.4 B, Figure 5.4, Figure 5.6 A).

Tropical vs. Temperate Biomes. There was no discernible pattern between warmer (temperate) and cooler biomes (tropical) for initial similarity levels and distance decay rates based on S_{jac} (Table 5.4 A, Figure 5.4, Figure 5.6 A). In contrast, levels of initial similarity based on S_{sim} were lower within warmer biomes (tropical) than within cooler biomes (temperate) for both forest and grassland biomes. Distance decay rates based on S_{sim} were faster within warmer biomes than within cooler biomes for both forest and grassland biomes (Table 5.4 B, Figure 5.4, Figure 5.6 A).

[BIOMES/Realm]: Within Each Realm, Does Beta-Diversity Vary Among Biomes and Is the Relative Rank of Biomes Consistent Across Realms?

For comparisons across the biomes within each biogeographic realm, initial similarity based on S_{jac} and initial similarity based on S_{sim} differed both in terms of the *number* of biome comparisons that had significantly different levels of initial similarity, as well as *which* biomes comparisons were significantly different (Figure 5.4, Figure 5.7). Based on S_{jac} , initial similarity levels were significantly different between all biomes within five of the six biogeographic realms (Table 5.4 A, Figure 5.4, Figure 5.7). Based on S_{sim} , however, only one realm (Indomalaya) had significantly different levels of initial similarity between all biomes (Table 5.4 B, Figure 5.4, Figure 5.7). Within one realm, the Palearctic, there was no significant difference in initial similarity levels based on S_{sim} between any of the biomes in that realm (Table 5.4 B, Figure 5.4).

For distance decay rates as well, the *number* of biome comparisons that had significantly different levels of distance decay rates, and *which* biomes comparisons were significantly different, were not

the same for the two similarity metrics (Figure 5.4, Figure 5.7). Based on S_{jac} , distance decay rates were significantly different among all biomes within three of the six realms: the Indomalayan, the Neotropical, and the Afrotropical (Table 5.4 A, Figure 5.4, Figure 5.7). Within each of the other three realms (Australasia, the Nearctic, and the Palearctic), at least two biomes did not have significantly different distance decay rates based on S_{jac} . TBF was one of the biomes with overlapping initial similarity levels in all three of these realms (Figure 5.4). Distance decay rates based on S_{sim} , in contrast, were significantly different between all biome comparisons for each of the six realms (Table 5.4 B, Figure 5.4, Figure 5.7).

The rank order of biomes for initial similarity within a realm, and the degree to which biomes were consistent in their relative levels of initial similarity across realms, differed between the two similarity metrics (Figure 5.4, Figure 5.7). In particular, when initial similarity was based on S_{jac} there was a trend of lower levels of initial similarity in wetter biomes and higher levels in drier biomes for three of the realms, but for the other three realms there was an opposite trend of increasing initial similarity from the drier biomes to the wetter biomes. When based on S_{sim} , however, initial similarity was generally lower in wetter biomes and higher in drier biomes for almost all the realms.

For distance decay rates, the rank orders of biomes within each realm based on S_{jac} were largely similar to the rank orders based on S_{sim} (Figure 5.4, Figure 5.7). There was a trend of more rapid distance decay rates in drier biomes and slower distance decay rates in wetter biomes for both S_{jac} and S_{sim} , but the trend was stronger for distance decay rates based on S_{sim} . The relative difference in similarity at a particular distance between biomes within a realm, however, depends on their relative ranks for both initial similarity and rate of distance decay (Figure 5.8). In Australasia, for instance, similarity at near distances is lower in TRG than in DXS, but similarity at greater distances is lower in DXS than in TRG (Figure 5.8).

I compared forest and grassland biomes within each realm that they co-occur in to determine whether the distance decay parameters vary consistently across a wetter to drier gradient regardless of biogeographic history. I also compared tropical and temperate biomes co-occurring in different

regions to look at the consistency of variation in the distance decay parameters across a warmer to cooler gradient.

Forest vs. Grassland Biomes. Wetter (forest) and drier (grassland) biomes were found adjacent within both tropical (Neotropical and Afrotropical realms) and temperate (Australasian, Nearctic, and Palearctic realms) regions (Figure 5.2). For distance decay regressions based on S_{jac} , grassland and forest biomes did not have consistent relative ranks of initial similarity levels or distance decay rates (Table 5.4 A, Figure 5.4, Figure 5.8). For regressions based on S_{sim} , in contrast, initial similarity levels and distance decay rates were generally lower in forest biomes than in grassland biomes within both tropical and temperate regions (Table 5.4 B, Figure 5.4, Figure 5.8).

Tropical vs. Temperate Biomes. Warmer (tropical) and cooler (temperate) grassland biomes occur together in two realms (Australasian and Neotropical) (Figure 5.2). Warmer and cooler forest biomes did not co-occur within any single realm, but the two biomes did co-occur in both the New World and in the Old World (Figure 5.2). Initial similarity levels and distance decay rates based on S_{jac} showed no clear difference in relative rank between tropical and temperate biomes for either forests or grasslands (Table 5.4 A, Figure 5.4, Figure 5.8). Initial similarity based on S_{sim} also had no obvious differences between warm and cool regions, but distance decay rates based on S_{sim} did show a distinct pattern (Table 5.4 B, Figure 5.4, Figure 5.8); the rate of distance decay was greater within tropical forests than within temperate forests in both the New World and Old World. For grasslands, conversely, the rate of distance decay was greater within temperate regions than in tropical regions of both Australasia and the Neotropics.

[REALMS]: Does Beta-Diversity Vary Among Realms, Without Regard to Biome?

Levels of initial similarity for the overall realm distance decay regressions were significantly different within all six biogeographic realms when based on S_{jac} (Table 5.4 A, Figure 5.4, Figure 5.5 B). Based on S_{sim} , however, initial similarity levels was not significantly different between the Nearctic and Neotropical realms (Table 5.4 B, Figure 5.4, Figure 5.5 B). Rates of distance decay for

the overall realm regressions differed significantly between all realms when based on S_{jac} and when based on S_{sim} (Table 5.4, Figure 5.4, Figure 5.5 B).

The rank order of the realms for initial similarity based on S_{jac} and initial similarity based on S_{sim} were slightly different, but the rank order of the realms for distance decay rates was the same for both similarity metric (Figure 5.4). For both distance decay parameters, the Indomalayan realm ranked highest and the Palearctic realm ranked lowest. For initial similarity based on S_{jac} , the Afrotropics and Neotropical realms also ranked low. For initial similarity based on S_{sim} , the two New World realms (Nearctic and Palearctic) ranked higher than the Old World realms, with the exception of the Indomalayan. For distance decay rates based on both metrics, the two New World realms ranked lower than the Old World realms, with the exception of the Palearctic. Of course, for any give distance, the relative difference in similarity between realms depends on their relative differences in both initial similarity and rate of distance decay (Figure 5.6 B).

To better assess variation in beta-diversity between the New World and the Old World, I examined the distance decay parameters for certain pairs of realms without regard to their relative ranks among all realms. I compared each realm in the New World to a realm in the Old World having most of the same biomes

Afrotropical vs. Neotropical Realms. Based on S_{jac} , the level of initial similarity within the Afrotropics was lower than the level within the Neotropics. The rate of distance decay based on S_{jac} was faster within the Afrotropics than within the Neotropics (Table 5.4 A, Figure 5.4, Figure 5.6 B). Based on S_{sim} , the Neotropics had a lower level of initial similarity than the Afrotropics, and again the Afrotropics had the faster rate of distance decay (Table 5.4 B, Figure 5.4, Figure 5.6 B).

Nearctic vs. Palearctic Realms. For both S_{jac} and S_{sim} , the initial similarity level within the Nearctic realm was lower than within the Palearctic, and the rate of distance decay within the Nearctic was faster than in the Palearctic (Table 5.4, Figure 5.4, Figure 5.6 B).

[REALMS/Biome]: Within a Biome, Does Beta-Diversity Vary Among Realms and Is the Relative Rank of Realms Consistent Across Biomes?

For comparisons across the biogeographic realms in which each biome occurred, initial similarity based on S_{jac} and initial similarity based on S_{sim} differed both in terms of the *number* of realm comparisons having significantly different initial similarity levels, as well as *which* realm comparisons had significantly different levels (Figure 5.4, Figure 5.9). Based on S_{jac} , initial similarity differed significantly between all realms for only one biome, TRG (Table 5.4 A, Figure 5.4, Figure 5.9). The four other biomes all had overlapping levels of initial similarity based on S_{jac} in at least two realms. However, the realms which did not differ in initial similarity level were not the same for these biomes (Table 5.4 A, Figure 5.4, Figure 5.9). Based on S_{sim} , initial similarity levels were significantly different between all realms for two biomes, TMF and TRG (Table 5.4 B, Figure 5.4, Figure 5.9).

Distance decay rates based the two similarity metrics also differed in terms of the *number* of biome comparisons with significantly different levels of distance decay rates, and *which* biomes comparisons were significantly different (Figure 5.4, Figure 5.9). Based on S_{jac} , distance decay were significantly different within each realm in which a biome occurred only for one biome, TMF (Table 5.4 A, Figure 5.4, Figure 5.9). Based on S_{sim} , distance decay rates differed significantly between all realms for two biomes, TMF and TRG (Table 5.4 B, Figure 5.4, Figure 5.9).

The rank order of realms within a biome for initial similarity, and the degree to which the relative ranks of realms were consistent across biomes, differed for the two similarity metrics. Based on S_{jac} , biomes generally had lower levels of initial similarity in the Nearctic realm than they did in the other realms in which they occurred (Figure 5.4, Figure 5.9). Biomes also tended to have higher levels of initial similarity based on S_{jac} in the Neotropical and Palearctic realms relative to their levels in other realms. Based on S_{sim} , in contrast, biomes did not always have lower levels of initial similarity in the Nearctic realm relative to other realms (Figure 5.4, Figure 5.9). Biomes also did not have consistently higher initial similarity based on S_{sim} in the Neotropical realm relative to other realms. However, for initial similarity based on S_{sim} , biomes generally had low levels of initial similarity in the Australasian

realm relative to levels in other realms. Biomes also tended to have relatively high levels of initial similarity based on S_{sim} in the Afrotropical realm compared to other realms.

The rank orders of realms within a biome were largely consistent for distance decay rates based on S_{jac} and based on S_{sim} (Figures 5.4, 5.9). While the relative ranks of realms were not always the same across biomes, there were some realms which generally had higher or lower rates of distance decay compared their rates in other realms. For example, biomes generally showed higher distance decay rates in the Afrotropical realm than they did in other realms. Biomes in the Palearctic, however, tended to have lower distance decay rates compared to other realms.

The relative difference in similarity at a particular distance between the realms in which a biome occurs, however, depends on the relative ranks of the realms for both initial similarity and rate of distance decay (Figure 5.10). For example, although the rate of distance decay in TBF is higher in the eastern Palearctic than in any other realm, similarity is lower in Australasia than in the eastern Palearctic at most distances (Figure 5.10).

Comparing distance decay parameters between certain realms apart from their relative ranks among all realms may reveal patterns not apparent from the ranks orders described above. I compared pairs of realms having at least two biomes in common between the New World and the Old World. For one pair, the realms are tropical (Afrotropics and Neotropics). For the other pair, both have largely temperate climates (Nearctic and Palearctic).

Afrotropical vs. Neotropical Realms. Initial similarity based on S_{jac} was not consistently higher in either the Afrotropics or Neotropics for the two biomes occurring in both realms (TMF and TRG), but distance decay rates for both biomes were faster in the Afrotropics than within the Neotropics (Table 5.4 A, Figure 5.4, Figure 5.10). When based on S_{sim} , initial similarity within TMF and TRG was lower in the Neotropics than in the Afrotropics, but distance decay rates of both biomes were faster in the Afrotropics than in the Neotropics (Table 5.4 B, Figure 5.4, Figure 5.10).

