TAXONOMIC, FUNCTIONAL, AND PHENETIC COMPONENTS OF LATITUDINAL
GRADIENTS IN BIODIVERSITY: PERSPECTIVES
ON THE COMMUNITY ECOLOGY OF NEW WORLD BATS

by

RICHARD D. STEVENS, B.S., M.S.
A DISSERTATION
IN
BIOLOGY
Submitted to the Graduate Faculty
of Texas Tech University in
Partial Fulfillment of
the Requirements for
the Degree of
DOCTOR OF PHILOSOPHY
Approved

[Signatures]

Co-Chairperson of the Committee

[Signatures]

Co-Chairperson of the Committee

[Signatures]

Accepted

[Signatures]

Dean of the Graduate School

December, 2002
ACKNOWLEDGMENTS

I would like to first thank my major advisors, Drs. Michael Willig and Richard Strauss, for their friendship, criticism, direction, encouragement, and financial support. In particular, I would like to thank Mike for making one of my long held academic dreams possible—a comparative intensive investigation of bat community ecology at two sites in eastern Paraguay, one that forever changed my life both personally and professionally. Similarly, I would like to thank Rich for revolutionizing my life, but in a much different way. Rich taught me how to use Matlab which has which has liberated me of my dependence on other people to write programs to conduct many of the randomization techniques necessary to address problems in community ecology. Moreover, learning how to program in Matlab has also deepened my understanding of univariate and multivariate statistics as well as had an immense impact on how I approach problems as a scientist.

I would like to thank Drs. Mark McGinley, Robert Owen, and David Schmidly for serving on my committee as well as for their interaction and direction. Their involvement has certainly broadened my knowledge of biology, particularly from the perspectives of community ecology, mammalogy, and systematics.

Ed Sobek, Dr. Stephen Cox, and Dr. John Zak have contributed substantially to my understanding of the concept of functional diversity. Interaction with many other faculty members and fellow graduate students have aided my academic development while at Texas Tech University. These include: Dr. Charles Werth, Dr. Robert Hollander, Dr. Michael Gannon, Dr. Elizabeth Sandlin, Dr. Steven Cox, Dr. Celia López-Gonzáles, Dr. Kate Lyons, Dr. Dawn Kaufman, Dr. Dave Chalcraft, Ed Sobek, Steven
Presley, Federico Hoffman, Carl Dick, Dr. Darin Carol, Chris Bloch and Marcos Gorresen.

I was very fortunate to be able to collect data on 2 of the 32 bat communities that are included in my analyses. Nonetheless, I did so with much help. Mike Willig and Robert Owen provided funding as well as much of the logistical infrastructure (via a grant from the National Science Foundation, DEB-9741543 and DEB-9741134) necessary to do extensive fieldwork in Paraguay. The National Museum of Natural History of Paraguay provided me with a truck while I was there. In particular, Oscar Romero and Isabel Gamarra de Fox put forth much effort to make that possible. Aida Luz Aquino and the Paraguayan C.I.T.E.S office provided continuous logistical assistance and a continuous “life-line” in times of need. Heidi Stevens, Rosalia Faríña Luis Jimenez, and Javier Pintos shared the fieldwork with me. The Fundacion Moises Bertoni and Yaguareté Forests allowed access to the two sites. In particular, I thank Paul Mueller and Alberto Yanosky for their cooperation while working at those sites. Marcos Gorresen, Steven Presley, and Dr. Celia López-Gonzáles offered much assistance and friendship while I was in Paraguay.

Lastly, I would like to thank my family both in the United States and Paraguay, for their constant patience and encouragement. In particular, I want to thank my wife Heidi for greatly enhancing the experience of all of the good times, for carrying me through the bad times, and for patience regarding the manic-depressive final stages of composing a dissertation. I also would like to thank my son Marco for broadening the context of my life and for enlightening my perspective on many aspects of it.
TABLE OF CONTENTS

ACKNOWLEDGMENTS...........................................................................................................ii

LIST OF TABLES................................................................................................................ix

LIST OF FIGURES................................................................................................................xi

CHAPTER

I. INTRODUCTION..............................................................................................................1

References.......................................................................................................................4

II. LATITUDINAL GRADIENTS IN THE TAXONOMIC DIVERSITY OF NEW WORLD BAT COMMUNITIES........................................................................................................5

Abstract.........................................................................................................................5

Introduction......................................................................................................................6

New World Bats...............................................................................................................9

Materials and Methods................................................................................................11

Available Data.................................................................................................................11

Characterization of Diversity......................................................................................14

Inferential Analyses......................................................................................................16

Results............................................................................................................................17

Measures of Diversity..................................................................................................17

Latitudinal Gradients....................................................................................................19

Scale-Dependence of Latitudinal Richness Gradients..............................................20

Local and Regional Richness.........................................................................................21
References.................................................. 72

IV. LATITUDINAL GRADIENTS IN THE PHENETIC DIVERSITY OF NEW WORLD BAT COMMUNITIES........89

Abstract................................................... 89
Introduction............................................ 90
Materials and Methods.............................. 93
Results..................................................... 97
  Characterization of Phenetic Diversity............ 97
  Empirical Patterns................................... 98
  Empirical Versus Simulated Gradients............. 99
Discussion.............................................. 100
  Differences Between Bats and Terrestrial Mammals............. 101
  Nearest-Neighbor and Community-Wide Perspectives........... 104
References............................................. 108

V. INTERACTIONS AMONG TAXONOMIC, FUNCTIONAL, AND PHENETIC COMPONENTS OF BIODIVERSITY AND THE CORRESPONDENCE OF THEIR LATITUDINAL GRADIENTS......126

Abstract................................................ 126
Introduction......................................... 127
  Components of Biodiversity........................ 128
Materials and Methods.............................. 130
  Components of Biodiversity........................ 130

vi
Taxonomic Diversity..................................130

Functional Diversity..................................131

Phenetic Diversity..................................131

Relationships between Components of Biodiversity..................................133

Characterization of Latitudinal Gradients.................................135

Differences in the Strength of Latitudinal Gradients Among Components of Biodiversity..........135

Results..................................................137

Relationships between Components of Biodiversity.................................137

Taxonomic versus Functional Diversity..137

Taxonomic versus Phenetic Diversity.....137

Functional versus Phenetic Diversity......138

Characterization of Latitudinal Gradients.........................140

Differences in the Strength of Latitudinal Gradients among Components of Biodiversity....140

Discussion..............................................141

References.............................................146

VI. SYNTHESIS.............................................175

References.............................................178
APPENDIX

A. MATLAB FUNCTION TO CALCULATE MEASURES OF TAXONOMIC DIVERSITY.................................170
B. MATLAB FUNCTION TO CALCULATE MEASURES OF FUNCTIONAL DIVERSITY.............................174
C. MATLAB FUNCTION TO SIMULATE EFFECTS OF CHANGES IN SPECIES RICHNESS ON FUNCTIONAL DIVERSITY GRADIENTS..........................................................177
D. MATLAB FUNCTION TO CALCULATE MEASURES OF PHENETIC DIVERSITY.............................184
E. MATLAB FUNCTION TO SIMULATE EFFECTS OF CHANGES IN SPECIES RICHNESS ON PHENETIC DIVERSITY GRADIENTS..........................................................186
E. MATLAB FUNCTION TO CONDUCT CANONICAL CORRELATION ANALYSES STANDARDIZED TO A PARTICULAR NUMBER OF VARIABLES...........................................192
LIST OF TABLES

2.1 Geographic and environmental characteristics of each of 32 bat communities used to evaluate patterns of taxonomic diversity in the New World..........................39

2.2 Fourteen measures of taxonomic diversity used to characterize New World bat communities.................................................................41

2.3 Empirical estimates of diversity and factor scores characterizing structure of 32 bat communities from the New World........................................42

2.4 Comparisons of aspects of diversity among tropical, subtropical, and temperate communities based on principal components as well as factors.......44

2.5 Results of simple linear regression analyses between latitude and each of the measures of diversity .........................................................45

3.1 Geographic and environmental characteristics of each of 32 bat communities used to evaluate patterns of functional diversity in the New World.......................80

3.2 Latitude and functional diversity for each of 32 bat communities in the New World..................................................................................82

3.3 Comparisons of aspects of functional diversity among tropical, subtropical, and temperate communities......................................................84

3.4 Results from orthogonal polynomial regression analyses (Dutka and Ewens 1971) estimating relationships of local functional diversity with species richness and latitude......................................................85

3.5 Results from simulation analyses determining the degree to which latitudinal gradients in functional diversity could be produced by a latitudinal gradient in species richness..................................................86

4.1 Geographic and environmental characteristics of each of 32 bat communities used to evaluate patterns of phenetic diversity in the New World..................113

4.2 Measures of phenetic diversity for each of 32 New World bat communities.................................................................115

4.3 Results from orthogonal polynomial regression analyses (Dutka and Ewens 1971) estimating relationships of local phenetic diversity with species richness and latitude......................................................117
4.4 Comparisons of aspects of phenetic diversity among tropical, subtropical, and temperate zones.............................................118

4.5 Results from simulation analyses determining the degree to which latitudinal gradients in phenetic diversity could be produced by the empirical latitudinal gradient in species richness.............................................119

5.1 Geographic and environmental characteristics of each of 32 bat communities used to evaluate patterns of diversity in the New World.............................................151

5.2 Results of canonical correlation analyses between taxonomic, functional, or phenetic components of biodiversity.........................................................154

5.3 Results of canonical correlation analyses between latitude and taxonomic, functional, and phenetic components of biodiversity.....................................156

5.3 Results from t-tests evaluating significant differences regarding the correlation of taxonomic, functional, and taxonomic with latitude.....................................157
LIST OF FIGURES

2.1 Location of 32 New World bat communities (solid dots) used to evaluate geographic patterns of diversity ........................................... 47

2.2 The projection of each of 32 communities in two-dimensional diversity space (left column) defined by principal components (a) and rotated factors (c) .... 48

2.3 Relationships of principal components and rotated factors with latitude for New World bats ............................................................... 49

2.4 Relationships between the number of rare (a) and common (b) species and latitude ........................................................................... 50

2.5 The ability of diversity indices to detect a latitudinal gradient, as measured by the correlation coefficient, is not greatly affected by changes in sampling intensity ....................................................................................... 51

2.6 Significant relationships between local species richness (solid line) and regional species richness (dashed line) with latitude for New World bats (a) .......................................................... 52

3.1 Location of 32 New World bat communities (solid dots) used to evaluate geographic patterns of diversity ........................................... 87

3.2 Gradients in four components of functional diversity of New World bat communities with respect to latitude (right column) and species richness (left column) ........................................................................ 88

4.1 Location of 32 New World bat communities (solid dots) used to evaluate geographic patterns of diversity ........................................... 120

4.2 Diagramatic representation of variation in phenetic diversity ........... 121

4.3 Correlogram depicting the magnitude and direction of correlations of the original morphological variables with the first two axes from principal components analysis ................................................................. 122

4.4 Relationships between aspects of morphological diversity and species richness .................................................................................. 123

4.5 Latitudinal gradients in morphological diversity with regard to both size (left column) and shape (right column) .............................................. 124
4.6 Latitudinal gradients in morphological diversity of terrestrial mammals (redrawn from Shepherd 1998) ........................................ 125

5.1 Location of 32 New World bat communities (solid dots) used to evaluate geographic patterns of diversity ........................................ 158

5.2 Correlations of original measures of taxonomic (upper) and functional (lower) diversity to the first set of canonical variates derived from canonical correlation analysis evaluating the relationship between taxonomic and functional components of biodiversity ........................................ 159

5.3 Correlations of original measures of taxonomic (upper) and phenetic (lower) diversity to the first set of canonical variates derived from canonical correlation analysis evaluating the relationship between taxonomic and phenetic components of biodiversity ........................................ 160

5.4 Correlations of original measures of functional (upper) and phenetic (lower) diversity to the first set of canonical variates derived from canonical correlation analysis evaluating the relationship between functional and phenetic components of biodiversity ........................................ 161

5.5 Correlations of original measures of functional (upper) and phenetic (lower) diversity to the second set of canonical variates derived from canonical correlation analysis evaluating the relationship between functional and phenetic components of biodiversity ........................................ 162

5.6 Correlations of original measures of functional (upper) and phenetic (lower) diversity to the third set of canonical variates derived from canonical correlation analysis evaluating the relationship between functional and phenetic components of biodiversity ........................................ 163

5.7 Correlations of original measures of taxonomic (upper), functional (middle), and phenetic (lower) diversity with canonical variates derived from canonical correlation analyses between latitude and each of the three components of biodiversity ........................................ 164

5.8 Frequency distributions characterizing bootstrapped canonical correlation coefficients between latitude and taxonomic (hatched), functional (grey) and phenetic (black) components of biodiversity ........................................ 165
CHAPTER 1
INTRODUCTION

Over the last century, our understanding of the various ways in which taxa diversify has expanded at an accelerating rate. This consequently has driven the expansion of the science of biology into a large number of disciplines including systematics, ecology, physiology, molecular biology, and biogeography. This expansion has been driven primarily by reductionist approaches resulting in specialization with only a few attempts to synthesize information across disparate disciplines or even integrate paradigms within disciplines (Pickett et al. 1994). A prime example of this characterizes advances in the field of ecology. Ecologists seek to understand the diversification of taxa by evaluating the distribution and abundance of organisms from a variety of temporal, spatial, and taxonomic perspectives (Ricklefs 1990). Second only to the theory of natural selection, the concept of biodiversity is central to investigations involving the diversification of taxa. Contributions from ecology have resulted from independent investigation in different sub-disciplines that focus on issues such as species diversity, ecosystem function and dynamics, metapopulations, ecomorphology, or competition.