Nearctic vs. Palearctic Realms. Based on S_{jac} , there was no consistent pattern in relative ranks of initial similarity or distance decay rate between Nearctic and Palearctic for three biomes occurring in

both realms (TMF, TRG, and DXS) (Table 5.4 A, Figure 5.4, Figure 5.10). Based on S_{sim} , however, initial similarity of biomes within the Nearctic has generally lower than within the Palearctic. Distance decay rates based on S_{sim} within the Nearctic were usually faster than within the Palearctic (Table 5.4 B, Figure 5.4, Figure 5.10).

Discussion

Topographic Complexity

Correlations measured across all regions between the distance decay parameters and topographic complexity suggest that initial similarity is strongly related to topography complexity, but distance decay rates are not. However, within the sets of regions for which beta-diversity was compared, there was considerable variation in the rank orders of regions for topographic complexity compared to their rank orders both for initial similarity and for distance decay rates (see Table 5.1, Figure 5.4). For some comparisons, such as for biomes in the Nearctic realm, the rank orders of regions for topographic complexity and for initial similarity were identical. The rank orders of regions for some comparisons were also identical for topographic complexity and distance decay rates, such as for Neotropical biomes. There were also comparisons for which rank orders for topographic complexity were the inverse of the rank orders for one of the distance decay parameters. Coincident rank orders between topographic complexity and one or both of the distance decay parameters occurred more often for comparisons across the biomes found within a realm than it did for comparisons across the realms in which a biome occurs. This suggests that the relationships between topography and distance decay may be contingent upon historical factors. Furthermore, the rank order of regions for topographic complexity coincided more often with the rank orders for initial similarity than with the rank orders for distance decay rate.

Comparison of Similarity Metrics (S_{jac} vs. S_{sim})

The removal of richness gradients from distance decay regressions had a much stronger effect on level of initial similarity than on rate of distance decay. The effect of richness gradients on initial similarity is consistent with previous findings at near distances (Lennon *et al.* 2001), but there are no

previous results relating to distance decay rates and richness gradients. It is unclear whether distance decay rates are robust to differences in richness because richness gradients are not the same as turnover gradients or because richness gradients as measured in this study have little effect on rates of distance decay. The effect of removing richness gradients on the relative ranking of distance decay rates among biomes or realms was largely quantitative, in that it made patterns of variation more pronounced, rather than qualitative, or changing the direction of rankings, as happened for initial similarity. In general, however, removing richness gradients made the overall patterns of variation stronger.

There appeared to be a slightly stronger effect of removing local richness gradients for comparisons between biomes within a realm than for comparisons across the realms in which a biome occurred. This suggests that differences in local richness gradients may have a stronger relationship with differences in environment than with variation in biogeographic history.

Biomes vs. Realms

Beta-diversity is a complex phenomenon, particularly at a global scale, where there are many combinations of biogeographic history and environment. Although not all variation was systematic in this study, there were some results that were generalizable across biomes and/or realms. There was a greater degree of systematic variation in initial similarity among realms than among biomes (most biomes of a realm had similar rank levels of initial similarity relative to their rank level in other realms). This suggests that aspects of biogeographic history may play a strong role in determining the relative degree of turnover at near distances. There were also consistent trends among certain realms for distance decay rates. For example, Nearctic biomes generally had more rapid distance decay rates than found for the same biomes in the Palearctic. Likewise, there were some strong patterns between certain biomes, although in general comparisons among biomes were less consistent those among realms. For instance, in each realm in which the tropical grasslands and tropical moist forests biomes occurred together, the rate of distance decay was more rapid within the former biome.

Biomes and realms in this study were first approximation surrogates for environment and biogeographic history, and therefore cannot yield more detailed insight to the relative contributions of the specific factors responsible for variation in beta-diversity. However, it is worthwhile to discuss the processes which biomes and realms, as surrogates, might represent. Below, I use two examples from my results – one for biomes and one for realms – to illustrate some possible environmental and biogeographic factors that may contribute to differences in initial similarity level and distance decay rate found in this study.

Temperate Forests vs. Grasslands. What might explain the general trend of lower initial similarity in the temperate forests but higher rates of distance decay in temperate grasslands across the biogeographic realms containing both these biomes? The lower initial similarity within forests is consistent with the high correlation between topographic complexity and initial similarity found for the study overall, as the average standard deviation of elevation in grid cells was greater in the forest biomes than grassland biomes. Topography, range size, and beta-diversity are closely related (Arita & Rodríguez 2002). Mountainous areas have been shown to be associated with high levels of amphibian endemism (Baillie *et al.* 2004) as well as high amphibian beta-diversity (calculated at near distances; see Chapter 3). In the Nearctic realm, for example, endemism and beta-diversity (at near distances) of amphibians is highest in the southern Appalachian Mountains of the temperate broadleaf forest biome (Ricketts *et al.* 1999; Chapters 3, 4). It is also important to note that by restricting analyses to biome interiors, major mountain chains, where amphibian endemism is highest, were excluded. This occurred because mountainous regions often contain multiple biomes or biogeographic realms, in which case grid cells in these areas would not have at least 95% of their area in single biome or realm (a criterion for the study). Distance decay rates across whole realms may be lower than would be if all areas were included.

Qian *et al.* (2005) suggested that topography relates to turnover between near locations through environmental differences, because of elevation gradients, and to turnover between distant locations through biogeographic history, because of barriers to dispersal. Harrison *et al.* (1992) proposed that

the distribution of species' range sizes (e.g., the proportion of widespread species vs. the proportion of smaller ranged species), as well as the actual range sizes, will likely have a greater effect on comparisons at closer distances than farther distances. In this sense, turnover between close locations could be influenced by dispersal barriers, as well as elevation gradients. The strength of such influences relate to the grain and extent of analysis, and would likely be stronger when grain size is large relative to the range size of the more restricted species being analyzed, such as studies at broad scales or those of species having relatively poor vagility.

Temperate forests in this study had a slower rate of distance decay but a higher level of topographic complexity than temperate grasslands, and there was no significant correlation between topographic complexity and distance decay rates measured across all regions. This contradicts the expectation that greater topographic roughness will increase the rate distance decay (Qian *et al.* 2005). However, these results do not mean that topographic complexity does not effect on species turnover between distant locations. The rate of distance decay reflects the degree of the decrease in similarity that occurs between distant pairs and near pairs. If initial similarity levels are low, there is less similarity to decay, which may dampen distance decay rates. For example, Nekola and White (1999) found that when distance decay was measured only for the rarest species, there was little decrease in similarity with distance but the level of similarity at the origin was much lower than when measured for widespread species, for which the distance decay rate was much higher. The relationship between initial similarity and distance decay rate has not received much attention, although it has consequences for comparing distance decay rates between studies.

There are many other factors besides topography that may contribute to the more rapid decay of similarity of amphibian composition with distance across temperate grasslands compared to temperate forests. For instance, broad climatic gradients could affect compositional change between more distant locations, and therefore may influence distance decay rates. A more rapid rate of decay may be due to a steeper gradient, or because the gradient includes a threshold that strongly influences species distributions. For instance, amphibian distributions are strongly associated with precipitation

(Duellman 1999) and there is a gradient of decreasing precipitation that occurs longitudinally across the TBF and TPG biomes. The more rapid decay of amphibian similarity in the grassland biome could imply a steeper decrease in precipitation within grasslands or the presence in the biome of a particular rainfall level that corresponds to a rapid transition in the amphibian fauna. Soininen *et al.* (2007) suggested that initial similarity reflects beta-diversity at small spatial extents, while the rate of distance decay is a measure of the scale-dependency of beta-diversity, in that a low rate of decay indicates that beta-diversity is highly scale-dependent (scale in their study was defined as extent), and a low rate of decay implies that beta-diversity changes little with increasing scale (i.e., extent). By this thinking, beta-diversity as I measured is higher in temperate forests than in temperate grasslands at near extents but is more scale dependent in temperate grasslands than in forests.

Afrotropical Realm vs. Neotropical Realm. Comparisons of the Afrotropics and Neotropics have been of interest to ecologists studying many organisms and systems (e.g., Goldblatt 1993a and references therein; Corlett & Primack 2006) because the two realms have many commonalities yet are so strikingly different. For example, both realms are largely tropical and, within the biomes used in this study, have similar levels of topographic complexity (Table 5.1). Both have experienced long periods of isolation, as well as periods of contact with other landmasses and, relative to other regions of the world, the two realms have had similar levels of climatic stability (Corlett & Primack 2006). The Afrotropical realm, however, has a much greater proportion of arid places versus humid places and has been more arid historically than the Neotropical realm (Goldblatt 1993b; Duellman 1993). Furthermore, as fragments of the Gondwanaland supercontinent, the two realms have a certain degree of shared history, but the amphibian fauna of these realms have diverged considerably during their long separation, and the realms today share only four amphibian families (Duellman 1993).

Two biomes, TMF and TRG, occur in both the Neotropical and Afrotropical realms. While levels of initial similarity within these biomes were comparable between the realms, distance decay rates, particularly for the forest biome, were more rapid in the Afrotropics than in the Neotropics. What processes might result in greater turnover between distant sites in the Afrotropics than in the

Neotropics when the level of species turnover between near sites is the same for the realms? As noted above, one potential influence of a higher rate of distance decay could be greater degree of climatic heterogeneity in the Afrotropics. Similarly, the more rapid distance decay rate may be influenced by a greater variation in biogeographic history, or more barriers to dispersal within the Afrotropical biomes than within biomes in the Neotropics. This last possibility is particularly interesting in light of the historical differences in aridity between the realms, as in arid environments resistance to movement may arise from physiological traits or life history phases relating to moisture. Previous comparisons of the Afrotropical and Neotropical amphibian fauna have shown that there is a marked disparity in these species traits between the two realms (Duellman 1993). For example, the Afrotropical fauna has a much higher proportion of riparian species than the Neotropical fauna. Riparian species would likely face greater restriction to dispersal within the higher aridity of the Afrotropics. In contrast, the Neotropics has a higher proportion of species with direct development or that have non-aquatic eggs, which may facilitate dispersal (Duellman 1993).

Studies at several scales have found amphibian richness to be higher in the Neotropics than in the Afrotropics (Duellman 1993, 1999; Baillie *et al.* 2004). At the scale of my analyses, average grid cell richness within biomes in the Neotropics was far greater than within the Afrotropics. The finding of similar initial similarity levels but faster distance decay rates in the Afrotropics compared to the Neotropics poses an interesting question: Where does the higher richness of the Neotropics come from? One possibility, of course, is greater rates of turnover within a grid cell, but interestingly, studies at smaller scales have found that amphibian communities in lowland tropical rain forests and tropical savanna-grassland vegetation types within the Neotropics had twice the number of species as communities in the same vegetation types within the Afrotropics (reported in Duellman 1993). This was attributed to greater vertical differentiation, particularly of arboreal species, which compose a higher proportion of the Neotropical fauna than the Afrotropical fauna (Duellman 1993). Several other hypotheses have been suggested for the higher amphibian richness of the Neotropics compared to Afrotropics at various scales, for instance, the higher proportion of humid regions and presence of

water-holding bromeliads in the Neotropics, the connectivity between the South American and Central American tropics compared to the greater isolation of the modern Afrotropical forests, and the greater contiguity of moist forests in the Afrotropics compared to the multiple moist forest regions in the Neotropics (i.e., Amazon, Atlantic Forests, Chocóan forests) (Duellman 1993). While some of these hypotheses relate more to the inventory component of diversity than the differentiation component because they generate higher richness through the accumulation of species in an area (e.g., because greater habitat availability), others are possible influences on differentiation diversity (e.g., dispersal limitations). Studies comparing the way in which the two diversity components are partitioned at different scales in these realms can help elucidate the influence of beta-diversity on the generation of tropical richness.