This body of research has demonstrated that changes in species richness or the equability of species abundances are not the only manifestations of the diversification of taxa across space and time (Heywood and Watson 1995, Gaston 1996, Levin 2001). Consequently, the current paradigm defines biodiversity as the totality of variation in living things (Tilman 2001), and reflects evolution of the concept from one that characterized variation in numbers of species to one that embraces complex forms of variation such as temporal
and spatial changes in community structure and ecosystem function. Although the concept of biodiversity reflects integrated understanding based on information coming from areas within and outside of ecology, the failure to achieve integration has limited progress in understanding how biodiversity varies spatially and temporally in nature. In fact, most of the research evaluating variation in biodiversity across environmental gradients still focuses exclusively on patterns of species richness measured at relatively large spatial scales in terms of both grain and extent (Willig 2001, Stevens and Willig 2002). Clearly, the use of species richness as a surrogate for biodiversity has led to considerable advances in understanding the spatial and temporal distribution of organisms. Nonetheless, the extent to which such surrogates capture the salient spatial and temporal dynamics underlying patterns in biodiversity largely remains unexplored and conjectural.

Latitudinal gradients in species richness have been investigated across a number of spatial, temporal, and taxonomic extents (Willig 2001). Increases in the number of species toward the equator have been demonstrated on all continents except Antarctica, throughout geologic time, and across most higher taxa of plants or animals. Nonetheless, changes in species richness do not directly correspond to changes in other components of biodiversity such as functional diversity (Martinez 1996), character diversity (Williams and Humphries 1996), or phenetic diversity (Findley 1976, 1993, Schum 1984). Moreover, uncertainty concerning the degree to which components of biodiversity vary independently of species richness in particular and each other in general highlights the need to integrate patterns of variation and to better understand their environmental gradients.
Herein, I attempt more comprehensively to characterize spatial variation in the biodiversity of New World bat communities by integrating information regarding taxonomic, functional, and phenetic components. Although this approach does not include all of the numerous possible components of biodiversity, it represents a more holistic perspective to understanding latitudinal gradients in biodiversity. In Chapter II, I evaluate latitudinal gradients of taxonomic diversity that are characterized by measures sensitive to variation in species richness, as well as species diversity, species evenness and species dominance. In Chapter III, I evaluate latitudinal gradients of functional diversity. In Chapter IV, I describe latitudinal gradients of phenetic diversity. Finally, in Chapter VI, I compare and contrast the strength of associations of each component of biodiversity with latitude and evaluate the interrelationships among components of biodiversity.
References


CHAPTER II
LATITUDINAL GRADIENTS IN THE TAXONOMIC
DIVERSITY OF NEW WORLD BAT COMMUNITIES

Abstract

The ubiquity of the latitudinal gradient of species richness is well documented at coarse scales of resolution, but the extent to which the pattern is recapitulated at the level of local communities for any aspect of taxonomic diversity (i.e., richness, evenness, or diversity) is unclear. I examined how attributes of New World bat taxonomic diversity vary with each other and with latitude at two scales of resolution, local communities and regional species pools. I calculated 14 indices of taxonomic diversity (species richness [3], evenness [4], dominance [3], and diversity [4]) from species abundance distributions for 32 intensively sampled local sites between 42.25° N and 24.12° S latitude. The species richness of each corresponding regional pool was estimated from published range maps. In general, the gradient of local species richness was less steep than the corresponding gradient of regional species richness—beta diversity in the tropics is greater than that for temperate communities. All aspects of taxonomic diversity at the local scale did not vary with latitude in the same manner. The latitudinal gradient in taxonomic diversity of local communities was primarily a consequence of the corresponding gradient in species richness. Local richness increased and became more variable with decreasing latitude. In contrast, species evenness did not vary in a systematic fashion with latitude. Although the absolute number of rare species in
communities increased faster with latitude than did that of common species, both 
abundance classes proportionately increased with latitude in equivalent ways throughout 
the New World. In general, latitudinal variation at the community level was detected in 
diversity indices that were insensitive to the abundance of species. The dramatic increase 
in species richness at broad scales of resolution toward the tropics (gamma diversity) was 
as much a consequence of increased richness at the local level (alpha diversity) as it was 
a consequence of the latitudinal increase in species turnover among communities (beta 
diversity). Future theoretical research should examine the correlates of latitude that 
enhance differentiation among communities at low latitudes (i.e., those which enjoy high 
productivities). Conservation strategies based on assessments of diversity at coarse levels 
of resolution (gamma diversity) should be implemented with caution because beta 
diversity inflates regional estimates of diversity.

Introduction

Quantifying broad-scale spatial patterns in the distribution and abundance of 
organisms (Fischer 1960, Pianka 1966, MacArthur 1972), and postulating causative 
mechanisms (MacArthur 1972, Colwell and Hurtt 1994, Rosenzweig 1995, Rohde 1997), 
have dominated much of contemporary ecological research over the last two decades 
(Gaston and Blackburn 1999). Studies of latitudinal gradients have contributed greatly to 
our understanding of the geographic distribution of diversity (Willig 2000). These 
 studies primarily have examined patterns of species richness at or above the regional 
scale (sampling units ≥ 25 km²), and typically are based on data garnered from
distribution maps, field guides, atlases, or checklists that characterize the distribution of taxa across broad geographic areas at coarse scales of resolution (e.g., Fischer 1960, Cook 1969, Kiefer 1971, Willig and Scler 1989, Rohde 1992, Rex et al. 1993). This approach has documented one of the most pervasive patterns characterizing the spatial distribution of organisms. Systematic increases in the number of species with decreases in latitude have been demonstrated for plants and animals, in terrestrial and aquatic environments, and during contemporary and past times (see Gaston 1994, Brown 1995, Rosenzweig 1995, Willig 2000). Moreover, this pattern is robust with respect to systematic hierarchy and can be demonstrated at specific, generic, familial, and ordinal levels (e.g., Fischer 1960, Kaufmann 1995). Ecologists, however, have become bogged down in a quagmire of contention concerning the mechanisms that produce the gradient (see Rohde 1997, Rosenzweig and Sandin 1997). Moreover, distinguishing the process or subset of mechanisms that are responsible for latitudinal patterns will be a daunting task because most mechanisms only lead to qualitative predictions that are not mutually exclusive, and because null models can give rise to latitudinal gradients in the absence of underlying environmental heterogeneity (Colwell and Hunt 1994, Willig and Lyons 1998, Colwell and Lees 2000).

Many factors limit the development of theory. For example, much of what has been learned regarding spatial variation in taxonomic diversity comes from two distinct approaches. The first uses species richness as a surrogate of diversity and then evaluates patterns at large spatial scales. Because differences in relative abundances of species are ignored, such an approach provides limited understanding of the ways in which
taxonomic diversity *per se* responds to environmental variation. The second evaluates simultaneous changes in richness and evenness along environmental gradients (e.g., productivity), but this typically is done at relatively small spatial scales in terms of both focus or extent (Rotenberry 1978, Wilson and Gitay 1995, Drobner et al. 1998, Weiher and Keddy 1999, Wilsey and Potvin 2000). The way in which species richness and evenness interact and give rise to empirical patterns of diversity at large scales, especially along extensive environmental gradients, remains poorly understood. The marriage of these two approaches likely will hasten a unified understanding of patterns of taxonomic diversity.

Advancement of theory also has been stymied by the scale-dependent nature of patterns of taxonomic diversity. Studies of the productivity-diversity relationship offer a good example (Pastor et al. 1996, Waide et al. 1999, Gross et al. 2000, Mittlebach et al. 2001). The consensus is that productivity affects species diversity; however, little agreement exists regarding the form of this relationship from either theoretical or empirical perspectives. Productivity increases diversity at some spatial scales, whereas at others it can decrease diversity. Along extensive gradients the relationship between diversity and productivity can be unimodal or linear. The generalization of patterns of species diversity across spatial scales, and hence the production of unified theories, depends on understanding scale-dependence from both qualitative and quantitative perspectives (Scheiner et al. 2000). Scale-dependence should be expected as long as species richness increases with area in a non-linear way (Lyons and Willig 1999, 2001).
The greatest obstacles that impede the description of broad-scale patterns of diversity are practical. Detailed information from intensive sampling of numerous local sites across a variety of latitudes must be accurate and comparable. Because ecological communities generally comprise more relatively rare species than common ones (Gaston 1994), especially in tropical environments, intensive efforts are necessary to estimate confidently the right-hand tail of species abundance distributions. Moreover, the collection of such information across a number of sites is too prodigious a task for any one investigator, and the only practical way to amass such data is to wait patiently for a number of investigators independently to collect detailed data on species composition at a variety of sites. Only recently has such information become available for even common taxa. Fortunately, studies quantifying bat species composition at a number of New World locales have accumulated over the last 25 years and make such broad analyses a feasible endeavor (Table 2.1).

**New World Bats**

Bats are exceptional in that they generally have broad geographic distributions and exhibit high degrees of taxonomic and functional diversity (Findley 1993, Stevens and Willig 2000, Patterson et al. 2001). They exhibit pronounced latitudinal gradients of species richness at the regional scale (Willig and Selcer 1989, Willig and Sandlin 1991, Kaufman and Willig 1998) that are not solely a consequence of stochastic processes (Willig and Lyons 1998). Moreover, bats are often the most abundant vertebrates at the level of local communities and often the most species-rich mammalian taxon in the
tropics (Patterson et al. 2001). Functionally, compositionally, and structurally, New
World bat communities are highly variable (Findley 1993, Stevens and Willig 1999,
2000). Communities comprise species from a single feeding guild (aerial insectivores) at
high latitudes, and exhibit an increase in the number of functional groups to at least seven
(aerial insectivores, frugivores, gleaning animalivores, high-flying insectivore,
nectarivores, sanguinivores, and piscivores) at the equator (Stevens and Willig 2000).
Moreover, communities vary considerably in morphological and numerical patterns
related to size assortment and density compensation (Stevens and Willig 1999, 2000).
Nonetheless, it is unclear if such community characteristics, or even more basic attributes
like taxonomic diversity, are related to latitude and its primary correlates of temperature,
seasonality, or energy.

I quantitatively describe taxonomic diversity in 32 bat communities from
throughout the New World. I also evaluate 14 popular indices of diversity based on how
they reflect species richness, evenness, or dominance, and evaluate the sensitivity of
these measures to detect a gradient when data are based on successively less effort at
each site. I then quantify latitudinal gradients in diversity at the community level and
evaluate scale-dependence in latitudinal gradients of species richness by determining the
linkage between the latitudinal gradient of species richness at regional and local scales.
Materials and Methods

Available Data

Data on species composition of 32 bat communities were obtained from the literature (Table 2.1, Figure 2.1). Although data based on samples from local communities provide finer-grain resolution than do studies based solely on distribution maps, they suffer from a suite of unique limitations. For example, a number of different investigators collected data across a number of different years; inter-investigator differences in sampling protocol and inter-year environmental differences may affect the number of individuals obtained at a site. Moreover, these communities span environmental gradients that I did not attempt to control, such as elevation and precipitation, and these gradients often may be influenced by edaphic characteristics. These environmental factors may not vary with latitude in simple ways and may obscure relationships between taxonomic diversity and latitude. Nonetheless, data from these sites represent taxonomic and functional subsets of real communities (i.e., groups of species, which as a consequence of spatial and temporal constraints, have the potential to interact and affect local demographics), and if broad-scale geographic patterns are the result of strong structuring mechanisms operating at the community level, then such uncontrolled factors should cause only minor departures from true relationships and not affect a bias.