The life-history and physiological traits particular to amphibians may affect levels of beta-diversity in ways that would not apply to other groups, particularly in arid regions. For example, other terrestrial vertebrates may not face the same restrictions on dispersal in arid environments as do amphibians. The generally smaller range sizes and lower vagility of amphibians especially compared to birds and mammals might also have implications for distance decay relationships. A recent meta-analysis of distance decay relationships, for instance, found that compared to homoiotherms, ectotherms had much lower initial similarity levels, but only slightly faster distance decay rates (Soininen *et al.* 2007). Beta-diversity was also found to be effected by dispersal type and body weight (Soininen *et al.* 2007). It remains to be seen whether patterns for other taxonomic groups will be similar to those reported here for amphibians.

Conclusions and Implications for Conservation

Broad-scale beta-diversity across biomes and realms is complex, particularly in comparison with species richness. Beta-diversity was neither convergent across biogeographic realms nor predicted by environment (as represented by biomes) within a biogeographic realm, however, some interesting contrasts emerged for certain biomes (e.g., forests vs. grasslands), as well as for certain realms (e.g., Afrotropics vs. Neotropics, Nearctic vs. Palearctic).

Initial similarity level and distance decay rate provide different information regarding beta-diversity. These metrics did not vary in tandem across biomes and realms. Realms showed greater consistency in their variation of initial similarity levels than their distance decay rates. The results of this study demonstrate the importance of testing patterns for both initial similarity levels and distance decay rates.

The two distance decay parameters, initial similarity and the rate of distance decay, inform different aspects of conservation network design. The level of initial similarity, because it reflects beta-diversity at near distances, relates to size of protected areas which must be larger in areas with low initial similarity in order to capture the rapid change in species between locations of close proximity. The rate of distance decay, as it reflects the degree of change in species composition with increasing distance, relates to the spacing of protected areas which will require close spacing in regions of rapid distance decay in order to capture gradients of species turnover across the full extent of the region. The variation found in initial similarity and distance decay rate across biomes and realms also has implications for conservation. Such variation suggests that the optimal spacing of conservation areas to capture all species is driven by both environment and biogeographic history and cautions against a one-size-fits-all approach to conservation planning. This especially true for large-scale surrogate methods, the success of which often depend on consistent patterns of beta-diversity across realms.

References

- Arita, H.T. & Rodríguez, P. (2002) Geographic range, turnover rate and the scaling of species diversity. *Ecography* 25, 541-550.
- Baillie, J.E.M., Hilton-Taylor, C. & Stuart, S.N. (2004) *2004 IUCN Red List of threatened species: a global species assessment*. IUCN, Gland, Switzerland.
- Cody, M.L. (1975) Towards a theory of continental species diversities: bird distributions over Mediterranean habitat gradients. *Ecology and evolution of communities* (ed. by M.L. Cody and J.M. Diamond), pp. 214-257. Harvard University Press, Cambridge, MA.
- Cody, M.L. (1986) Diversity, rarity, and conservation in Mediterranean-climate ecosystems. *Conservation biology: the science of scarcity and diversity* (ed. by M.E. Soulé), pp. 122-152. Sinauer Associates, Sunderland, MA.
- Condit, R., Pitman, N., Leigh, E.G. Jr., Chave, J., Terborgh, J., Foster, R.B., Núñez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. & Hubbell, S.P. (2002) Beta-diversity in tropical forest trees. *Science* 295, 666-669.
- Corlett, R.T. & Primack, R.B. (2006) Tropical rainforests and the need for cross-continental comparisons. *Trends in Ecology and Evolution* 21, 104-110.
- Currie, D.J. & Paquin, V. (1987) Large-scale biogeographical patterns of species richness of trees. *Nature* 329, 326-327.
- Duellman, W.E. (1993) Amphibians in Africa and South America: evolutionary history and ecological comparisons. *Biological relationships between Africa and South America* (ed. by P. Goldblatt), pp. 200-243. Yale University Press, New Haven, CT.
- Duellman, W.E. (1999) *Patterns of distribution of amphibians: a global perspective*. The Johns Hopkins University Press, Baltimore, MD.
- Ferrier, S., Powell, G.V.N., Richardson, K.S., Manion, G., Overton, J.M., Allnutt, T.F., Cameron, S.E., Mantle, K., Burgess, N.D., Faith, D.P., Lamoreux, J.F., Kier, G., Hijmans, R.J., Funk, V.A., Cassis, G.A., Fisher, B.L., Flemons, P., Lees, D., Lovett, J.C. & Rompaey, R.S.A.R. (2004) Mapping more of terrestrial biodiversity for global conservation assessment. *BioScience* 54, 1101-1109.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature* 405, 220-227.
- Goldblatt, P. (1993a) *Biological relationships between Africa and South America*. Yale University Press, New Haven, CT.
- Goldblatt, P. (1993b) Biological relationships between Africa and South America: an overview. *Biological relationships between Africa and South America* (ed. by P. Goldblatt), pp. 3-14. Yale University Press, New Haven, CT.
- Harrison, S., Ross, S.J. & Lawton, J.H. (1992) Beta-diversity on geographic gradients in Britain. *Journal of Animal Ecology* 61, 151-158.

- IUCN, Conservation International & NatureServe (2004) *Global amphibian assessment*. IUCN/Conservation International/NatureServe, Washington, D.C. and Arlington, VA.
- Lamoreux, J.F., Morrison, J.M., Ricketts, T.H., Olson, D.M., Dinerstein, E., McKnight, M.W. & Shugart, H.H. (2006) Global tests of biodiversity concordance and the importance of endemism. *Nature* 440, 212-214.
- Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology* 70, 966-979.
- Manly, B.F.J. (1997) *Randomization, bootstrap and Monte Carlo methods in biology*. Chapman and Hall, London, UK.
- Mantel, N. (1967) The detection of disease clustering and a generalized regression approach. *Cancer Research* 27, 209-220.
- McDonald, R., McKnight, M., Weiss, D., Selig, E., O'Connor, M., Violin, C. & Moody, A. (2005) Species compositional similarity and ecoregions: do ecoregion boundaries represent zones of high species turnover? *Biological Conservation* 126, 24-40.
- Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* 26, 867-878.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* 51, 933-938.
- Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sánchez-Azofeifa, G.A., Still, C.J. & Young, B.E. (2006) Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439, 161-167.
- Qian, H., Ricklefs, R.E. & White, P.S. (2005) Beta diversity of angiosperms in temperate floras of eastern Asia and eastern North America. *Ecology Letters* 8, 15-22.
- Qian, H., Klinka, K. & Kayahara, G.J. (1998) Longitudinal patterns of plant diversity in the North American boreal forest. *Plant Ecology* 138, 161-178.
- Ricketts, T.H., Dinerstein, E., Olson, D.M., Loucks, C.J., Eichbaum, W., DellaSala, D., Kavanagh, K., Hedao, P., Hurley, P.T., Carney, K.M., Abell, R. & Walters, S. (1999) Terrestrial ecoregions of North America: a conservation assessment. Island Press, Washington, D.C.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.
- Roy, K., David, J., Valentine, J.W. & Rosenberg, G. (1998). Marine latitudinal diversity gradients: tests of causal hypotheses. *Proceedings of the National Academy of Sciences, USA* 95, 3699-3702.

- Simpson, G.G. (1943) Mammals and the nature of continents. *American Journal of Science* 241, 1-31.
- Soininen, J., McDonald, R. & Hillebrand, H. (2007) The distance decay of similarity in ecological communities. *Ecography* 30, 3-12.
- S-PLUS 7.0 Release 1 (2005) Insightful Corporation, Seattle, WA.
- Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L. & Waller, R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science* 306, 1783-1786.
- Tuomisto, H., Ruokolainen, K. & Yli-Halla, M. (2003) Dispersal, environment, and floristic variation of western Amazonian forests. *Science* 299, 241-244.
- Westoby, M. (1993) Biodiversity in Australia compared with other continents. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 147-158. University of Chicago Press, Chicago, IL.

Table 5.1. Area, topographic complexity, average species richness for overall biomes, overall biogeographic realms, and the nineteen unique biome/biogeographic realm regions. The number of grid cells (*n*), pairwise comparisons (*np*), average standard deviation of within-grid cell elevation (*E.SD* (m)), and average grid cell species richness (*R*) are shown. Biome abbreviations: Tropical Moist Forests (TMF); Temperate Broadleaf Forests (TBF); Tropical Grasslands and Savannas (TRG); Temperate Grasslands and Savannas (TPG); and Deserts and Xeric Scrub (DXS). Realm abbreviations: Australasian (AA), Afrotropical (AT), Indomalayan (IM), Nearctic (NA), Neotropical (NT), and Palearctic (PA: eastern Palearctic TBF, TPG, and DXS; PA W: western Palearctic TBF).

		TMF	TBF	TRG	TPG	DXS	All Realm
AA	<i>n/np</i>		22/212	171/7169	31/406	294/16826	518/24613
	<i>E.SD</i>		190.49	57.69	31.18	46.63	55.60
	<i>R</i>		33.32	17.94	15.13	5.40	11.31
AT	<i>n/np</i>	141/7379		344/24299		78/2381	563/34059
	<i>E.SD</i>	61.08		95.53		91.83	85.87
	<i>R</i>	41.13		33.69		9.77	32.24
IM	<i>n/np</i>	169/9294				44/373	213/9667
	<i>E.SD</i>	275.09				25.95	217.99
	<i>R</i>	31.70				5.32	26.25
NA	<i>n/np</i>		172/7906		235/11977	34/515	441/20398
	<i>E.SD</i>		87.55		60.51	144.27	77.52
	<i>R</i>		31.84		12.55	14.47	20.22
NT	<i>n/np</i>	554/55767		190/8251	129/4744		873/68762
	<i>E.SD</i>	67.66		80.88	104.46		75.97
	<i>R</i>	84.08		40.33	6.73		63.13
PA	<i>n/np</i>		173/6551		53/594	124/3901	652/20335
	<i>E.SD</i>		185.42		97.12	89.16	108.56
	<i>R</i>		12.55		3.25	2.32	8.89
PA W	<i>n/np</i>		295/9145				
	<i>E.SD</i>		74.93				
	<i>R</i>		10.95				
All Biome	<i>n/np</i>	856/72440	648/23814	705/39719	455/17865	574/23996	
	<i>E.SD</i>	103.13	110.41	81.76	75.67	66.26	
	<i>R</i>	66.83	17.41	31.66	9.85	5.86	

Table 5.2. Coefficients from distance decay regressions for overall biomes, overall biogeographic realms, and the nineteen unique biome/biogeographic realm regressions. Shown are coefficients for regressions based on S_{jac} and S_{sim} (intercept (I); slope (SL) and R^2 values; $P = 0.001$ for all). Biome abbreviations: Tropical Moist Forests (TMF); Temperate Broadleaf Forests (TBF); Tropical Grasslands and Savannas (TRG); Temperate Grasslands and Savannas (TPG); and Deserts and Xeric Scrub (DXS). Realm abbreviations: Australasian (AA), Afrotropical (AT), Indomalayan (IM), Nearctic (NA), Neotropical (NT), and Palearctic (PA: eastern Palearctic TBF, TPG, and DXS; PA W: western Palearctic TBF).