I used several criteria to select sites for inclusion in analyses. Data must have been based on collections from more than one location in a community, but the area of
sampling must have been constrained spatially so that information likely was from a single community. This criterion was somewhat subjective. Many facets of bat community ecology remain enigmatic (Findley 1993). For example, no estimates currently exist as to the aerial extent of bat communities. Moreover, it is unknown whether the boundaries of bat communities are sharp and correspond to boundaries elicited by the environment, such as those between habitats or between life zones, or whether boundaries are spatially broad and represent gradual transitions whereby communities progressively intergrade into each other along environmental gradients. In general, I incorporated studies that sampled bats within an area of approximately 1000 km² (ca. 32 km by 32 km). Although some studies included data from more than one habitat in heterogeneous environments or from more than one life zone in montane environments, the data characterizing each study always came from a single biome and were bounded spatially so that it would not be unreasonable to encounter the same individuals across the entire suite of habitats encompassed in the study. Additionally, sampling must have been conducted on a regular basis, in all seasons during which bats were active, for at least one but not exceeding five years. Clearly, the most effective means to increase the probability of encountering rare species is to increase sampling effort. Nonetheless, if the time period over which sampling is conducted is too long, samples may include species that do not coexist in time and may be biased in the alternate direction of overestimating the richness of a community and underestimating its evenness or dominance. A 1-5 year time span is a tradeoff that minimizes the possibility of missing rare species and increases the accuracy of relative abundances while
minimizing the possibility of including species that, due to temporal changes in
community structure, may not coexist in time. As a final safeguard, I constructed
collectors curves for all communities, and included only those communities whose
taxonomic diversity was at the asymptote of a collectors curve representing diversity as a
function of numbers of captured individuals. Two of the thirty-two communities did not
meet all criteria. The Nevada community did not meet spatial sampling criteria and the
Linhares community did not meet temporal sampling criteria. Neither of these sites
greatly influenced statistical results nor did they represent outliers in any analysis.
Because these sites enhance our ability to describe the great variety of bat communities
found in the New World and increase our ability to obtain sufficiently large samples sizes
to resolve patterns in diversity, I included them in analyses.

To determine the regional species richness of a site, I counted the number of bat
species whose geographic distributions overlapped that site. Distribution maps for each
species were prepared using Hall (1981), Eisenberg (1989), Koopman (1982), and
Redford and Eisenberg (1992). Following Kaufman (1998), I used the equation (1 – local
species richness/regional species richness) as an estimate of species turnover or beta
diversity for each of the 32 communities. Based on latitude, communities were classified
into one of three geographic zones: tropical (12° N to 12° S), subtropical (13° N to 23.45°
N and 13° S to 23.45° S), or temperate (> 23.45° N or 23.45° S).
Characterization of Diversity

The multifaceted nature of diversity presents a number of methodological complications. Changes in diversity can result from changes in species richness, changes in equability, or both. Accordingly, attempts to differentially weight richness and evenness have resulted in more than 20 measures of diversity. Many are mathematically complex and disguise the relative degree to which evenness and richness are weighted in a composite index. Indeed, no one measure has achieved hegemony.

Fourteen measures of taxonomic diversity (Table 2.2) were calculated using a program written in Matlab for the Macintosh (The Math Works, 1995). These measures differentially reflect species richness, evenness, dominance, or diversity. Species richness ($R_e$) was estimated as the number of species sampled from the community. In addition, Margalef's index (Margalef 1957) and Menhinick's index (Menhinick 1964) were used because they take into account the increases in species richness with increases in effort. The equability of species abundances (evenness) was estimated using an index reflecting the probability of an interspecific encounter (Pie, Hurlbert 1971), Schoener's index (O, Schoener 1970, Camargo 1995), Shannon's index (SHE, Pielou 1975), and Camargo's index (CE, Camargo 1993). Diversity measures that capture simultaneous variation in richness and evenness were estimated by log-series alpha (A, Fisher et al. 1943), Shannon's index (SHD, Pielou 1975), Brillouin's index (B, Pielou 1969, 1975), and Camargo's index (CD, Camargo 1993). Finally, the degree to which community composition is dominated by one or a few abundant species (dominance) was estimated using Simpson's index (SI, Simpson 1949), Berger-Parker index (BP, Berger and Parker...
1970), and McIntosh D-index (McIntosh, 1967). Following Magurran (1988), BP and SI were scaled so that a large index represents low dominance and high diversity. All indices are well-described in the literature (e.g., Peet 1974, Magurran 1988, Camargo 1995, Biesel et al. 1996, Smith and Wilson 1996, Camargo, 1997) and will not be defined in additional detail here. This is not an exhaustive survey of diversity measures. Rather, I selected measures that were easy to calculate, commonly used, or proposed to be improvements over previously described and commonly used indices. Taken together, I expect this suite of measures to reveal variation in the complexion of diversity throughout the range of sites from which I have data.

I conducted a factor analysis ("Procedure FACTOR," SPSS 1990) to construct derived measures of diversity based on the original fourteen indices. Factor analysis derives variables that are linear combinations of the original ones. My analysis constrained factors to be orthogonal. Thus, because original indices were correlated, fewer than fourteen factors were necessary to represent the structure of the original data (i.e., accurately reflect intersite differences in empirical diversity). Analysis began with a principal components analysis (PCA) of the correlation matrix. PCA extracts derived orthogonal variables such that each subsequent axis accounts for a maximal amount of residual variation. Thus, the first few principal components characterize the main axes of variation in taxonomic diversity embodied in the 32 communities. Only those principal components with eigenvalues greater than unity (i.e., accounted for more variation on average than one of the original indices) were included in inferential analyses and subsequent aspects of the factor analysis. These principal components were rotated via a
varimax procedure to produce factors. Rotation causes variation in each of the original indices to be maximal on one factor and minimal on all others, predisposing correlated variables to have maximal loadings on the same factor, and equalizing variation among factors. The varimax rotation facilitated the decomposition of variation in diversity into constituents of evenness and richness.

Inferential Analyses

I used linear regression analyses ("Procedure REGRESSION," SPSS Inc. 1990) to determine if latitude accounted for a significant proportion of the variation among sites in each of the original diversity measures separately, as well as for each of the orthogonal axes derived from factor analyses. I maintained experiment-wise-error rate at 5% by conducting separate sequential Bonferroni adjustments (Rice 1989) for the set of 14 indices, as well as for each set of derived variables. Linear regression may lack power to detect latitudinal effects related to differences among broad climatological regions. Thus, I used MANOVA ("Procedure MANOVA," SPSS Inc. 1990) to evaluate differences regarding taxonomic diversity among temperate, subtropical, and tropical communities. Subsequently, I used Student-Newman-Keuls tests (Sokal and Rohlf 1995) to further resolve mean differences with respect to each of the derived variables provided that their associated ANOVAs were significant. To evaluate differences between local and regional richness regarding their relationship with latitude, I compared the 95% confidence intervals of both the slopes and intercepts generated from least-squares linear regressions.
In addition, I categorized species as common or rare based on four considerations of abundance (i.e., rare species are those with less than $1/R_c$, 5%, 2%, or 1% of all individuals in the community). To evaluate if the absolute rate of increase in species richness with decreasing latitude is the same for rare and common taxa, I compared slopes from least-squares regressions of the number or rare and common taxa and latitude. To evaluate if the proportional rate of increase in species richness with decreases in latitude is the same for rare and common species, I compared slopes from least squares-regressions of the log of the numbers of rare and common taxa and latitude.

Finally, I conducted a sensitivity analysis to explore the effect of sampling intensity on latitudinal gradients of diversity. I randomly sampled individuals from each community until their number in a subsample equaled a particular percentage of the total number of individuals in the entire sample. Diversity measures for each community were recalculated, and the correlation was determined between diversity and latitude. I then used the mean and two standard deviations of one hundred iterations of this process for each subsample (defined by a percent of total sampling effort) as measures of the average latitudinal gradient and its variability.

Results

Measures of Diversity

All measures of diversity were quite variable among the 32 bat communities (Table 2.3). In general, indices of richness and dominance were most variable and indices of evenness were least variable among sites based on relative measures of
dispersion (CV). More specifically, PIE (CV = 21.20) and O (CV = 21.74) exhibited the least relative variation among sites, whereas A (CV = 58.65) and SI (CV = 57.31) exhibited the most relative variation among sites. The degree of association between pairs of measures of diversity was generally high but variable. Correlations ranged from -0.01 between CE and MAR to approximately 1.00 between SHD and B.

Factor analysis reduced the 14 measures of diversity to two major axes (Figure 2.2a). Eigenvalues for the first two principal components were 9.88 and 2.72, and together accounted for 90.0 percent of the variation among communities regarding all measures of diversity. All variables were significantly ($P < 0.05$) correlated with PC1, and correlations were positive (Figure 2.2b). Thus, PC1 reflects a general component of variation in the magnitude of diversity among sites. PC2 was correlated most highly with indices of species richness and evenness (Figure 2.2b). Indices of species richness were correlated negatively and indices of evenness were correlated positively with this component. PC2 reflected the tradeoffs between richness and evenness that integrate empirically to constitute local diversity.

The varimax procedure decomposed variation in diversity into aspects of species richness and evenness (Fig 2.2c). The first rotated factor was significantly ($P < 0.05$) and most highly correlated with measures of species richness (Figure 2.2d). The second factor was correlated significantly and most highly with measures of evenness (Figure 2.2d).

Diversity differed among communities based on latitudinal affiliation (Figure 2.2a; MANOVA, $F_{3,32} = 2.25$, $P = 0.014$). Regarding PC1 (Table 2.4), temperate
communities were significantly less diverse than were tropical or subtropical communities whereas tropical and subtropical communities were indistinguishable. No significant differences among regions existed on PC2 (Table 2.4). Differences in diversity among sites also can be distinguished by examination of derived factors of evenness and richness (Figure 2.2d). Temperate communities were different from both tropical and subtropical communities on the richness factor (Factor 1), whereas differences between tropical and subtropical communities were detectable on Factor 2. Temperate communities evinced relatively low species richness and low evenness. Tropical and sub-tropical communities evinced similar levels of diversity. Tropical communities attained high diversity primarily as a consequence of species richness, whereas subtropical communities attained high diversity as a consequence of more even abundances.

**Latitudinal Gradients**

Differences among regions reflected a continuous latitudinal gradient in Factor 1 and the two principal components (Figure 2.3). Two of the three measures of species richness and two of the four measures of diversity also were significant linear functions of latitude (Table 2.5). The amount of variation in an index that was related significantly to latitude ranged from 0.27 for SHD to 0.35 for $R_c$. In general, evenness and dominance did not exhibit latitudinal gradients.

Because results were qualitatively the same regardless of the criterion for rarity, I only present those based on $1/ R_c$. Latitudinal gradients exist regarding the number of
both common and rare taxa, however, latitude had a stronger effect on the number of rare species. Compared to common species (95% CI for $b_1$: -0.30 to -0.07), rare species (95% CI for $b_1$: -1.05 to -0.34) increased more rapidly in richness toward the tropics (Figure 2.4). Nonetheless, the proportional rate of increase in species richness towards the tropics was indistinguishable for common species (95% CI for $b_1$: -0.02 to -0.01) and rare species (95% CI for $b_1$: -0.02 to -0.01).

Sensitivity analyses indicated that measures of diversity for subsamples, on average, recapitulated the latitudinal gradient to the same degree as did the complete samples, even when subsamples constituted a small percentage of the original data (Figure 2.5). Results within index classes based on richness, diversity, evenness, and dominance were always similar. Consequently, I illustrate results for only two of the available indices for each of the four diversity classes. The environmental pattern among sites embodied by latitude is strong, and not extremely sensitive to the number of individuals sampled from each of the communities. Although mean characteristics of diversity were stable, variability increased with decreases in the size of subsamples. Nonetheless, even very small samples, on average, evinced the observed significant latitudinal gradient in species diversity.

Scale-Dependence of Latitudinal Richness Gradients

Latitude accounted for much more of the variation in regional richness ($r^2 = 0.88$) than in local richness ($r^2 = 0.35$). Nonetheless, both relationships were significant (Figure 2.6a). More specifically, almost three times as many species of bats are predicted
to occur at the equator in regional faunas ($b = 124 \pm 4$) than in local communities ($b = 44 \pm 4$), and this difference was significant. Nonetheless, the rate of decrease of the number of species with increasing latitude was significantly higher for regions ($b = -2.89 \pm 0.20$) than for local communities ($b = -0.88 \pm 0.22$), suggesting that environmental filters (the proportion of the regional fauna occupying a local community) are most selective in tropical areas.

Local and Regional Richness

Species richness at the regional level accounted for a significant amount of the variation in species richness at the local level (Figure 2.6b, $b = 0.30$, $F_{1,39} = 17.91, r^2 = 0.37, P << 0.001$) and no evidence exists for a quadratic component (i.e., a non-significant [$P = 0.509$] quadratic coefficient in the second-degree polynomial with a $\Delta R^2$ of only 0.01) in the relationship. As the number of species increased in regional faunas, so did the number of species in local communities. Although this relationship was linear, it was more variable when the richness of regional pools was higher. Beta diversity, measured as species turnover between faunal pools and local communities, increased significantly with decreases in latitude (Figure 2.6c, $b = -0.009$, $F_{1,39} = 11.72, r^2 = 0.28, P = 0.002$) for the entire New World.

Discussion

The latitudinal gradient in taxonomic diversity is one of the most well-recognized and frequently substantiated patterns known to biogeographers. Nonetheless, this pattern
rarely is evaluated for local communities, and almost all studies, regardless of spatial scale, consider only species richness. I substantiate that, albeit weaker than at the regional scale, a latitudinal gradient in species richness exists at the community level for bats. In addition, latitude affects other aspects of taxonomic diversity. Many of the existing measures of diversity are robust and can detect latitudinal patterns even with relatively small sampling effort. I demonstrate that latitudinal gradients at local and regional levels are quantitatively different, with regional species richness being more strongly influenced by latitude than is community species richness. Moreover, the scale-dependence of latitudinal species richness gradients is further suggested by latitudinal increases in the magnitude of beta diversity.

Gradients of Diversity

Classically, latitudinal gradients of taxonomic diversity have been explored by evaluating the relationship between regional species richness and latitude. Indeed, our results regarding latitudinal gradients in species richness at both the regional and local level corroborate previous findings. Gradients in species richness should result when environmental variation affects the number and diversity of resources (Rodenberry 1978). Latitudinal increases in the kinds of resources utilized by New World bats are implied by latitudinal increases in the number of trophic guilds (Stevens and Willig 2000, Willig 2000). The trophic diversity of bats in the New World ranges from only aerial insectivores at the highest latitudes to the full compliment of trophic strategies (7) at the equator. Thus, latitudinal gradients in species richness result at least in part because
increases in the number of resource types (e.g., seeds, fruit, insects, nectar, fish) allow for
increases in the number of trophic guilds. Furthermore, increases in resource abundance
with latitude may also affect the number of species within trophic guilds. Thus, the
latitudinal gradient in bat species richness likely results from the interaction of a number
of environmental gradients that affect community composition at a number of different
levels.

Few empirical investigations have explored variation in evenness along
environmental gradients (Drochner et al. 1998, Willer and Keddy 1999). Moreover,
theory to explain changes in species evenness is not as well developed as that for species
richness or diversity. Changes in evenness have been predicted to be associated with
changes in stability (Rotenberry 1978) as well as stress and biomass (Drochner et al.
1998). Communities should be less even in situations of low stress and high biomass
because these circumstances allow a few species to dominate community composition
(Grime 1973a, b, Drochner et al. 1998). I find no empirical support for this prediction
given the degree to which decreases in latitude can be associated with decreases in
environmental variability and increases in productivity (Rosenzweig 1995). No
latitudinal gradient existed with respect to the evenness axis derived from factor analysis.
Moreover, the lack of a latitudinal gradient was not just a consequence of the derived
evenness axis being an amalgam of all diversity indices; it was also true of those
evenness indices which were orthogonal to species richness.

Although latitude likely reflects global changes in productivity, it significantly
affects only the richness component of taxonomic diversity. Nonetheless, changes in
taxonomic diversity due primarily to changes in evenness may only be detected over relatively short environmental gradients, or those that only entail changes in the amounts of common resources and not changes in the number of resources. When gradients become sufficiently extensive so as to entail variation in both the amount and kinds of resources, variation in taxonomic diversity may stem primarily from changes in species richness. If changes in species richness reflect changes in available energy, and changes in evenness reflect variation in environmental stability, then the types of environmental changes associated with latitude are more linked to considerations of energy than to stability. Indeed, theoretical predictions addressing how taxonomic diversity might change along environmental gradients need to be tempered to take into account that gradients reflecting qualitative environmental differences may affect patterns of taxonomic diversity differently than do gradients that reflect only quantitative environmental differences.

From a mathematical perspective, indices of species richness and evenness should be independent components of diversity (Smith and Wilson 1996). Although this need not be true from an empirical perspective, spatial variation in the magnitude of species richness and evenness are independent (two orthogonal factors distinguished by factor analysis) for New World bats. Moreover, spatial variation in two evenness indices (CE and O) was uncorrelated with species richness (Re). Nonetheless, the independence of these two components of diversity when measured along a gradient of latitude for New World bats applies only to magnitude. These components are related by virtue of their variances. As the magnitude of species richness increases, variation in species evenness
decreases. Similarly, as the magnitude of species evenness increases, the variation in species richness decreases. Although this pattern has been reported for plant communities (Wetler and Keddy 1999), this is the first report for animal communities and may suggest a general characteristic of how taxonomic diversity varies in nature. Thus, to the degree that latitude reflects a gradient in productivity, concomitant changes in taxonomic diversity and productivity are constrained. The relationship between species richness and evenness may reflect the naturally constrained way in which species are added to species-rich communities. With decreases in latitude, the number of rare species increases at a faster rate than does the number of common species. Moreover, when species richness is high, the addition of rare species affects richness disproportionately more than it affects evenness; the increment in richness is relatively greater than the decrement in evenness. At high species richness, the addition of rare species has a dampened effect on evenness, giving rise to a situation where variation in evenness is low.

Scale-Dependence

Although latitude accounts for a significant amount of the variation in species richness at the community level, this relationship is much weaker than at the regional level. At least two explanations may account for such scale-dependence.

First, mechanisms that give rise to latitudinal gradients may be scale-dependent. The weak latitudinal gradient at the community level may simply reflect effects of latitude on species richness at the regional level. Latitude, or those environmental
gradients with which it is correlated, may only set the upper limit to local species richness. From this upper bound is subtracted species who cannot tolerate particular environmental regimes or competitive interactions germane to the structure of the actual community. Although regional richness sets the upper bound, local conditions determine the realized number of species in the community. If the richness of only a few communities approaches the limit set by regional species pools and there is a latitudinal gradient at the regional scale, a weaker yet significant latitudinal gradient in species richness at the community level may result.

Second, scale-dependence may be a pervasive characteristic of macroecological patterns. For example, distributions of body size are right-skewed at continental scales, log-normal at regional scales, and log-uniform at local scales (Brown and Nicoletto 1991). Moreover, scale-dependence in the strength of macroecological patterns could be the common result of two interacting factors. Sample sizes underlying most macroecological patterns are smaller for communities than for regions. Thus, the reason many ecological patterns are scale-dependent may be because regional scales comprise more data and naturally manifest stronger patterns (Gaston and Blackburn 1999). Alternatively, larger scales likely integrate greater quantities of environmental variability than do smaller scales. If local sites are variable when combined to form regional patterns, this variability will be homogenized and likely will cause local and regional patterns to differ. The greater the variability among sites within a region, the less the regional characteristic will characterize any one of the
sites. The scale dependence of macroecological patterns makes generalization tenuous, and only by improved understanding of how mechanisms and resultant patterns translate across spatial scales will macroecologists be able to attain a broader synthesis.

**Beta Diversity**

Tropical and subtropical communities attain similar degrees of high taxonomic diversity, but they do so in different ways. Tropical communities are characterized by relatively high species richness and relatively low species evenness, whereas subtropical communities are characterized by the opposite pattern. Tradeoffs between increasing richness or increasing evenness that facilitate increases in taxonomic diversity may be related to levels of beta diversity. In situations where beta diversity is high, relatively more species are available to colonize communities and increases in diversity may be facilitated more easily by increases in species richness. When beta diversity is low, however, relatively fewer species are available for colonization and increases in diversity may be facilitated more easily by changes in the evenness of species already in the community. Beta diversity of communities differs between tropical and subtropical zones and these differences may account for how these sites achieve similarly high levels of species diversity while exhibiting consistent differences regarding evenness and richness.
Increases in beta diversity with decreases in latitude may be a consistent attribute of mammalian faunas. Kaufman (1998) found that terrestrial mammals in North America exhibited a similar latitudinal pattern of beta diversity to that quantified here. Although she found no significant difference in beta diversity between the temperate and tropical zones, species turnover increased significantly with decreases in latitude. The latitudinal gradient in beta diversity was stronger for terrestrial mammals than for bats (terrestrial mammals, $r^2 = 0.50$; bats, $r^2 = 0.28$). Beta diversity of terrestrial mammals was a significant function of latitude in the temperate zone and unassociated with latitude in the tropics.

The ecological interpretation of beta diversity is straightforward. Beta diversity results from species-specific responses to variation along environmental gradients (Shmida and Wilson 1985). Thus, beta diversity should increase with the magnitude of environmental heterogeneity within a region. Significant increases in beta diversity with decreases in latitude for both terrestrial and volant mammals suggest that both groups perceive the tropics as more heterogeneous than temperate areas. Variation in beta diversity also is a reflection of species- or group-specific niche breadth. Taxa with relatively high beta diversities should exhibit relatively narrow tolerances for heterogeneity (Harrison et al. 1992). Kaufman’s terrestrial mammals disproportionately comprise small mammals (rodents and marsupials). Compared to bats, these small mammals were influenced more by environmental heterogeneity characterized by changes in latitude, and this may reflect differences in mobility, and hence, differences in the way these two groups deal with environmental heterogeneity.
The volant nature of bats has major implications for their foraging behavior, population dynamics, and ultimately community organization (Willig 1986, Willig and Moulton 1989, Findley 1993, Stevens and Willig 1999 2000). Instead of specializing on particular facets of heterogeneity, the best strategy for bats may be to exploit their high mobility and integrate the environmental heterogeneity encountered over relatively larger spatial scales. Thus, patterns of beta diversity may reflect both the amount of variability along an environmental gradient and the grain at which a group of organisms perceives its environment. To this end, interpretations of differences in beta diversity should consider not only environmental differences among sites but also ecological differences among organisms.

Implications for the Conservation of New World Bats

Bats exhibit their highest levels of alpha, gamma, and beta diversity in the tropics, intermediate levels in the subtropics, and lowest levels in the temperate zones. Coincident with the increase in beta diversity, as one moves toward the equator, gamma diversity of a region becomes less reflective of the actual number of species residing at the local level. Gamma diversity (the number of species whose geographic distributions overlap a point on a range map) has often been used to characterize biogeographic patterns in local diversity and to make decisions regarding conservation priorities (Rebelo and Siegfried 1992, Pomeroy 1993, Lombard et al. 1995, 1997, Williams et al. 1996, Kerr 1997). Ironically, tropical and subtropical areas represent the greatest conservation priorities (Myers 1980, Soule and Kohm 1989, Mares 1992), but the metric typically used
to determine places of greatest importance for conservation efforts (gamma diversity) may provide only limited utility towards identifying areas of elevated local species richness. As data continue to be collected regarding the composition of local communities, dependence on surrogates such as gamma diversity will lessen. Nonetheless, latitudinal changes in beta diversity should admonish the conservation community of the potentially loose linkage between gamma and alpha diversity in tropical and subtropical systems, and emphasize the importance of continued collection of intensive inventories at the community level to accurately chart conservation priorities.
References


Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, Massachusetts, USA.


SPSS, Inc. 1990. The SPSS base system user’s guide. SPSS, Inc., Chicago, USA.