		TMF		TBF		TRG		TPG		DXS		All Realm	
		S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}
AA	I			0.726	0.821	0.781	0.979	0.903	0.974	0.859	1.031	0.842	1.014
	SL			-0.456	-0.321	-0.502	-0.540	-0.499	-0.404	-0.662	-0.637	-0.624	-0.608
	R^2			0.578	0.338	0.405	0.378	0.618	0.459	0.340	0.169	0.359	0.198
AT	I	0.941	1.012			0.912	1.031			0.787	1.000	0.901	1.024
	SL	-0.628	-0.486			-0.611	-0.600			-0.558	-0.646	-0.601	-0.579
	R^2	0.650	0.471			0.493	0.518			0.472	0.387	0.510	0.482
IM	I	0.702	0.875							0.946	0.989	0.790	0.952
	SL	-0.569	-0.697							-0.241	-0.050	-0.642	-0.748
	R^2	0.596	0.574							0.184	0.014	0.474	0.464
NA	I			0.841	0.905			0.895	1.062	0.780	0.876	0.872	0.996
	SL			-0.434	-0.283			-0.562	-0.505	-0.431	-0.420	-0.514	-0.417
	R^2			0.441	0.162			0.448	0.256	0.388	0.334	0.438	0.218
NT	I	0.948	1.001			0.924	1.003	0.912	1.070			0.917	0.991
	SL	-0.414	-0.341			-0.516	-0.499	-0.826	-0.750			-0.423	-0.369
	R^2	0.345	0.317			0.545	0.559	0.546	0.286			0.263	0.231
PA	I			0.856	1.031			0.777	1.035	1.022	1.034	0.930	1.034
	SL			-0.563	-0.523			-0.540	-0.407	-0.278	-0.083	-0.369	-0.289
	R^2			0.317	0.261			0.298	0.113	0.127	0.031	0.131	0.101
PA W	I			0.982	1.041								
	SL			-0.335	-0.247								
	R^2			0.208	0.126								
All Biome	I	0.882	0.959	0.896	0.991	0.886	1.014	0.878	1.053	0.924	1.053		
	SL	-0.408	-0.362	-0.401	-0.314	-0.568	-0.568	-0.606	-0.547	-0.624	-0.558		
	R^2	0.221	0.182	0.185	0.130	0.462	0.487	0.404	0.228	0.241	0.144		

Table 5.3. Effect of similarity coefficient choice on observed variation in beta-diversity. Shown for each distance decay parameter (initial similarity (*I*, intercept) or distance decay rate (*SL*, slope)): the percent of all comparisons within each category that have significant differences when based on S_{jac} but not when based on S_{sim} (loss of significance), significant differences when based on S_{sim} but not when based on S_{jac} (gain of significance), and changes in rank order when S_{sim} is used instead of S_{jac} (change in rank order). Italic numbers in parentheses are the percent of realms in the [BIOMES/Realm] and percent of biomes in the [REALMS/Biome] categories which are affected by the changes in rank order.

		Loss of Significance	Gain of Significance	Change of Rank Order
[BIOMES]	<i>I</i>	30	10	40
	<i>SL</i>	10	20	20
[BIOMES/Realm]	<i>I</i>	43	4	39 (67)
	<i>SL</i>	4	11	17 (33)
[REALMS]	<i>I</i>	0	7	27
	<i>SL</i>	0	0	0
[REALMS/Biome]	<i>I</i>	11	14	21 (80)
	<i>SL</i>	0	22	11 (60)

Table 5.4. Bootstrapped 90% confidence intervals for distance decay regression parameters. For overall biomes, overall biogeographic realms, and the 19 unique biome/biogeographic realm regions, the 5% and 95% empirical percentile values for intercept (*I*) and slope (*SL*) coefficients of distance decay regressions based on S_{sim} are shown. Biome abbreviations: Tropical Moist Forests (TMF); Temperate Broadleaf Forests (TBF); Tropical Grasslands and Savannas (TRG); Temperate Grasslands and Savannas (TPG); and Deserts and Xeric Scrub (DXS). Realm abbreviations: Australasian (AA), Afrotropical (AT), Indomalayan (IM), Nearctic (NA), Neotropical (NT), and Palearctic (PA: eastern Palearctic TBF, TPG, and DXS; PA W: western Palearctic TBF). (A) Regressions based on S_{jac} . (B) Regressions based on S_{sim} .

A

		TMF		TBF		TRG		TPG		DXS		All Realm	
		5%	95%	5%	95%	5%	95%	5%	95%	5%	95%	5%	95%
AA	<i>I</i>			0.698	0.753	0.772	0.789	0.888	0.919	0.851	0.866	0.836	0.847
	<i>SL</i>			-0.498	-0.414	-0.512	-0.489	-0.527	-0.469	-0.672	-0.653	-0.631	-0.617
AT	<i>I</i>	0.935	0.948			0.907	0.916			0.773	0.801	0.897	0.905
	<i>SL</i>	-0.636	-0.620			-0.617	-0.605			-0.576	-0.538	-0.606	-0.597
IM	<i>I</i>	0.696	0.708							0.932	0.961	0.782	0.798
	<i>SL</i>	-0.577	-0.561							-0.268	-0.215	-0.652	-0.632
NA	<i>I</i>			0.835	0.847			0.889	0.901	0.757	0.805	0.868	0.877
	<i>SL</i>			-0.442	-0.425			-0.569	-0.554	-0.466	-0.399	-0.519	-0.508
NT	<i>I</i>	0.946	0.951			0.918	0.929	0.900	0.925			0.914	0.920
	<i>SL</i>	-0.418	-0.411			-0.523	-0.507	-0.843	-0.811			-0.427	-0.419
PA	<i>I</i>			0.845	0.865			0.753	0.798	1.013	1.031	0.925	0.935
	<i>SL</i>			-0.576	-0.550			-0.573	-0.505	-0.291	-0.264	-0.376	-0.361
PA W	<i>I</i>			0.977	0.987								
	<i>SL</i>			-0.343	-0.327								
All Biome	<i>I</i>	0.879	0.886	0.891	0.901	0.883	0.890	0.873	0.884	0.917	0.930		
	<i>SL</i>	-0.412	-0.404	-0.407	-0.394	-0.573	-0.564	-0.613	-0.599	-0.633	-0.615		

B

		TMF		TBF		TRG		TPG		DXS		All Realm	
		5%	95%	5%	95%	5%	95%	5%	95%	5%	95%	5%	95%
AA	<i>I</i>			0.789	0.849	0.970	0.987	0.958	0.991	1.022	1.039	1.008	1.020
	<i>SL</i>			-0.361	-0.277	-0.551	-0.529	-0.441	-0.368	-0.650	-0.624	-0.617	-0.599
AT	<i>I</i>	1.007	1.018			1.027	1.035			0.986	1.016	1.021	1.027
	<i>SL</i>	-0.495	-0.478			-0.605	-0.594			-0.667	-0.625	-0.583	-0.574
IM	<i>I</i>	0.868	0.882							0.980	0.998	0.944	0.961
	<i>SL</i>	-0.707	-0.687							-0.070	-0.031	-0.760	-0.738
NA	<i>I</i>			0.899	0.912			1.056	1.069	0.848	0.901	0.992	1.001
	<i>SL</i>			-0.293	-0.273			-0.514	-0.495	-0.459	-0.381	-0.424	-0.410
NT	<i>I</i>	0.999	1.003			0.998	1.009	1.056	1.084			0.989	0.994
	<i>SL</i>	-0.344	-0.339			-0.506	-0.491	-0.771	-0.728			-0.372	-0.366
PA	<i>I</i>			1.022	1.039			1.017	1.053	1.030	1.039	1.030	1.038
	<i>SL</i>			-0.536	-0.509			-0.444	-0.373	-0.092	-0.073	-0.295	-0.282
PA W	<i>I</i>			1.037	1.046								
	<i>SL</i>			-0.255	-0.240								
All Biome	<i>I</i>	0.956	0.962	0.987	0.995	1.011	1.017	1.048	1.059	1.046	1.059		
	<i>SL</i>	-0.366	-0.358	-0.320	-0.307	-0.572	-0.563	-0.556	-0.538	-0.567	-0.548		

Figure 5.1. Distance decay regression parameters. The relative ranks of similarity for the two distance decay regressions depends both on initial similarity levels and the distance decay rates. In this example, the blue line has a faster rate of distance decay than the orange line, but the orange line has a lower initial similarity (I_{or}) than the blue line (I_{bl}), so that at some distance (d_x), the lines cross. For distances less than d_x (such as d_A) the similarity predicted by the orange line (\hat{S}_{or}) will be lower than the similarity predicted by the blue line (\hat{S}_{bl}) even though the decay rate is faster on the blue line because of the much lower initial similarity of the orange line (I_{or}). For distances greater than d_x (such as d_B) the similarity predicted by the blue line (\hat{S}_{bl}) will be lower than the similarity predicted by orange line (\hat{S}_{or}), despite the lower initial similarity of the orange line, because of the blue line's faster rate of decay.

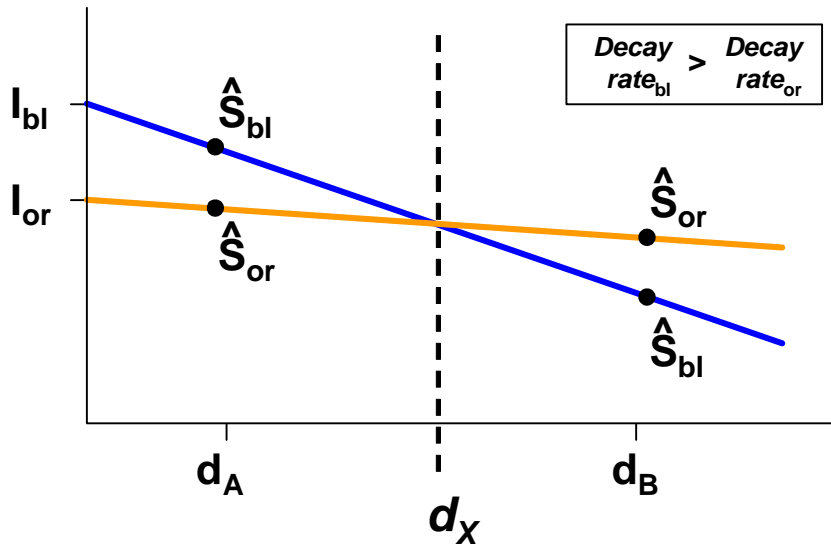


Figure 5.2. The nineteen unique biome/biogeographic realm regions. Tropical Moist Forests (TMF): Bright green; Temperate Broadleaf Forests (TBF): Teal; Tropical Grasslands and Savannas (TRG): Yellow; Temperate Grasslands and Savannas (TPG): Green – grey; and Deserts and Xeric Scrub (DXS): Orange. Realm boundaries are depicted by black lines: Australasian (AA), Afrotropical (AT), Indomalayan (IM), Nearctic (NA), Neotropical (NT), and Palearctic (PA).

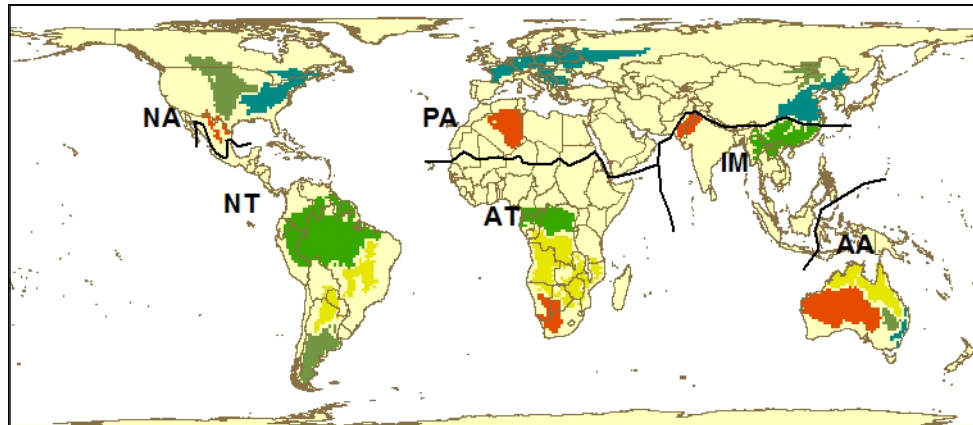


Figure 5.3. Schematic representation of the four comparison categories used to group the results from the distance decay regressions. Each category addresses a different question regarding systematic variation in beta-diversity across biomes or realms: [BIOMES], “Does beta-diversity vary among biomes, without regard to biogeographic realm?”; [BIOMES/Realm], “Within each realm, does beta-diversity vary among biomes and is the relative rank of biomes consistent across realms?”; [REALMS], “Does beta-diversity vary among realms, without regard to biome?”; [REALMS/Biome], “Within a biome, does beta-diversity vary among realms and is the relative rank of realms consistent across biomes?”

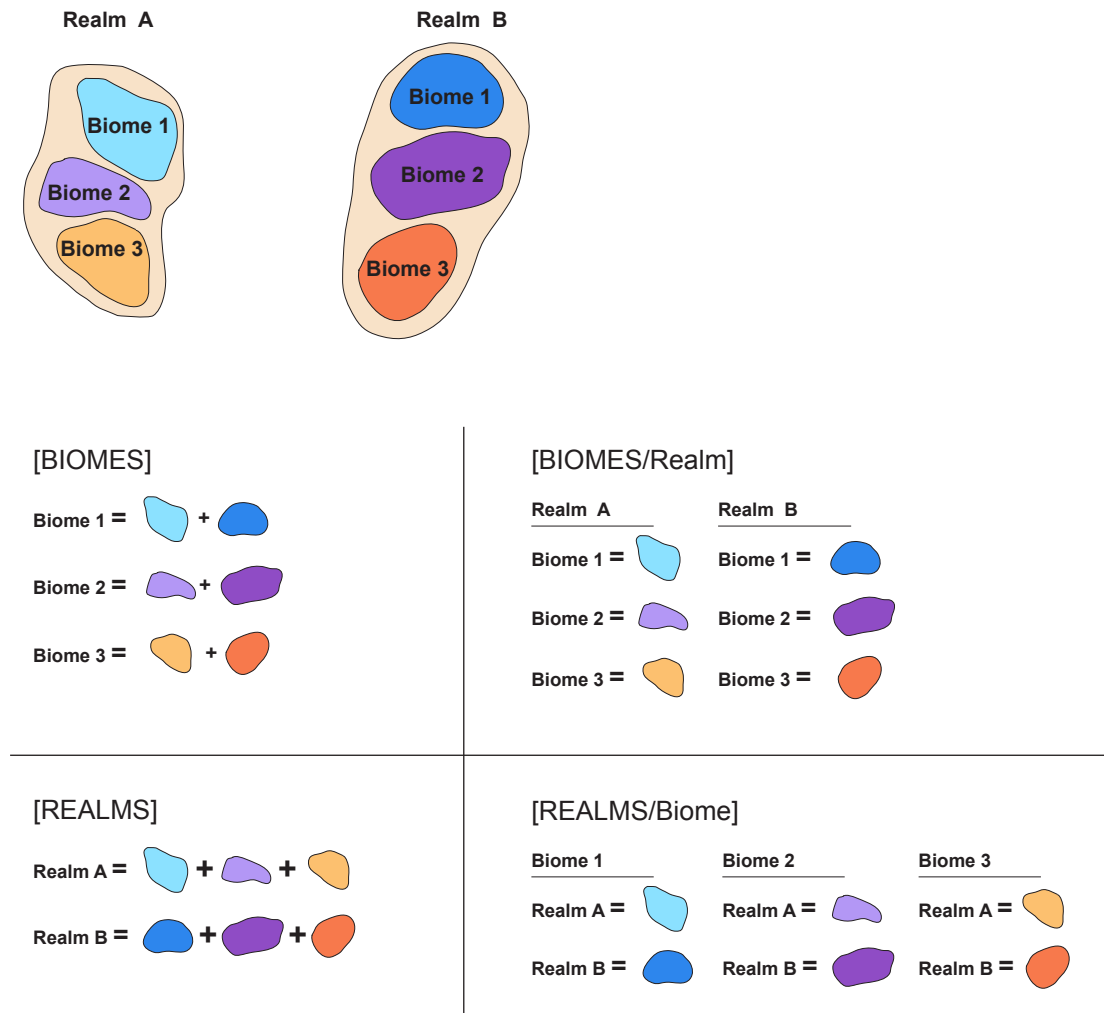


Figure 5.4. Rank order of regions within each of the four comparison categories for initial similarity levels and for distance decay rates based on S_{jac} and S_{sim} . Red circles show regions which do not differ significantly in the distance decay parameter. Biome abbreviations: Tropical Moist Forests (TMF); Temperate Broadleaf Forests (TBF); Tropical Grasslands and Savannas (TRG); Temperate Grasslands and Savannas (TPG); and Deserts and Xeric Scrub (DXS). Realm abbreviations: Australasian (AA), Afrotropical (AT), Indomalayan (IM), Nearctic (NA), Neotropical (NT), and Palearctic (PA). Palearctic TBF in eastern portion of the realm and western portion of the realm are designated by (e) and (w) respectively. Within each group, the rank order of regions for topographic complexity is indicated in parentheses.

[BIOMES]			[BIOMES/Realm]											
Initial Similarity	S_{jac}	S_{sim}	AA		AT		IM		NA		NT		PA	
			S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}
	TPG (4)	TMF (2)	TBF (1)	TBF (1)	DXS (2)	DXS (2)	TMF (1)	TMF (1)	DXS (1)	DXS (1)	TPG (1)	TMF (1)	TPG (2)	TBF _e (1)
	TMF (2)	TBF (1)	TRG (2)	TPG (4)	TRG (1)	TMF (3)	DXS (2)	DXS (2)	TBF (2)	TBF (2)	TRG (2)	TRG (2)	TBF _e (1)	DXS (2)
	TRG (3)	TRG (3)	TBF (1)	TPG (4)	TMF (3)	TRG (1)	DXS (2)	DXS (2)	TPG (3)	TPG (3)	TMF (3)	TMF (3)	TBF _w (4)	TPG (2)
	TBF (1)	TPG (4)	DXS (3)	TRG (2)	TMF (3)	TRG (3)	TRG (1)	TRG (1)	TPG (3)	TPG (3)	TPG (3)	TPG (3)	TBF _w (4)	TPG (2)
	DXS (5)	DXS (5)	TPG (4)	DXS (3)	TPG (4)	DXS (3)	TPG (4)	DXS (3)	TPG (3)	TPG (3)	TPG (3)	TPG (3)	TBF _w (4)	TPG (2)
	DXS (5)	DXS (5)	TPG (4)	DXS (3)	TPG (4)	DXS (3)	TPG (4)	DXS (3)	TPG (3)	TPG (3)	TPG (3)	TPG (3)	TBF _w (4)	TPG (2)
Distance Decay Rate	S_{jac}	S_{sim}	AA		AT		IM		NA		NT		PA	
			S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}
	DXS (5)	TRG (3)	DXS (3)	DXS (3)	TMF (3)	DXS (2)	TMF (1)	TMF (1)	TPG (3)	TPG (3)	TPG (1)	TPG (1)	TBF _e (1)	TPG (2)
	TPG (4)	DXS (5)	TRG (2)	TRG (2)	TRG (1)	TRG (1)	DXS (2)	DXS (2)	TBF (2)	TBF (2)	TRG (2)	TRG (2)	TBF _w (4)	TPG (2)
	TRG (3)	TPG (4)	TPG (4)	TPG (4)	TPG (4)	TPG (4)	DXS (2)	DXS (2)	DXS (1)	DXS (1)	TMF (3)	TMF (3)	TBF _w (4)	TPG (2)
	TMF (2)	TMF (2)	TPG (4)	TPG (4)	TPG (4)	TPG (4)	TPG (4)	TPG (4)	DXS (1)	DXS (1)	TMF (3)	TMF (3)	TBF _w (4)	TPG (2)
	TBF (1)	TBF (1)	TBF (1)	TBF (1)	TBF (1)	TBF (1)	TBF (1)	TBF (1)	DXS (1)	DXS (1)	TMF (3)	TMF (3)	TBF _w (4)	TPG (2)
[REALMS]			[REALMS/Biome]											
Initial Similarity	S_{jac}	S_{sim}	TMF		TBF		TRG		TPG		DXS			
			S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}		
	IM (1)	IM (1)	IM (1)	IM (1)	AA (1)	AA (1)	AA (3)	AA (3)	PA (2)	AA (4)	NA (1)	NA (1)		
	AA (6)	NT (5)	AT (3)	NT (2)	NA (3)	NA (3)	AT (1)	NT (2)	NA (3)	PA (2)	AT (2)	IM (5)		
	NA (4)	NA (4)	AT (3)	NT (2)	PA _e (2)	PA _e (2)	NT (2)	AT (1)	AA (4)	NT (1)	AA (4)	AT (2)		
	AT (3)	AA (6)	NT (2)	AT (3)	PA _w (4)	PA _w (4)	NT (2)	AT (1)	AA (4)	NT (1)	AA (4)	AT (2)		
	NT (5)	AT (3)	NT (2)	AT (3)	PA _w (4)	PA _w (4)	NT (2)	AT (1)	AA (4)	NT (1)	AA (4)	AT (2)		
	PA (2)	PA (2)	NT (2)	AT (3)	PA _w (4)	PA _w (4)	NT (2)	AT (1)	AA (4)	NT (1)	AA (4)	AT (2)		
Distance Decay Rate	S_{jac}	S_{sim}	TMF		TBF		TRG		TPG		DXS			
			S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}	S_{jac}	S_{sim}		
	IM (1)	IM (1)	AT (3)	IM (1)	PA _e (2)	PA _e (2)	AT (1)	AT (1)	NT (1)	NT (1)	AA (4)	AT (2)		
	AA (6)	AA (6)	IM (1)	AT (3)	AA (1)	AA (1)	NT (2)	AA (3)	NA (3)	NA (3)	AT (2)	AA (4)		
	AT (3)	AT (3)	NT (2)	NT (2)	NA (3)	NA (3)	AA (3)	AA (3)	PA (2)	PA (2)	NA (1)	NA (1)		
	NA (4)	NA (4)	NT (2)	NT (2)	PA _w (4)	PA _w (4)	AA (3)	AA (3)	AA (4)	AA (4)	PA (3)	PA (3)		
	NT (5)	NT (5)	NT (2)	NT (2)	PA _w (4)	PA _w (4)	AA (3)	AA (3)	AA (4)	AA (4)	IM (5)	IM (5)		
	PA (2)	PA (2)	NT (2)	NT (2)	PA _w (4)	PA _w (4)	AA (3)	AA (3)	AA (4)	AA (4)	IM (5)	IM (5)		

Figure 5.5. Regression coefficients from distance decay regressions for overall biomes and biogeographic realms. Left panel shows initial similarity levels (Intercept, y-axis), right panel shows distance decay rates (Slope, y-axis) for each biome or biogeographic realm on the x-axis. Magenta diamonds represent values for S_{jac} , blue ovals show values for S_{sim} . Lines around each symbol are 90% confidence intervals. Biome abbreviations: Tropical Moist Forests (TMF); Temperate Broadleaf Forests (TBF); Tropical Grasslands and Savannas (TRG); Temperate Grasslands and Savannas (TPG); and Deserts and Xeric Scrub (DXS). Realm abbreviations: Australasian (AA), Afrotropical (AT), Indomalayan (IM), Nearctic (NA), Neotropical (NT), and Palearctic (PA). (A) Biomes. (B) Biogeographic realms.