Yancey, F. D. 1996. The mammals of Big Bend Ranch State Park. Dissertation, Texas Tech University, Lubbock, Texas, USA.
Table 2.1. Geographic and environmental characteristics of each of 32 bat communities used to evaluate patterns of taxonomic diversity in the New World.

<table>
<thead>
<tr>
<th>Community</th>
<th>Country</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Habitat</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Iowa</td>
<td>USA</td>
<td>42.5°N</td>
<td>93.0°W</td>
<td>Riggins</td>
<td>Kuntz 1973</td>
</tr>
<tr>
<td>California</td>
<td>USA</td>
<td>36.5°N</td>
<td>117.3°W</td>
<td>Desert</td>
<td>Suprenant 1977</td>
</tr>
<tr>
<td>Nevada</td>
<td>USA</td>
<td>36.2°N</td>
<td>115.2°W</td>
<td>Desert</td>
<td>O’Farrell and Bradley 1970</td>
</tr>
<tr>
<td>New Mexico</td>
<td>USA</td>
<td>33.9°N</td>
<td>107.4°W</td>
<td>Desert</td>
<td>Black 1974</td>
</tr>
<tr>
<td>Big Bend Ranch</td>
<td>USA</td>
<td>29.8°N</td>
<td>101.8°W</td>
<td>Desert</td>
<td>Yancy 1996</td>
</tr>
<tr>
<td>Querétaro</td>
<td>Mexico</td>
<td>21.1°N</td>
<td>99.3°W</td>
<td>Montane Tropical Forest</td>
<td>Navarro L. and Lemos-Paniagua 1995</td>
</tr>
<tr>
<td>Manantial</td>
<td>Mexico</td>
<td>19.3°N</td>
<td>104.0°W</td>
<td>Montane Tropical Forest</td>
<td>Iniguez Davalos 1995</td>
</tr>
<tr>
<td>Ixtapan del Oro</td>
<td>Mexico</td>
<td>19.3°N</td>
<td>100.2°W</td>
<td>Montane Tropical Forest</td>
<td>Alvarez and Alvarez-Castaneda 1996</td>
</tr>
<tr>
<td>Los Tuxtlas</td>
<td>Mexico</td>
<td>18.4°N</td>
<td>95.0°W</td>
<td>Wet Tropical Forest</td>
<td>Estrada et al. 1993</td>
</tr>
<tr>
<td>Chiapas</td>
<td>Mexico</td>
<td>16.1°N</td>
<td>91.0°W</td>
<td>Wet Tropical Forest</td>
<td>Medellin 1993</td>
</tr>
<tr>
<td>Guanacaste-1</td>
<td>Costa Rica</td>
<td>9.5°N</td>
<td>85.2°W</td>
<td>Wet Tropical Forest</td>
<td>LaVal and Fitch 1977</td>
</tr>
<tr>
<td>Guanacaste-2</td>
<td>Costa Rica</td>
<td>9.5°N</td>
<td>85.2°W</td>
<td>Wet Tropical Forest</td>
<td>Fleming et al. 1972</td>
</tr>
<tr>
<td>Panamans</td>
<td>Costa Rica</td>
<td>10.0°N</td>
<td>84.5°W</td>
<td>Montane Tropical Forest</td>
<td>LaVal and Fitch 1977</td>
</tr>
<tr>
<td>Heredia</td>
<td>Costa Rica</td>
<td>10.5°N</td>
<td>83.5°W</td>
<td>Wet Tropical Forest</td>
<td>LaVal and Fitch 1977</td>
</tr>
<tr>
<td>Sherman</td>
<td>Panama</td>
<td>9.3°N</td>
<td>86.0°W</td>
<td>Wet Tropical Forest</td>
<td>Fleming et al. 1972</td>
</tr>
<tr>
<td>Rodman</td>
<td>Panama</td>
<td>9.0°N</td>
<td>79.6°W</td>
<td>Dry Tropical Forest</td>
<td>Fleming et al. 1972</td>
</tr>
<tr>
<td>BCI</td>
<td>Panama</td>
<td>9.2°N</td>
<td>79.8°W</td>
<td>Wet Tropical Forest</td>
<td>Handley et al. 1991</td>
</tr>
<tr>
<td>Paracou</td>
<td>French Guiana</td>
<td>5.3°N</td>
<td>52.9°W</td>
<td>Wet Tropical Forest</td>
<td>Simmons and Voss 1998</td>
</tr>
<tr>
<td>Community</td>
<td>Country</td>
<td>Latitude</td>
<td>Longitude</td>
<td>Habitat</td>
<td>Reference</td>
</tr>
<tr>
<td>-----------------</td>
<td>-------------</td>
<td>----------</td>
<td>-----------</td>
<td>--------------------------</td>
<td>-----------------</td>
</tr>
<tr>
<td>Zabelitas</td>
<td>Colombia</td>
<td>4.0° N</td>
<td>76.5° W</td>
<td>Wet Tropical Forest</td>
<td>Thomas 1972</td>
</tr>
<tr>
<td>Macareva</td>
<td>Colombia</td>
<td>3.3° N</td>
<td>73.9° W</td>
<td>Wet Tropical Forest</td>
<td>Sanchez-Palomino et al. 1993</td>
</tr>
<tr>
<td>Pase</td>
<td>Colombia</td>
<td>3.0° N</td>
<td>76.4° W</td>
<td>Montane Tropical Forest</td>
<td>Thomas 1972</td>
</tr>
<tr>
<td>Hormiguerro</td>
<td>Colombia</td>
<td>3.0° N</td>
<td>76.0° W</td>
<td>Montane Tropical Forest</td>
<td>Thomas 1972</td>
</tr>
<tr>
<td>Manz et</td>
<td>Brazil</td>
<td>3.0° S</td>
<td>60.0° W</td>
<td>Wet Tropical Forest</td>
<td>Dos Reis 1984</td>
</tr>
<tr>
<td>Edaphic Carrado</td>
<td>Brazil</td>
<td>7.2° S</td>
<td>39.4° W</td>
<td>Tropical Woodland-Savannah</td>
<td>Willig 1982</td>
</tr>
<tr>
<td>Caatinga</td>
<td>Brazil</td>
<td>7.9° S</td>
<td>39.9° W</td>
<td>Dry Tropical Forest</td>
<td>Willig 1982</td>
</tr>
<tr>
<td>Linhares</td>
<td>Brazil</td>
<td>19.0° S</td>
<td>40.3° W</td>
<td>Wet Semi-Tropical Forest</td>
<td>Peracchi and Albuquerque 1993</td>
</tr>
<tr>
<td>Panga</td>
<td>Brazil</td>
<td>19.3° S</td>
<td>48.4° W</td>
<td>Wet Semi-Tropical Forest</td>
<td>Pedro and Taddei 1997</td>
</tr>
<tr>
<td>Minas Gerais</td>
<td>Brazil</td>
<td>19.8° S</td>
<td>41.8° W</td>
<td>Wet Semi-Tropical Forest</td>
<td>Moura de Souza Aguiar 1994</td>
</tr>
<tr>
<td>Jureno Herrera</td>
<td>Peru</td>
<td>4.9° S</td>
<td>72.8° W</td>
<td>Wet Tropical Forest</td>
<td>Gorchow and Ascoras in litt.</td>
</tr>
<tr>
<td>Manu</td>
<td>Peru</td>
<td>11.5° S</td>
<td>71.3° W</td>
<td>Wet Tropical Forest</td>
<td>Ascoras et al. 1996</td>
</tr>
<tr>
<td>Mharazayu</td>
<td>Paraguay</td>
<td>24.1° S</td>
<td>55.5° W</td>
<td>Wet Semi-Tropical Forest</td>
<td>Stevens and Willig in litt.</td>
</tr>
<tr>
<td>Rio Verde</td>
<td>Paraguay</td>
<td>33.5° S</td>
<td>56.1° W</td>
<td>Dry Semi-Tropical Forest</td>
<td>Stevens and Willig in litt.</td>
</tr>
</tbody>
</table>
Table 2.2. Fourteen measures of taxonomic diversity used to characterize New World bat communities.

<table>
<thead>
<tr>
<th>Measure</th>
<th>Source</th>
<th>Code</th>
<th>Aspect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species Richness</td>
<td></td>
<td>$R_s$</td>
<td>Richness (Magurran 1988)</td>
</tr>
<tr>
<td>Margalef Index</td>
<td>Clifford and Stephenson 1975</td>
<td>MAR</td>
<td>Richness (Magurran 1988)</td>
</tr>
<tr>
<td>Menhinick Index</td>
<td>Whittaker 1977</td>
<td>MER</td>
<td>Richness (Magurran 1988)</td>
</tr>
<tr>
<td>Shannon Diversity</td>
<td>Pielou 1975</td>
<td>SHD</td>
<td>Diversity (Magurran 1988)</td>
</tr>
<tr>
<td>Shannon Evenness</td>
<td>Pielou 1975</td>
<td>SHE</td>
<td>Evenness (Magurran 1988)</td>
</tr>
<tr>
<td>Simpson Index</td>
<td>Simpson 1949</td>
<td>SI</td>
<td>Dominance (Magurran 1988)</td>
</tr>
<tr>
<td>Berger-Parker Index</td>
<td>Berger and Parker 1970</td>
<td>BP</td>
<td>Dominance (Magurran 1988)</td>
</tr>
<tr>
<td>McIntosh D-Index</td>
<td>McIntosh 1967</td>
<td>MD</td>
<td>Dominance (McIntosh 1967)</td>
</tr>
<tr>
<td>Log Series Alpha</td>
<td>Fisher et al. 1943</td>
<td>A</td>
<td>Diversity (Magurran 1988)</td>
</tr>
<tr>
<td>Brillouin Index</td>
<td>Pielou, 1975, 1969</td>
<td>B</td>
<td>Diversity (Magurran 1988)</td>
</tr>
<tr>
<td>PIE Index</td>
<td>Hurlbert 1971</td>
<td>PIE</td>
<td>Evenness (Hurlbert 1971)</td>
</tr>
<tr>
<td>Camargo Diversity</td>
<td>Camargo 1993</td>
<td>CD</td>
<td>Diversity (Camargo 1993)</td>
</tr>
<tr>
<td>Camargo Evenness</td>
<td>Camargo 1993</td>
<td>CE</td>
<td>Evenness (Smith and Wilson 1996)</td>
</tr>
<tr>
<td>Schoener's Index</td>
<td>Schoener 1970</td>
<td>O</td>
<td>Evenness (Smith and Wilson 1996)</td>
</tr>
<tr>
<td>Site</td>
<td>Latitude</td>
<td>Richness</td>
<td>Diversity</td>
</tr>
<tr>
<td>-----------------</td>
<td>----------</td>
<td>----------</td>
<td>-----------</td>
</tr>
<tr>
<td>Iowa</td>
<td>42.25</td>
<td>8.1</td>
<td>1.11</td>
</tr>
<tr>
<td>California</td>
<td>36.59</td>
<td>10</td>
<td>1.10</td>
</tr>
<tr>
<td>Nevada</td>
<td>36.20</td>
<td>8</td>
<td>1.04</td>
</tr>
<tr>
<td>New Mexico</td>
<td>33.87</td>
<td>16</td>
<td>2.22</td>
</tr>
<tr>
<td>Big Brother Ranch</td>
<td>29.75</td>
<td>14</td>
<td>2.07</td>
</tr>
<tr>
<td>Quentin</td>
<td>21.12</td>
<td>28</td>
<td>4.48</td>
</tr>
<tr>
<td>Massanutten</td>
<td>19.35</td>
<td>28</td>
<td>4.20</td>
</tr>
<tr>
<td>Espadon del Oro</td>
<td>19.25</td>
<td>25</td>
<td>3.85</td>
</tr>
<tr>
<td>Los Tuxles</td>
<td>18.42</td>
<td>35</td>
<td>4.33</td>
</tr>
<tr>
<td>Choctaw</td>
<td>16.10</td>
<td>30</td>
<td>7.12</td>
</tr>
<tr>
<td>Guanacaste-1</td>
<td>9.47</td>
<td>36</td>
<td>3.33</td>
</tr>
<tr>
<td>Guanacaste-2</td>
<td>9.47</td>
<td>27</td>
<td>3.73</td>
</tr>
<tr>
<td>Pantanal</td>
<td>10.00</td>
<td>24</td>
<td>3.38</td>
</tr>
<tr>
<td>Hesperia</td>
<td>10.50</td>
<td>57</td>
<td>7.44</td>
</tr>
<tr>
<td>Sherman</td>
<td>9.33</td>
<td>31</td>
<td>4.20</td>
</tr>
<tr>
<td>Redwood</td>
<td>8.95</td>
<td>28</td>
<td>3.88</td>
</tr>
<tr>
<td>Site</td>
<td>Latitude</td>
<td>Richness</td>
<td>Diversity</td>
</tr>
<tr>
<td>-----------------</td>
<td>----------</td>
<td>----------</td>
<td>-----------</td>
</tr>
<tr>
<td>BCI</td>
<td>9.17</td>
<td>39</td>
<td>4.17</td>
</tr>
<tr>
<td>Pantano</td>
<td>5.27</td>
<td>78</td>
<td>9.58</td>
</tr>
<tr>
<td>Zeballos</td>
<td>4.00</td>
<td>35</td>
<td>4.52</td>
</tr>
<tr>
<td>Macuareo</td>
<td>3.25</td>
<td>39</td>
<td>6.57</td>
</tr>
<tr>
<td>Pesoa</td>
<td>3.00</td>
<td>17</td>
<td>2.42</td>
</tr>
<tr>
<td>Hormiguero</td>
<td>3.00</td>
<td>14</td>
<td>1.87</td>
</tr>
<tr>
<td>Mares</td>
<td>3.00</td>
<td>52</td>
<td>7.22</td>
</tr>
<tr>
<td>Edaphic Corredo</td>
<td>7.23</td>
<td>25</td>
<td>3.18</td>
</tr>
<tr>
<td>Caatinga</td>
<td>7.58</td>
<td>34</td>
<td>4.50</td>
</tr>
<tr>
<td>Limares</td>
<td>19.01</td>
<td>37</td>
<td>5.73</td>
</tr>
<tr>
<td>Ponga</td>
<td>19.25</td>
<td>17</td>
<td>2.94</td>
</tr>
<tr>
<td>Minas Gerais</td>
<td>19.83</td>
<td>20</td>
<td>3.26</td>
</tr>
<tr>
<td>Jangar Herrera</td>
<td>4.92</td>
<td>59</td>
<td>7.52</td>
</tr>
<tr>
<td>Muli</td>
<td>11.93</td>
<td>50</td>
<td>7.63</td>
</tr>
<tr>
<td>Minas Encayay</td>
<td>24.12</td>
<td>15</td>
<td>1.66</td>
</tr>
<tr>
<td>Río Verde</td>
<td>22.49</td>
<td>29</td>
<td>3.54</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>30.78</td>
<td>4.21</td>
</tr>
<tr>
<td>Variance</td>
<td></td>
<td>267.72</td>
<td>4.63</td>
</tr>
<tr>
<td>CV</td>
<td></td>
<td>53.16</td>
<td>51.06</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>r_s</th>
<th>MAR</th>
<th>MER</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.10</td>
<td>-1.33</td>
<td></td>
</tr>
</tbody>
</table>
Table 2.4. Comparisons of aspects of taxonomic diversity among tropical, subtropical, and temperate communities based on principal components as well as factors. Means for latitudinal regions that share an alphabetic superscript are statistically indistinguishable (Student-Newman-Keuls tests, comparison-wise error rate held constant at five percent).