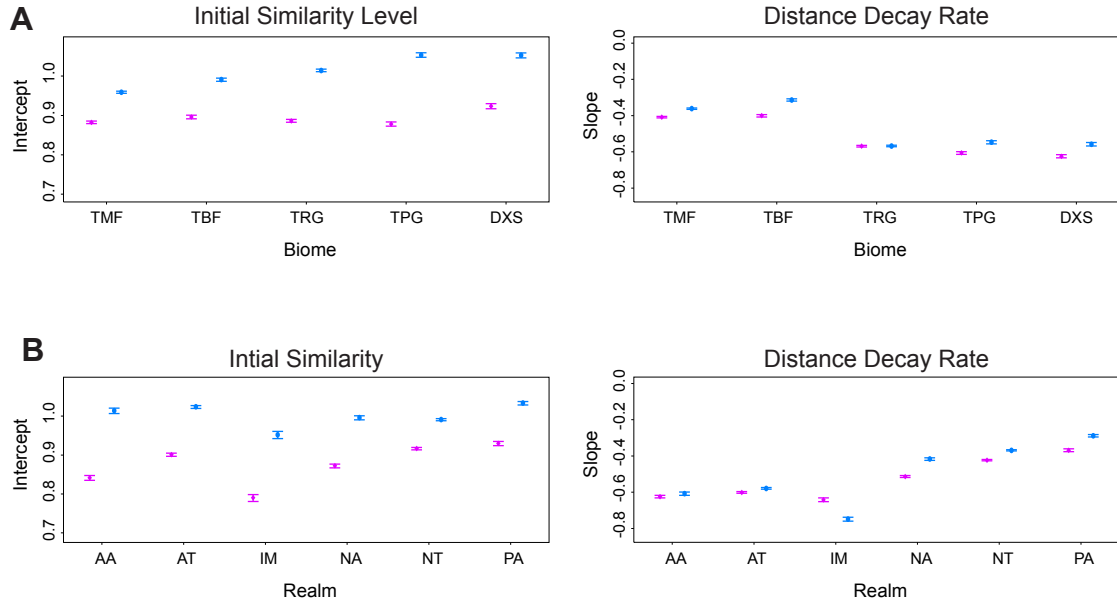


Figure 5.6. Distance decay relationships for overall biomes and biogeographic realms. Modeled distance decay relationships (solid lines) based on S_{jac} (left panel) and based on S_{sim} (right panel) for each biome or biogeographic realm (differentiated by color of line, see key). Dashed lines are 90% confidence intervals. Biome abbreviations: Tropical Moist Forests (TMF); Temperate Broadleaf Forests (TBF); Tropical Grasslands and Savannas (TRG); Temperate Grasslands and Savannas (TPG); and Deserts and Xeric Scrub (DXS). Realm abbreviations: Australasian (AA), Afrotropical (AT), Indomalayan (IM), Nearctic (NA), Neotropical (NT), and Palearctic (PA). (A) Biomes. (B) Biogeographic realms.

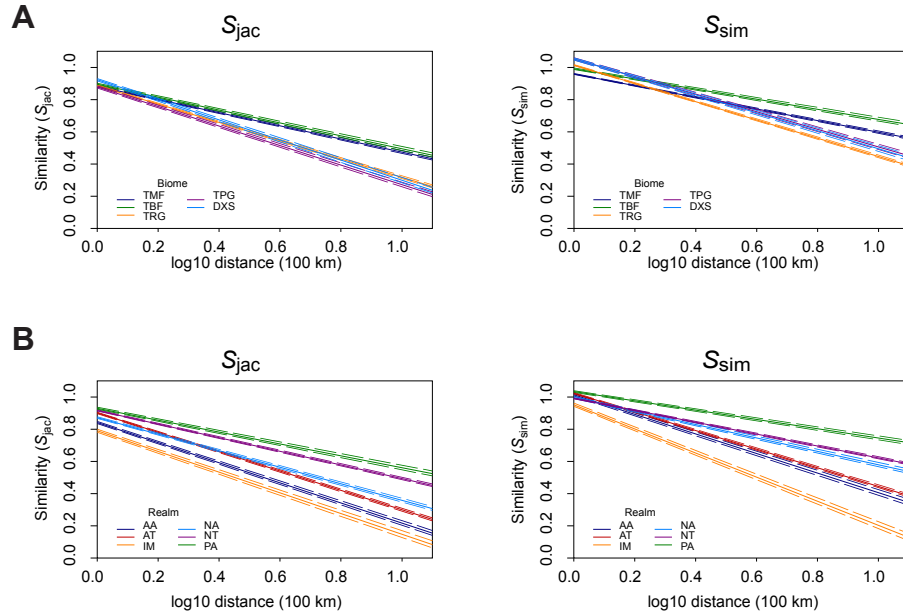


Figure 5.7. Regression coefficients from distance decay regressions for biomes within each of the six biogeographic realms. Left panel shows initial similarity levels (Intercept, y-axis), right panel shows distance decay rates (Slope, y-axis) for biomes within each biogeographic realm (x-axis). Magenta diamonds represent values for S_{jac} , blue ovals show values for S_{sim} . Lines around each symbol are 90% confidence intervals. Biome abbreviations: Tropical Moist Forests (TMF); Temperate Broadleaf Forests (TBF); Tropical Grasslands and Savannas (TRG); Temperate Grasslands and Savannas (TPG); and Deserts and Xeric Scrub (DXS). For the Palearctic, two sets of symbols are drawn for TBF (right-hand: western Palearctic TBF; left-hand: eastern Palearctic TBF).

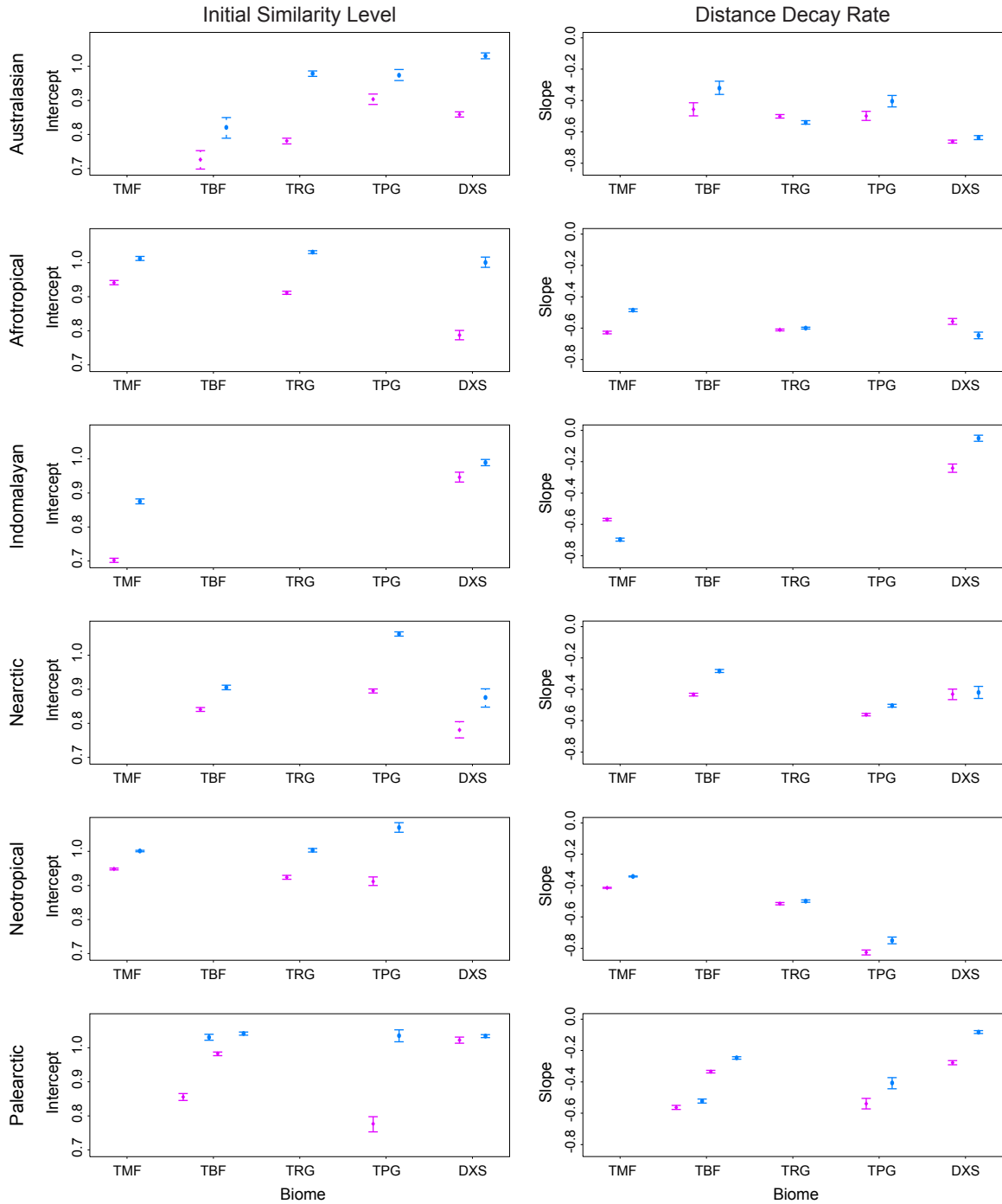


Figure 5.8. Distance decay relationships for biomes within each of the six biogeographic realms. Modeled distance decay relationships (solid lines) based on S_{jac} (left panel) and based on S_{sim} (right panel) for biomes (differentiated by color of line, see key) within each biogeographic realm. Dashed lines are 90% confidence intervals. Biome abbreviations: Tropical Moist Forests (TMF); Temperate Broadleaf Forests (TBF1 denotes all TBF regions except the western Palearctic TBF, which is denoted by TBF2); Tropical Grasslands and Savannas (TRG); Temperate Grasslands and Savannas (TPG); and Deserts and Xeric Scrub (DXS).