<table>
<thead>
<tr>
<th>Independent Variable</th>
<th>ANOVA</th>
<th>Means</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Tropical</td>
<td>Subtropical</td>
</tr>
<tr>
<td></td>
<td>F</td>
<td>P</td>
<td></td>
</tr>
<tr>
<td>Principal Components</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PC1</td>
<td>10.54</td>
<td>&lt; 0.001</td>
<td>0.24&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>PC2</td>
<td>2.93</td>
<td>0.069</td>
<td>-0.37&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Factors</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Factor 1</td>
<td>8.72</td>
<td>0.001</td>
<td>0.43&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Factor 2</td>
<td>3.94</td>
<td>0.031</td>
<td>-0.12&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
Table 2.5. Results of simple linear regression analyses between latitude and each of the measures of taxonomic diversity (Table 2.1). An asterisk indicates significant regressions between latitude and a particular measure of diversity. Experiment-wise error rate was held constant at five percent by application of a Bonferroni sequential adjustment (Rice 1989) within each of three separate analyses (principal components, derived factors, and the entire suite of diversity measures).

<table>
<thead>
<tr>
<th>Measure</th>
<th>Intercept</th>
<th>Slope</th>
<th>$r^2$</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>PC1</td>
<td>0.649</td>
<td>-0.042</td>
<td>0.209</td>
<td>0.009*</td>
</tr>
<tr>
<td>PC2</td>
<td>-0.571</td>
<td>0.037</td>
<td>0.162</td>
<td>0.022*</td>
</tr>
<tr>
<td>Factor 1</td>
<td>0.864</td>
<td>-0.055</td>
<td>0.371</td>
<td>&lt; 0.001*</td>
</tr>
<tr>
<td>Factor 2</td>
<td>-0.001</td>
<td>-0.001</td>
<td>0.000</td>
<td>0.999</td>
</tr>
<tr>
<td>Rc</td>
<td>44.438</td>
<td>-0.877</td>
<td>0.346</td>
<td>&lt; 0.001*</td>
</tr>
<tr>
<td>MAR</td>
<td>5.982</td>
<td>-0.114</td>
<td>0.337</td>
<td>&lt; 0.001*</td>
</tr>
<tr>
<td>A</td>
<td>8.740</td>
<td>-0.174</td>
<td>0.292</td>
<td>0.001*</td>
</tr>
<tr>
<td>B</td>
<td>2.498</td>
<td>-0.030</td>
<td>0.282</td>
<td>0.002*</td>
</tr>
<tr>
<td>SHD</td>
<td>2.564</td>
<td>-0.030</td>
<td>0.271</td>
<td>0.002*</td>
</tr>
<tr>
<td>CD</td>
<td>10.874</td>
<td>-0.189</td>
<td>0.217</td>
<td>0.007</td>
</tr>
<tr>
<td>PIE</td>
<td>0.868</td>
<td>-0.007</td>
<td>0.199</td>
<td>0.010</td>
</tr>
<tr>
<td>MER</td>
<td>1.206</td>
<td>-0.018</td>
<td>0.181</td>
<td>0.015</td>
</tr>
<tr>
<td>MD</td>
<td>0.645</td>
<td>-0.006</td>
<td>0.170</td>
<td>0.019</td>
</tr>
<tr>
<td>SI</td>
<td>7.548</td>
<td>-0.098</td>
<td>0.098</td>
<td>0.082</td>
</tr>
<tr>
<td>Measure</td>
<td>Intercept</td>
<td>Slope</td>
<td>$r^2$</td>
<td>Significance</td>
</tr>
<tr>
<td>---------</td>
<td>-----------</td>
<td>-------</td>
<td>-------</td>
<td>--------------</td>
</tr>
<tr>
<td>BP</td>
<td>4.191</td>
<td>-0.048</td>
<td>0.081</td>
<td>0.115</td>
</tr>
<tr>
<td>SHE</td>
<td>0.677</td>
<td>-0.003</td>
<td>0.060</td>
<td>0.177</td>
</tr>
<tr>
<td>CE</td>
<td>0.244</td>
<td>0.001</td>
<td>0.027</td>
<td>0.373</td>
</tr>
<tr>
<td>O</td>
<td>0.376</td>
<td>0.001</td>
<td>0.012</td>
<td>0.545</td>
</tr>
<tr>
<td>Re</td>
<td>123.729</td>
<td>-2.885</td>
<td>0.876</td>
<td>&lt; 0.001</td>
</tr>
</tbody>
</table>
Figure 2.1. Location of 32 New World bat communities (solid dots) used to evaluate geographic patterns of diversity. The letters a, b, and c denote temperate, subtropical and tropical latitudinal zones, respectively.
Figure 2.2. The projection of each of 32 communities in two-dimensional diversity space (left column) defined by principal components (a) and rotated factors (c). Principal components correspond to the two main axes of variation in taxonomic diversity among the 32 sites, whereas Factor 1 corresponds to species richness and Factor 2 corresponds to species evenness. Temperate, subtropical, and tropical communities are indicated by white, gray, and black circles, respectively. Relationship of each measure of diversity with principal components (b) and factors (d) are depicted in right columns. The length and direction of each arrow indicates the magnitude and sign of correlation of each index with the corresponding derived axis, respectively. The black, light gray, dark gray, and hatched arrows correspond to indices of diversity, richness, evenness, and dominance, respectively. Acronyms for each measure of taxonomic diversity appear in Table 2.2.
Figure 2.3. Relationships of principal components and rotated factors with latitude for New World bats. Latitude accounted for a significant amount of the variation in both principal components (a and b) as well as the first rotated factor (c). In contrast, the regression of the rotated factor of evenness (Factor 2) on latitude was not significant (d).
Figure 2.4. Relationships between the number of rare (a) and common (b) species and latitude. Rare species were those with an abundance less than 1/Re of the total number of individuals from a community. Latitude accounted for a significant amount of the variation in both abundance classes. White, gray, and black dots correspond to temperate, subtropical, and tropical communities, respectively.
Figure 2.5. The ability of diversity indices to detect a latitudinal gradient, as measured by the correlation coefficient, is not greatly affected by changes in sampling intensity. An index is insensitive when its correlation with latitude remains stable, regardless of sample size. Two representative indices for each class of measure (a, richness; b, diversity; c, evenness; d, dominance) illustrate the general trend. Because the number of communities is constant in all analyses, the correlation coefficient is significant at the 0.05 level if the absolute value of its magnitude exceeds 0.349 (area of gray shading). Vertical bars represent means plus or minus 2 standard deviations.
Figure 2.6. Significant relationships between local species richness (solid line) and regional species richness (dashed line) with latitude for New World bats (a). Significant relationship between local and regional richness of bats in the New World (b). Significant relationship between species turnover and latitude for New World bats (c). White, gray, and black dots correspond to temperate, subtropical, and tropical communities, respectively.
CHAPTER III
LATITUDINAL GRADIENTS IN THE FUNCTIONAL
DIVERSITY OF NEW WORLD BAT COMMUNITIES

Abstract

Although the examination of gradients in taxonomic components of biodiversity is common, much less attention has been given to latitudinal gradients regarding ecological function. Herein, I evaluate latitudinal gradients in the functional diversity of New World bats. Bat species from each of 32 communities distributed throughout the New World were assigned to one of seven functional groups (e.g., aerial insectivores, frugivores, gleaning animalivores, high-flying insectivores, nectarivores, piscivores, sanguinivores). Measures of richness, evenness, diversity, and dominance of functional groups were determined for each community. On average, communities from tropical and subtropical regions exhibited significantly higher richness and diversity, and significantly lower dominance of functional groups compared to communities from temperate regions. Moreover, latitudinal gradients existed for the richness, diversity, and dominance of functional groups. Simulation analyses indicated that these latitudinal gradients in functional diversity were not solely the product of gradients in species richness. However, when variation in species composition of the regional fauna surrounding each community was incorporated into simulation analyses, many significant differences in patterns of functional diversity between observed and simulated gradients disappeared. Community-wide responses to variation in the quantity and quality of
resources at local sites likely contribute to differences in functional diversity at local and regional levels. Differences among functional groups regarding beta diversity likely contribute to these differences as well. Current conservation efforts should broaden their focus to embrace more than only the taxonomic component of biodiversity. Efforts to maximize the conservation of the number of species may not necessarily conserve important ecosystem functions that are performed by a particular community of bats. Future conservation efforts should integrate taxonomic and functional components of biodiversity in an effort to conserve more comprehensively biodiversity in all of its facets.

**Introduction**

The latitudinal gradient of taxonomic diversity is one of the most well-described patterns in biogeography (see reviews by Gaston 1994, Brown 1995, Rosenzweig 1995, Willig 2001). Recent efforts to understand latitudinal effects on taxonomic diversity have established the ubiquity of gradients at various levels in the systematic hierarchy (Gaston et al. 1995, Kaufman 1995, Roy et al. 1996, Quián 1998), as well as at temporal (Rosenzweig 1995), spatial (Lyons and Willig 1999, 2001, Rahbek and Graves 2000) and ecological scales (Roy et al. 2000, Stevens and Willig 2002). For example, latitude accounts for much of the spatial variation in the number of functional groups of New World bats (Stevens and Willig 2001, Willig 2001), and is a good predictor of species richness at a number of spatial scales ranging from local communities (Stevens and Willig 2002) to those encompassed by 25,000 km² quadrats (Lyons and Willig 1999,
Although this research has improved our understanding of spatial variation in taxonomic diversity, it provides only limited resolution to our understanding of patterns of biodiversity in the broad sense. Taxonomic diversity may not reflect salient features of other components of biodiversity such as functional, genetic, phylogenetic, or phenetic components. Moreover, it is poorly understood whether different components of biodiversity respond similarly to environmental gradients in general or to latitude in particular.

Functional diversity represents the variety of ways that species are involved in ecological activities (Martinez 1996, Tilman 2001). Typically, investigations of functional diversity have focused on plant or soil-microbial communities (Zak et al. 1994, Troumbis and Memtsas 2000, Derry et al. 2001, Dukes 2001). For plants, functional diversity refers to the variety of ways that groups defined by photosynthetic pathway or growth form convert solar energy to biomass (i.e., production). For soil microbes, functional diversity has referred to the variety of ways that groups decompose organic matter into its constituent nutrients, and can be measured by the variety of carbon substrates a particular microbial assemblage is capable of catabolizing for metabolic maintenance and biomass production (Willig et al. 1996).

From a functional perspective, bats play several important roles in terrestrial ecosystems. As consumers, bats are involved intimately in the transfer of energy and cycling of nutrients within ecosystems via production, immobilization, and mineralization. Moreover, because of their high mobility, bats frequently redistribute large amounts of nutrients and energy. Such transport sometimes crosses habitat
boundaries (Fleming 1988, Cox et al. 1991, Fujita and Tuttle 1991, Ascorra and Wilson 1992, Rainey et al. 1992, Gorchov et al. 1993, Willig and Gannon 1996). For example, fishing bats (*Myotis vivesi* and *Noctilio leporinus*) feed largely on fish and redistribute most of the energy and nutrients obtained from aquatic habitats to terrestrial ones (Brooke 1994). Less dramatically, individuals of *Carollia perspicillata* in Costa Rica frequently disseminate seeds at distances of 2 km from parent plants (Fleming 1988). Because of their numerical dominance in some mammalian faunas, bats are keystone species in many ecosystems (Fleming 1988, Willig and Gannon 1996). Their high abundance and large metabolic demand (many bats eat from between 50 and 120% of their own body weight nightly [Fenton 1992]) likely translates to major effects on pathways of energy flow and nutrient cycling in foodwebs, spatial heterogeneity of nutrients in ecosystems, promotion of secondary succession and revegetation in disturbed areas, and the spatial distribution and genetic structure of plant populations within communities (Fleming 1988, Cox et al. 1991, Fujita and Tuttle 1991, Ascorra and Wilson 1992, Rainey et al. 1992, Gorchov et al. 1993, Willig and Gannon 1996). The unique ways that bats are involved in ecosystem processes related to the conversion of energy and nutrients to biomass (i.e. secondary production, immobilization, and mineralization) is associated with the spatial and temporal dynamics of their foraging as well as with the taxonomic identity of their prey. Such considerations can be used to define functional groups. Functional groups parallel classifications involving ecological guilds (Hawkins and McMahon 1989, Simberloff and Dayan 1991), foraging strategies (Lawton and Strong 1981, Moore et al. 1988), or behavioral syndromes (Cummins 1973) yet highlight
the roles of species from an ecosystem perspective. Furthermore, the number of functional groups as well as the distribution of species among those groups can be used to form measures of functional diversity. Herein, I characterize the functional diversity of New World bat communities, quantify latitudinal gradients, and explore the relationship of functional diversity to taxonomic diversity.

Materials and Methods

Available Data and Definition of Functional Groups

Data on the species composition of 32 New World bat communities (Figure 3.1, Table 3.1) come from the literature (see Stevens and Willig 2002, Chapters II, and III). Based on latitude, communities were classified into one of three geographic zones: tropical (12.00° N to 12.00° S), subtropical (13.00° N to 23.45° N and 13.00° S to 23.45° S), or temperate (>23.45° N or 23.45° S).

Feeding guilds represent discrete trophic strategies that reflect related ecosystem functions. For example, frugivory, nectarivory, and insectivory all involve secondary production, immobilization, and nutrient cycling within ecosystems, but do so from three distinct resource bases. I categorized species of bats to one of seven functional groups (e.g., aerial insectivores, frugivores, gleaning animalivores, high-flying insectivores, nectarivores, piscivores, sanguinivores) based on the distinct resource bases that bats use while involved in production, mineralization, and immobilization (sensu Stevens and Willig 1999, 2001).
Quantification of Functional Diversity

Aspects of the number of functional groups and the proportional distribution of species within functional groups can be used to estimate the functional diversity of a particular community. In this chapter, I use the term “functional diversity” as the all-inclusive term describing the ways that communities can differ regarding the richness and evenness of functional groups, whereas I use other terms to refer to the particular way that I measured functional diversity. For example, the richness of functional groups represents the number of functional groups in a local community. The diversity of functional groups reflects the number of groups and equability of species richness among groups and was determined by calculating the Shannon index (Pielou 1975) on data of the number of species in each functional group. The evenness of functional groups reflects equability in the distribution of species among functional groups and was calculated using the Camargo evenness index (Camargo 1993). The dominance of functional groups describes the degree to which the number of species in the most species-rich functional group dominates the community in terms of species richness, and was determined by calculating the Berger-Parker index (Berger and Parker 1970). Following Magurran (1988), dominance was scaled so that a large index represents low dominance and high diversity. These measures were selected because they represent salient features of richness, diversity, evenness, and dominance, respectively (see Chapter II, also Magurran 1988, Hubalek 2000).
Quantitative Analyses

Multivariate analysis of variance (MANOVA) was used to evaluate categorical differences among temperate, subtropical, and tropical sites based on the richness, evenness, diversity, and dominance of functional groups. Univariate analysis of variance (ANOVA) was used to infer which of the four measures of functional diversity were different among zones. Experiment-wise error rate was held at 5 percent by application of a Bonferroni sequential adjustment (Rice 1989). Finally, *a posteriori* Student-Newman-Keuls tests were used to determine the significance of all possible pair-wise differences. All analyses of differences of latitudinal zones regarding their functional diversity were performed using SPSS (SPSS Inc 1990).

I used orthogonal polynomial regression (Dutka and Ewens 1971) to determine the relationship of each measure of functional diversity with species richness and latitude. In these analyses, I used a first order term to explore linear rates of change in functional diversity with latitude as well as a quadratic term to explore nonlinearity (i.e., both modal and asymptotic associations) in relationships. The advantage of orthogonal polynomial regression analysis is that linear, quadratic, and higher order regression coefficients are independent of each other thereby allowing the decomposition of relationships into their linear and nonlinear components (Sokal and Rohlf 1995).

Because values of the independent variable (latitude) were not uniformly spaced, the calculation of regression coefficients is quantitatively lengthy. I used a function written in Matlab (Math Works 1995) to conduct the procedure described in Dutka and Ewens (1971) for determining orthogonal polynomial regressions when values of the
independent variable are not evenly spaced. Again, experiment-wise error rate was held at 5 percent by application of a Bonferroni sequential adjustment (Rice 1989).

**Simulation Analyses**

Latitudinal gradients of functional diversity could result from latitudinal gradients in species richness. More specifically, an increase in species richness predisposes an increase in functional diversity because it enhances the probability of obtaining a species that is a member of another functional group by chance alone. To determine if observed gradients in functional diversity could be generated by latitudinal increases in species richness, I conducted two suites of simulation analyses. In the first, species were drawn randomly from a pool comprising all continental New World bat species. I followed Koopman (1993) for a comprehensive list of New World bats. More specifically, for each real community, a simulated community was assembled by randomly selecting without replacement the same number of species as occurred in the actual community from the New World pool. Measures of functional diversity were calculated based on the number of species in each functional group and then each measure was regressed separately on latitude using orthogonal polynomial regression. This process was then iterated 1000 times to create a distribution of gradients in functional diversity that could be produced by a latitudinal gradient in species richness. Parameter estimates ($b_0$, $b_1$, $b_2$, and coefficients of determination) characterizing the empirical latitudinal gradient in functional diversity from actual communities were then compared to the distributions of such values from the simulated gradients to determine P-values. The position of the
parameter estimate for real communities relative to the distribution of simulated values describes the probability that the observed value is a random variate from the simulated distribution, and that the observed latitudinal gradient in functional diversity is a product of the latitudinal gradient in species richness. Parameter estimates for the actual relationship were deemed to be significant when they were not encompassed by the middle 1-α percent of the distribution of simulated values. The level of alpha was determined by a Bonferroni sequential adjustment in which experiment-wise error rate was equal to 5 percent (Rice 1989).

The second suite of analyses examined the extent to which variation in the composition of regional species pools (i.e., the richness and taxonomic identity of species) associated with the geographical location of a community affected latitudinal gradients in functional diversity. Simulations such as these not only control for evolutionary history and biogeographic processes (e.g., extinction and dispersal) that operate at larger regional scales but also provide the more realistic constraint that only those species with the dispersal potential to be part of a particular community were included in analyses. More specifically, species were drawn randomly from a pool comprising the regional bat fauna from which each community was potentially assembled. The regional fauna for a site was considered to be those species whose geographic distributions included the particular community. To define regional species pools, distribution maps for each species were modified from Willig and Selcer (1989) and Willig and Sandlin (1991) based on information in Hall (1981) and Koopman (1982),

Results

Empirical Patterns

Measures of functional diversity were quite variable among sites (Table 3.2). The Iowa community contained a single functional group (aerial insectivores), whereas 8 communities contained the full compliment of 7 functional groups (Chiapas, Sherman, Rodman, Paracou, Manaus, Edaphic Cerrado, Caatinga, and Manu). For communities with more than one functional group, the Puntarenas community had the highest evenness of functional groups whereas the Sherman and Manu communities had the lowest evenness of functional groups. The Iowa and Caatinga community had the lowest and highest dominance of functional groups, respectively. The Iowa and Caatinga communities had the lowest and highest diversity of functional groups, respectively. Based on measures of relative variability (CV), the dominance of functional groups was the most variable (31.54), whereas the evenness of functional groups was the least variable (16.67).

The richness, diversity, and dominance of functional groups varied with changes in species richness (Table 3.3, Figure 3.3). This was not true for the evenness of functional groups. Statistically significant coefficients of determination ranged from 0.40 between species richness and the dominance of functional groups to 0.48 between species
richness and the richness of functional groups. Communities with high species richness have higher functional diversity because functional groups are more numerous, more diverse, and less dominated by a single group than communities with low species richness.

Significant differences regarding functional diversity exist among temperate, subtropical, and tropical sites (MANOVA; \( F_{6,32} = 4.24, P = 0.001 \)). The richness, diversity, and dominance of functional groups, but not the evenness of functional groups, contributed to these significant differences among latitudinal zones (Table 3.4). In general, communities from the temperate zone exhibited lower levels of functional diversity and differed from tropical and subtropical zones as a group (Table 3.4).

Significant latitudinal gradients exist with respect to all aspects of functional except the evenness of functional groups (Table 3.4, Figure 3.2). Significant coefficients of determination ranged from 0.78 between latitude and the diversity of functional groups to 0.45 between latitude and the dominance of functional groups. In all significant cases, increases in functional diversity were associated with decreases in latitude with significant linear and quadratic components.

**Simulation Analyses**

Latitudinal increases in a number of measures of functional diversity could not be explained by latitudinal increases in species richness based on simulation analyses in which the species pool comprised all continental New World bats (Table 3.5). Significant differences between simulated and empirical latitudinal gradients existed for
all measures of functional diversity. More specifically, the richness and dominance of functional groups in real communities were larger and changed at faster rates with latitude than in simulated communities. In contrast, the diversity of functional groups was smaller, but increased toward the equator at a faster rate than in simulated communities. Latitude significantly accounted for more of the variation in empirical communities than in simulated communities regarding the richness, diversity and dominance of functional groups. Finally, evenness of functional groups was on average lower than in simulated communities, but the way in which it changed with latitude was indistinguishable in simulated and empirical communities.