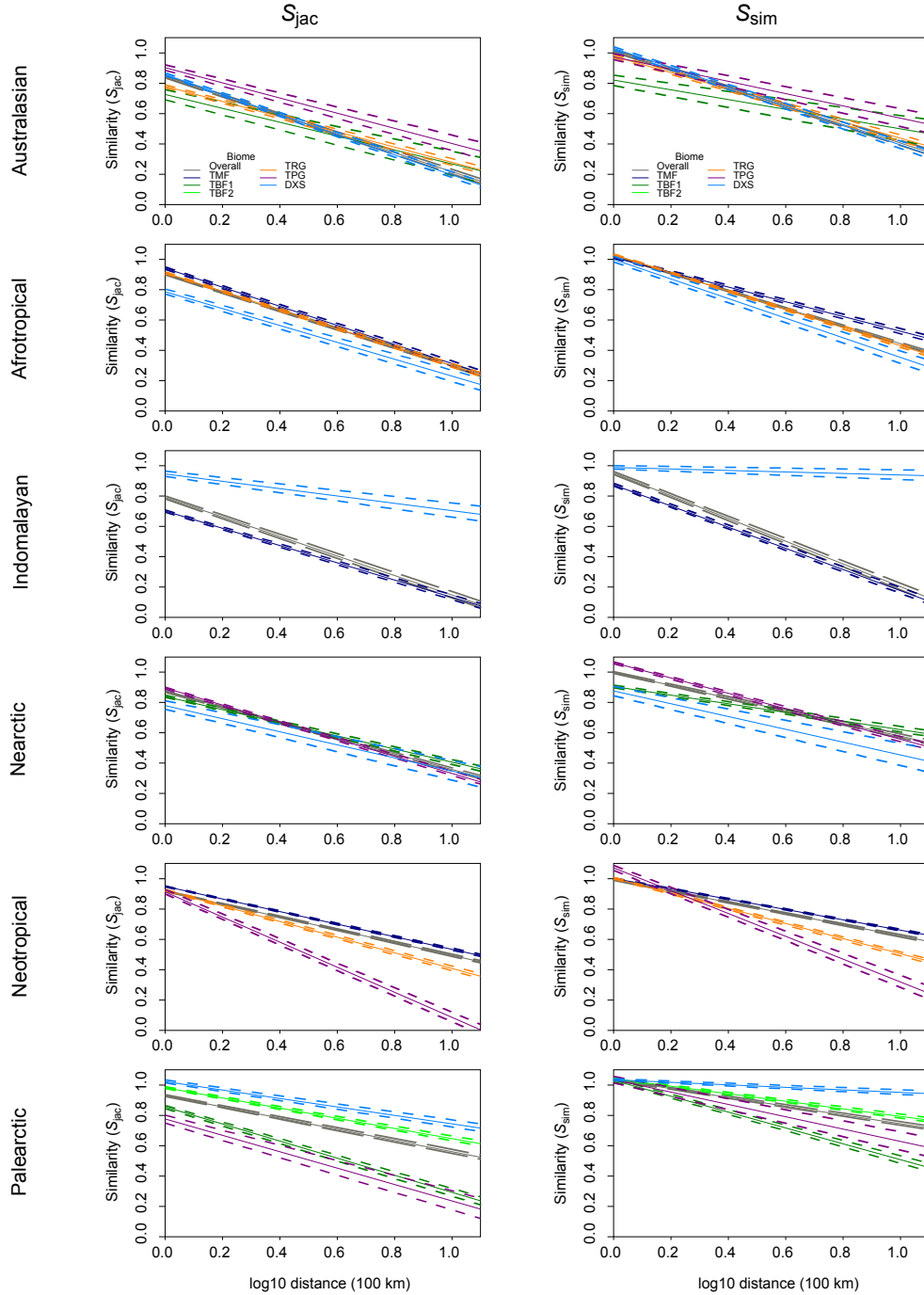


Figure 5.9. Regression coefficients from distance decay regressions of each of the five biomes within the biogeographic realms in which it occurs. Left panel shows initial similarity levels (Intercept, y-axis), right panel shows distance decay rates (Slope, y-axis) for realms in which each biome occurs (x-axis). Magenta diamonds represent values for S_{jac} , blue ovals show values for S_{sim} . Lines around each symbol are 90% confidence intervals. Realm abbreviations: Australasian (AA), Afrotropical (AT), Indomalayan (IM), Nearctic (NA), Neotropical (NT), and Palearctic (PA). For TBF, two sets of symbols are drawn for the Palearctic realm (right-hand: western Palearctic TBF; left-hand: eastern Palearctic TBF).

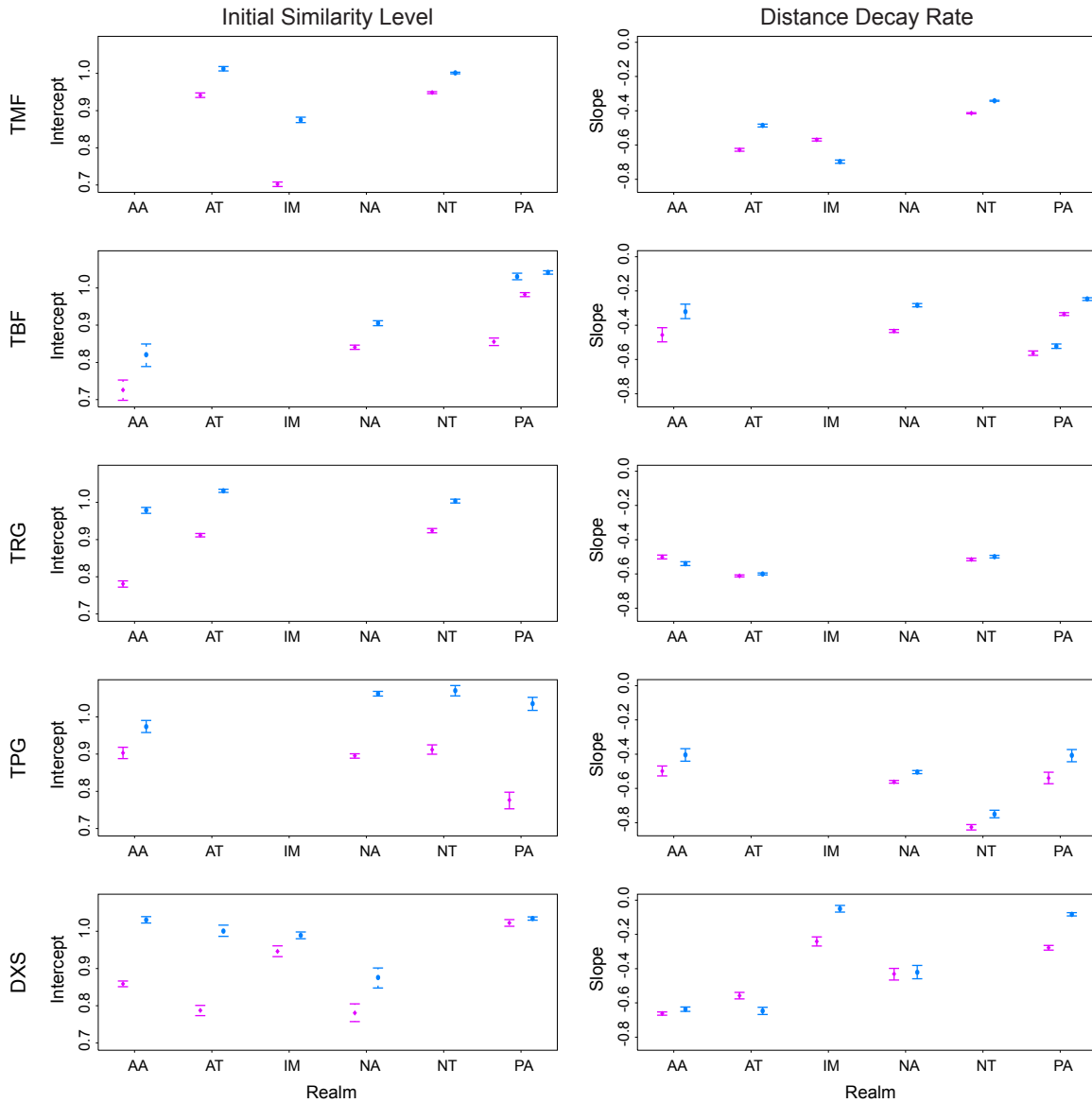
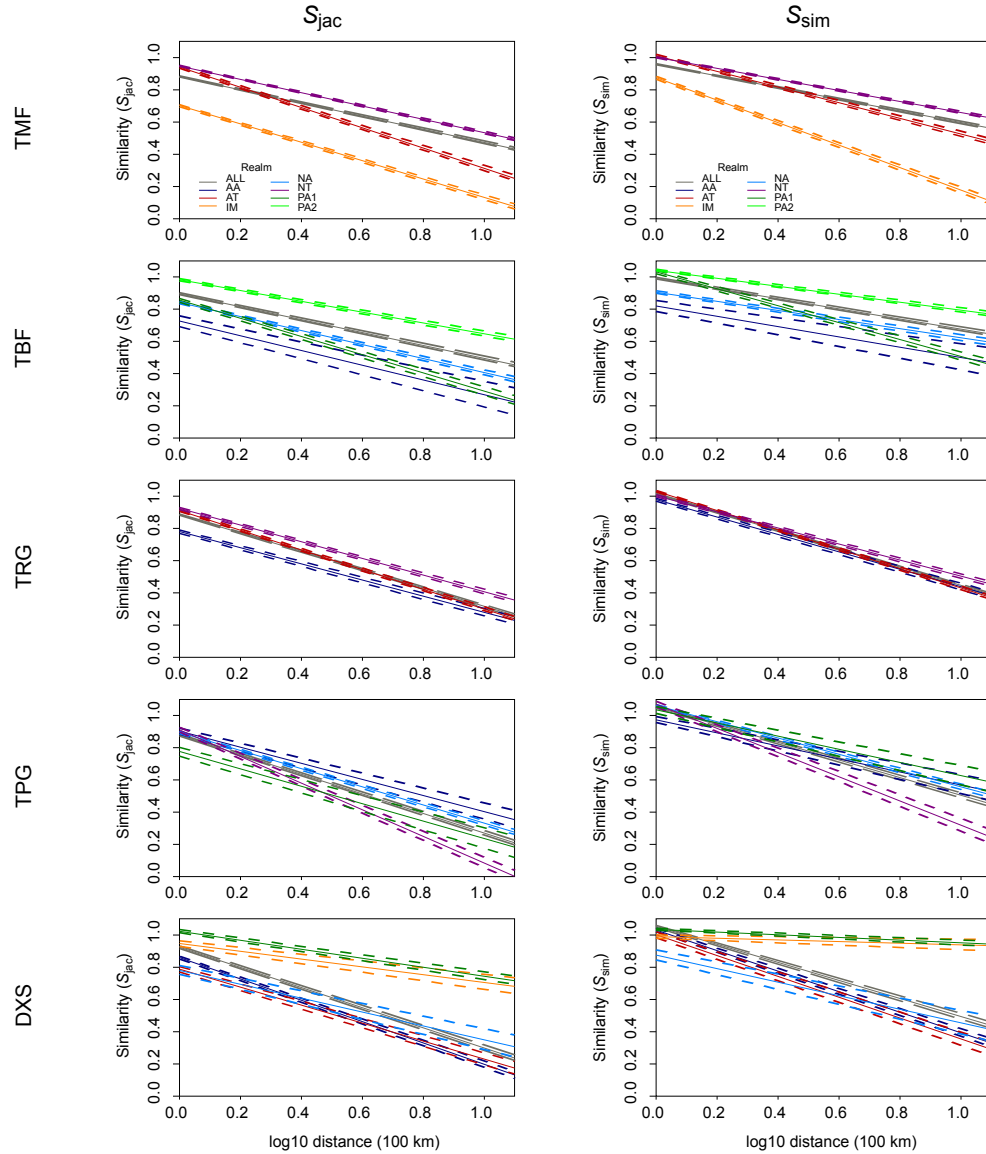


Figure 5.10. Distance decay relationships for each of the five biomes within the biogeographic realms in which it occurs. Modeled distance decay relationships (solid lines) based on S_{jac} (left panel) and based on S_{sim} (right panel) for the different realms (differentiated by color of line, see key) in which each biome occurs. Dashed lines are 90% confidence intervals. Realm abbreviations: Australasian (AA), Afrotropical (AT), Indomalayan (IM), Nearctic (NA), Neotropical (NT), and Palearctic (PA1: eastern Palearctic TBF, TPG, and DXS; PA2: western Palearctic TBF).



CHAPTER 6

Conclusions: Diversity's "Other Component"

The concept of diversity has two broad components: richness (also called inventory diversity) and beta-diversity (also called differentiation diversity). Beta-diversity is diversity's "other component" because it is less studied and more poorly understood than richness. This is partly due to confusion over terminology and concepts of beta-diversity and partly due to lack of data sets that can be used to compute beta-diversity over large areas. In this thesis, I addressed the obstacles to making generalizations about beta-diversity and presented the first empirical analyses of beta-diversity patterns at continental and global scales. In completing this thesis I produced the first maps of beta-diversity at the scale of the Western Hemisphere. While continental and global richness maps are familiar, my maps provide the only look to date at beta-diversity at this scale for multiple classes of terrestrial vertebrates, and offer a striking visual representation of this fundamental component of biological diversity.

In my review chapter, I traced the conceptual history of beta-diversity from its origins in community ecology to its many applications today. My review revealed the historical development of a single phenomenon of differentiation diversity, the compositional change in species regardless of scale or mechanism. I argued that this unifying concept ties together the various divisions previous authors have made. I further recommended that the term beta-diversity continue to be applied to this phenomenon because of the widespread use and the historical roots of this concept.

The three empirical chapters of this dissertation examined broad-scale beta-diversity of terrestrial vertebrates across multiple locations and extents, with the underlying purpose of determining whether

certain generalities exist. The taxonomic and geographic scope of my analyses of three terrestrial vertebrate classes (birds, mammals, and amphibians), 7,667 terrestrial vertebrate species across the Western Hemisphere and 5,817 amphibian species globally, exceeds that of any previous analyses of beta-diversity. I used the Western Hemisphere data, at a grain of 100 km x 100 km, to perform a thorough assessment of cross-taxon congruence in broad-scale beta-diversity and of the relationship between beta-diversity and species richness. With the global amphibian data, I conducted a thorough analysis of the distance decay relationship across biomes and biogeographic realms. These analyses used biogeographic realms as a surrogate for differences in history, biomes as a surrogate for differences in environment, and topographic complexity as a surrogate for local environmental heterogeneity and dispersal barriers. Similarly, the three vertebrate classes represented distinct taxonomic groups with different ranges of life history and dispersal abilities, and which can be expected to represent differences in historical patterns of evolution. While these are coarse surrogates of underlying mechanisms, they were used to explore basic broad-scale patterns in beta-diversity.

I addressed three general expectations for broad-scale beta-diversity: Are beta-diversity patterns congruent across taxa? Is there a relationship between beta-diversity and species richness (measured at the same scale)? Is there systematic variation in beta-diversity across biomes and biogeographic realms?

Many of my results from analyses at the Western Hemisphere extent were consistent for the three vertebrate classes. I also found strong patterns in global amphibian beta-diversity across certain contrasting sets of biomes and of realms. However, my results also showed interesting variation with differences in spatial extent and geographic location, between taxa, between the high and low extremes of diversity components, and between metrics (i.e., between initial similarity and distance decay rate, and between Jaccard's index of similarity and an index designed to remove the effect of species richness gradients).

In the following paragraphs I summarize the findings that support generalizations in cross-taxon congruence in beta-diversity, the relationship of beta-diversity to species richness, and systematic

variation in beta-diversity across biomes and biogeographic realms. I then outline the variations I found relating to each of these questions. Lastly, I make recommendations for future research.

Generalities in Broad-Scale Beta-Diversity

Are Beta-Diversity Patterns Congruent Across Taxa?

Amphibian, bird, and mammal beta-diversity patterns were largely congruent across the extent of the Western Hemisphere. There was a striking association of high beta-diversity and mountains apparent when mapped, which was also confirmed statistically for each taxon. My work showed an interesting discrepancy between congruence in highest beta-diversity areas, which were similarly distributed for the three taxa, and congruence in lowest beta-diversity areas, which were largely distinct. This suggests that similar processes lead to high levels of differentiation of these taxa, but the ecological and biogeographic factors influencing low levels of differentiation vary.

Is There a Relationship Between Beta-Diversity and Species Richness?

Beta-diversity and richness exhibited disparate patterns for all three taxa at the scale of the Western Hemisphere. For each taxon, there was considerable spatial segregation between the highest areas of the two diversity components. This demonstrates that patterns of beta-diversity contain information that cannot be provided by measures of species richness alone, and has implications for the mechanisms underlying broad-scale diversity patterns. That not all species-rich, tropical areas have rapid species turnover suggests that the role beta-diversity plays producing the high richness of the tropics is not straightforward, at least at the scales I measured.

The importance of mountains was apparent from my analyses of both cross-taxon congruence in beta-diversity and the relationship between beta-diversity and richness. As noted above, beta-diversity for all three taxa was high in mountainous areas. Moreover, the areas of highest beta-diversity for the three groups overlapped in the Northern Andes. Mountains were also at the intersection of the highest beta-diversity and richness areas for each taxon. That high levels of the two diversity components co-occur in topographically complex areas both within and outside of the tropics confirms the importance of history and topography in generating diversity.

Is There Systematic Variation in Beta-Diversity Across Biomes and Biogeographic Realms?

Variation in amphibian initial similarity and distance decay rates was complex, yet I found evidence suggesting that strong patterns may exist between certain broad climate contrasts or for particular historical differences. For instance, initial similarity within biomes in the Australasian realm were generally much lower than within their counterparts in other realms, and distance decay rates within Afrotropical biomes were more rapid than within the same biomes in the Neotropics. Another interesting trend was that distance decay rates in grasslands were more rapid than in forests within both temperate and tropical regions.

Such trends suggest that while biogeographic history and environment are both important in influencing the degree of change in species composition at near and far distances, the relative strength of each in determining differences in beta-diversity may be contingent upon particular aspects of climate or biogeographic history. Determining the mechanisms driving these differences, however, will require more detailed analyses. Comparing my findings for amphibians with distance decay rates for other taxa will help ascertain whether these results are indicative of a widespread trend or are particular to amphibians.

The preceding paragraphs have described, for three questions concerning broad-scale beta-diversity, the results I found to be general across taxa or regions. Below, I discuss the results relating to each of these questions which varied between taxa, geographic location and spatial extent, or metric used to measure beta-diversity.

Variations in Broad-Scale Beta-Diversity

Beta-Diversity Congruence

When measured at extents smaller than the Western Hemisphere, the strength of congruence in beta-diversity varied with geographic location and spatial extent, as well as between pairs of taxa. For example, each pair of taxa showed much stronger congruence within the Neotropical realm than within the Nearctic realm. Correlations measured at the same extent and location also differed between taxonomic pairs. Within the Nearctic realm, for instance, amphibian and mammal beta-

diversity showed a moderate degree of congruence, as did bird and mammal beta-diversity, but beta-diversity of amphibians and birds showed no significant congruence. The stronger congruence in beta-diversity within the Neotropics compared to the Nearctic is consistent with the historical differences between these realms. The Neotropics have experienced greater historical stability than the Nearctic, which had more severe climatic fluctuations and more extensive glaciation during the Pleistocene. Future research is needed to determine whether this pattern extends beyond the Western Hemisphere, for example, whether the high congruence in the Neotropics is also found in other tropical realms such as the Afrotropics, and how the level of congruence found in the Nearctic compares to the level in the Palearctic.

Relationship Between Beta-Diversity and Species Richness

For each taxon, the strength of the correlation between beta-diversity and richness, and whether the relationship was positive or negative, varied between biogeographic realms. Mammalian beta-diversity and richness, for example, were positively correlated in the Nearctic, but negatively correlated in the Neotropics. The results within one biogeographic realm also varied between taxa. For instance, in contrast to the positive correlation for mammals in the Nearctic, bird beta-diversity and richness in that realm had a weak negative correlation.

Variation in Beta-Diversity Across Biomes and Realms

My global analysis of distance decay relationships of amphibians revealed several interesting contrasts between the two distance decay parameters: initial similarity level and distance decay rate. For instance, there was a strong relationship between the topographic complexity in a region and initial similarity level, but there was no significant relationship between topographic complexity and distance decay rate. Moreover, the rate of distance decay measured for a region, and the variation in distance decay rates between regions, were much less affected by factoring out local richness gradients than were the level of initial similarity measured for a region and the variation in initial similarity between regions.

Future Research

My results provided support for the existence of general trends in beta-diversity at broad scales, at least for terrestrial vertebrates. Below I outline four areas of research which are either important to elucidating generalities about broad-scale beta-diversity or important to the practical application of beta-diversity to conservation.

Taxonomic and Geographic Scope

For the vertebrate classes I examined, cross-taxon congruence and the relationship between beta-diversity and richness should be examined on other continents and at different grains, and the global variation in distance decay should be investigated for birds and mammals. To be able to state with certainty that there are general trends in beta-diversity, however, the scope of study must be expanded beyond terrestrial vertebrates, with emphasis on analyzing beta-diversity patterns across a wide phylogenetic/taxonomic range of organisms. The marine and freshwater realms offer exciting prospects for testing beta-diversity generalities. Freshwater systems are naturally isolated, while marine systems are seemingly open, and the processes relating to dispersal are so different than in terrestrial systems (at least from the perspective of a terrestrial ecologist!). Although beta-diversity in marine and freshwater systems is studied at many scales, the vast majority of beta-diversity studies, including those at broad-scales, have been terrestrial.

Environmental and Historical Processes

In addition to increasing the taxonomic and geographic coverage of analysis, future research should include more detailed examination of the processes underlying broad-scale beta-diversity. In particular, understanding the relative influence of environment and history, and under what circumstances one is more important than the other, is central to determining whether or not underlying trends exist across taxa and regions; it also has practical application for surrogate methods in conservation planning.

Extending Analyses Beyond Presence-Absence Data

The analyses in this dissertation were all based on presence-absence data, which may produce different patterns than abundance data. In contrast with the community ecology roots of beta-diversity, beta-diversity studies at large scales are generally based on data sources limited to presence-absence data, such as range maps. As the availability of abundance data at large scales increases, studies comparing the two data types will provide another perspective on broad-scale beta-diversity. Another interesting avenue for measures of beta-diversity is a development of a metric that incorporates phylogenetic dissimilarity as well, so that more distantly related species counts as more distantly than more closely related species.

The Role of Beta-Diversity in Conservation Planning

Although beta-diversity has received indirect attention in the conservation literature for some time, notably in the early SLOSS debates (e.g., Simberloff & Abele 1976) and in the more recent profusion of complementarity algorithms (Sarkar 2006), few methods for directly addressing beta-diversity in conservation planning have been developed. Complementarity is an important principle for designing representative conservation networks, but beta-diversity has many benefits for conservation apart from its link with this principle. For example, beta-diversity analyses can help identify areas where species face increasing threat to persistence, because beta-diversity is often high where species' ranges are particularly susceptible to climatic variability such as steep environmental gradients and centers of endemism, or regions where successful conservation strategies may be resource intensive, because gradients of rapid species turnover will require closely spaced protected areas in order to effectively conserve biodiversity.

Fortunately, there is increasing interest in integrating beta-diversity into systematic conservation planning. One example is the development of conservation surrogates based on modeling compositional dissimilarity, which can improve biodiversity representation for data poor regions (Ferrier 2002; Ferrier *et al.* 2004; Steinitz *et al.* 2005). Several recent studies have incorporated turnover measures into area selection algorithms, with the goal of addressing persistence (Fairbanks *et al.* 2001). The application of distance decay relationships to the priority setting process as a means

of determining appropriate reserve spacing has also received recent attention (Wiersma & Urban 2005). These are all important issues in need of more in-depth research.

References

- Fairbanks, D.H.K., Reyers, B. & van Jaarsveld, A.S. (2001) Species and environment representation: selecting reserves for the retention of avian diversity in KwaZulu-Natal, South Africa. *Biological Conservation* 98, 365-379.
- Ferrier, S. (2002) Mapping spatial pattern in biodiversity for regional conservation planning: Where to from here? *Systematic Biology* 51, 331-363.
- Ferrier, S., Powell, G.V.N., Richardson, K.S., Manion, G., Overton, J.M., Allnutt, T.F., Cameron, S.E., Mantle, K., Burgess, N.D., Faith, D.P., Lamoreux, J.F., Kier, G., Hijmans, R.J., Funk, V.A., Cassis, G.A., Fisher, B.L., Flemons, P., Lees, D., Lovett, J.C. & Rompaey, R.S.A.R. (2004) Mapping more of terrestrial biodiversity for global conservation assessment. *BioScience* 54, 1101-1109.
- Sarkar, S. (2006) Ecological diversity and biodiversity as concepts for conservation planning: comments on Ricotta. *Acta Biotheoretica* 54, 133-140.
- Simberloff, D.S. & Abele, L.G. (1976) Island biogeography theory and conservation practice. *Science* 191, 285-286.
- Steinitz, O., Heller, J., Tsoar, A., Rotem, D. & Kadmon, R. (2005) Predicting regional patterns of similarity in species composition for conservation planning. *Conservation Biology* 19, 1978-1988.
- Wiersma, Y.E. & Urban, D.L. (2005) Beta diversity and nature reserve system design in the Yukon, Canada. *Conservation Biology* 19, 1262-1272.