The regionally constrained model illustrates how the nonrandom assembly of species from regional faunas into communities contributes to latitudinal gradients in functional diversity. Significant differences between empirical and simulated latitudinal gradients exist regarding diversity, evenness, and dominance but not the richness of functional groups (Table 3.5). On average, diversity and evenness of functional groups was less and richness and dominance of functional groups in actual communities was greater than in simulated communities. Nonetheless for each of these three components of functional diversity, the way in which latitude affected changes in magnitude were indistinguishable between empirical and simulated communities. The species composition of regional faunas contributes to the functional diversity of communities, but cannot account for all of the latitudinal variation in functional diversity at the community level.
Discussion

Empirical Patterns

A significant challenge to ecology in particular and to biology in general involves the integration of data at a level that allows the most effective description of patterns in nature (Korner 1993). Although ecologists have long emphasized species as the unit of analyses, considerations unrelated to taxonomy, per se, have provided many insights into patterns of diversity (Winemiller 1995). Examples include functional groups (Tilman 2001) guilds (Simberloff and Dayan 1991), and trophospecies (Yodzis 1993). An objective of functional groupings is to define the major flows of matter, nutrients, and energy effected by a particular taxon, and ultimately within the entire ecosystem (Korner 1993). Classifying species of bats to functional groups and evaluating latitudinal gradients in functional diversity provide unique insights into patterns of biodiversity. Although latitudinal gradients in the taxonomic and functional diversity of bats share a similar direction in the New World (i.e., they both increase with decreases in latitude), functional diversity represents a different facet of biodiversity than that described by taxonomic diversity. For example, functional groups in actual communities are less diverse, less even, and more dominated by a particular functional group than would be expected given the observed variation among communities regarding species richness. Moreover, taxonomic and functional components of biodiversity respond to latitude in quantitatively different ways. Rates of change in the richness, diversity, and dominance
of functional groups were significantly different than expectations based on latitudinal
to variation in the richness of faunal pools.

Although changes in species richness likely contribute to variation in functional
diversity, differences between simulated and empirical latitudinal gradients in functional
diversity may be a consequence of the tropical radiation of the New World family
Phyllostomidae. Although phyllostomid taxa are limited primarily to tropical and
subtropical portions of the New World, they exhibit strong latitudinal gradients in species
richness, with their greatest species richness at low latitudes (Willig and Selcer 1989).
Moreover, phyllostomid taxa often dominate local communities in the tropics and
subtropics (Voss and Emmons 1996). Of the nine families of bats found in the New
World, the Phyllostomidae is by far the most functionally diverse (Nowak 1999),
comprising four (e.g., frugivores, gleaning animalivores, nectarivores, sanguinivores) of
the seven functional groups found in New World bats. Thus, latitudinal changes in the
taxonomic diversity of the Phyllostomidae greatly influence latitudinal changes in
functional diversity. Although changes in the taxonomic diversity of other families of
bats in the New World may be important, they involve fewer species and contribute to
changes in functional diversity with relatively fewer functional groups (i.e., usually one
functional group per family).

When observed gradients were compared to those simulated by assembling
communities from corresponding regional faunas, differences between simulated and
empirical gradients regarding attributes of functional diversity disappeared. For example,
the rate of change in the richness, diversity, evenness, and dominance of functional
groups with latitude was similar to the rate of change in simulated communities. Nonetheless, on average, the diversity and evenness of functional groups was less and the dominance of functional groups was greater in the empirical communities than in simulated ones. The higher dominance and lower evenness of functional groups at the local level may simply reflect the response of bat species to spatial variation in the types and quantities of resources among sites. For example, spatial variation among communities in the availability of resources could cause regions to comprise more resource types than any one local area and would create a situation in which any one community within the region is less diverse and more dominated than the region overall regarding the resources they offer to bats. This in turn may cause the functional diversity of bats to be more dominated at the local level relative to the region. Moreover, any random draw of species from the faunal pool would not recapitulate this high dominance. An example of this likely occurs in many temperate communities of the southwest United States. In these communities, the most dominant functional group is aerial insectivores and this is likely because resource bases exploitable by bats in these areas are primarily insects. Nonetheless, rare members of these temperate faunas are members of functional groups that have strong tropical affinities, namely gleaning insectivores, sanguivores, and nectarivores (Hall 1981, Schmidly 1990, Findley 1993). Since these tropical species are in the faunal pool, they sometimes are selected to form a simulated community. If this happens enough, the functional diversity of communities that do not possess these tropical species will exhibit greater dominance of functional groups than you would expect based on simulation.
This is an extreme case that likely only transpires in the temperate zone where many functional groups reach their biogeographic termini. Nonetheless, it could be argued that increased dominance and decreased diversity of functional groups would be expected whenever there is spatial variation among communities within a region regarding the quality and quantity of resource bases. For example, a community with a higher species richness relative to the region in fruit-producing plant species should be expected to be relatively more dominated by frugivores than the regional fauna. Likewise, if communities exhibit variation in the richness of plant species that are pollinated by bats, there should be concomitant variation in the degree to which nectarivores dominate bat functional diversity. To this end, beta diversity of species representing the resource bases for a higher trophic level can in turn cause similar beta diversity at higher trophic levels. This potentially could give rise to functional beta diversity in which the relative importance or even the appearance and disappearance of functional groups varies across a landscape.

The biogeographic history of a taxon, regional dispersal processes, and local interactions can play important roles in determining the number and types of species that coexist at the local scale (Huston 1999, Loreau 2000, Smith 2001). In fact, determining the identity as well as the primacy of local versus regional processes in structuring local communities is currently a contentious debate in ecology (Ricklefs and Schluter 1993, Rosenzweig 1995, Caley and Schluter 1997, Huston 1999). Consistent with the current paradigm (Ricklefs and Schluter 1993), both regional and local phenomena likely determine the functional diversity of New World bat communities. Of the simulation
analyses in which observed latitudinal gradients were compared to those simulated by random assembly of communities from regional pools, only three of sixteen tests were significant. Regional processes that determine the number of functional groups and the number of species per functional group can account for much of the latitudinal variation in the functional diversity of local bat communities. Nonetheless, instances of significant differences between observed and simulated gradients indicate variation in functional diversity that cannot be explained by regional phenomena alone. For example, differences in the magnitude of diversity, evenness, and dominance of functional groups between empirical and simulated communities may be better understood by investigating local phenomena such as the distribution of resources among communities than regional phenomena such as the biogeography of higher taxa or the dispersal capabilities of species. Indeed, a better understanding of the joint effects of regional and local processes on the species composition of local communities as well as identifying which components of biodiversity they affect and under what circumstances will greatly enhance our understanding of the formation of patterns of biodiversity.

*Functional Considerations in the Conservation of New World Bats*

Contemporary conservation efforts often attempt to conserve taxonomic diversity, especially the number of species regardless of their functional roles in ecosystems. Little effort is placed on directly attempting to conserve ecological function. Nonetheless, in light of the important ecosystem functions performed by many species, from some perspectives it could be argued that the need to conserve functional diversity is more
urgent than the conservation of taxonomic diversity. This may be especially true for bats. For example, many phyllostomid bats play crucial roles in the promotion of revegetation in disturbed areas, and the conservation of functional groups involved in these services may maintain a natural buffer against disturbance as well as expedite future restoration and reclamation efforts. Although patterns of functional diversity are related to those of taxonomic diversity, there is no direct correspondence. Thus, conservation efforts that attempt to maximize species richness in a large region or in local sites may not maximize the ecological functions performed by a particular taxon at local sites or in the region. Moreover, if functional groups are differentially susceptible to the effects of habitat modification, then aiming conservation efforts at maximizing species richness may disproportionately conserve only a minority of the functional groups, thereby having potentially harmful effects on ecosystem functioning and ultimately sustainability. Indeed, future conservation and management efforts, particularly those that attempt to maximize species richness, should take the functional aspects of species into consideration. For example, current reserve citing protocols (Freitag and Van Jaarsveld 1998, Polasky et al. 2001, Andelman and Willig in press) that attempt to maximize the number of species conserved given constraints on the number of sites or the overall budget of a reserve program should be modified so as to simultaneously maximize the number of species as well as the functional diversity inherent to those species. Indeed, the conservation of many components of biodiversity requires a multifaceted approach.
Only the incorporation of the complexity of biodiversity into current conservation practices can enhance the likelihood of conserving ecological integrity of local systems and the taxonomic diversity of the region.
References


Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, Massachusetts, USA.


Schmidtly, D. J. 1990. The bats of Texas. Texas A&M Press, College Station, Texas, USA.


SPSS, Inc. 1990. The SPSS base system user’s guide. SPSS, Inc., Chicago, Illinois, USA.


Yancey, F. D. 1996. The mammals of Big Bend Ranch State Park. Dissertation, Texas Tech University, Lubbock, Texas, USA.


Table 3.1. Geographic and environmental characteristics of each of 32 bat communities used to evaluate patterns of functional diversity in the New World.

<table>
<thead>
<tr>
<th>Community</th>
<th>Country</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Habitat</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Iowa</td>
<td>USA</td>
<td>42.3°N</td>
<td>93.0°W</td>
<td>Riparian</td>
<td>Kane 1973</td>
</tr>
<tr>
<td>California</td>
<td>USA</td>
<td>36.5°N</td>
<td>117.3°W</td>
<td>Desert</td>
<td>Suprenant 1977</td>
</tr>
<tr>
<td>Nevada</td>
<td>USA</td>
<td>36.2°N</td>
<td>115.2°W</td>
<td>Desert</td>
<td>O'Farrell and Bradley 1970</td>
</tr>
<tr>
<td>New Mexico</td>
<td>USA</td>
<td>33.9°N</td>
<td>107.4°W</td>
<td>Desert</td>
<td>Black 1974</td>
</tr>
<tr>
<td>Big Bend Ranch</td>
<td>USA</td>
<td>29.8°N</td>
<td>103.8°W</td>
<td>Desert</td>
<td>Yanecy 1996</td>
</tr>
<tr>
<td>Querétaro</td>
<td>Mexico</td>
<td>21.1°N</td>
<td>99.3°W</td>
<td>Montane Tropical Forest</td>
<td>Navarro L. and Leon-Paniagua 1995</td>
</tr>
<tr>
<td>Mazatlan</td>
<td>Mexico</td>
<td>19.3°N</td>
<td>104.0°W</td>
<td>Montane Tropical Forest</td>
<td>Ingles Davales 1993</td>
</tr>
<tr>
<td>Iztapán del Oro</td>
<td>Mexico</td>
<td>19.3°N</td>
<td>100.2°W</td>
<td>Montane Tropical Forest</td>
<td>Alvarez and Alvarez-Castanedo 1996</td>
</tr>
<tr>
<td>Los Tuxtlas</td>
<td>Mexico</td>
<td>18.4°N</td>
<td>95.0°W</td>
<td>Wet Tropical Forest</td>
<td>Estrada et al. 1993</td>
</tr>
<tr>
<td>Chiapas</td>
<td>Mexico</td>
<td>16.1°N*</td>
<td>91.0°W</td>
<td>Wet Tropical Forest</td>
<td>Medellin 1993</td>
</tr>
<tr>
<td>Guanacaste-1</td>
<td>Costa Rica</td>
<td>9.5°N</td>
<td>85.2°W</td>
<td>Wet Tropical Forest</td>
<td>LaVal and Fitch 1977</td>
</tr>
<tr>
<td>Guanacaste-2</td>
<td>Costa Rica</td>
<td>9.5°N</td>
<td>85.2°W</td>
<td>Wet Tropical Forest</td>
<td>Fleming et al. 1972</td>
</tr>
<tr>
<td>Panamericana</td>
<td>Costa Rica</td>
<td>10.0°N</td>
<td>84.8°W</td>
<td>Montane Tropical Forest</td>
<td>LaVal and Fitch 1977</td>
</tr>
<tr>
<td>Heredia</td>
<td>Costa Rica</td>
<td>10.5°N</td>
<td>83.8°W</td>
<td>Wet Tropical Forest</td>
<td>LaVal and Fitch 1977</td>
</tr>
<tr>
<td>Sherman</td>
<td>Panama</td>
<td>9.3°N</td>
<td>80.0°W</td>
<td>Wet Tropical Forest</td>
<td>Fleming et al. 1972</td>
</tr>
<tr>
<td>Rodeo</td>
<td>Panama</td>
<td>9.0°N</td>
<td>79.6°W</td>
<td>Dry Tropical Forest</td>
<td>Fleming et al. 1972</td>
</tr>
<tr>
<td>BCI</td>
<td>Panama</td>
<td>9.2°N</td>
<td>79.8°W</td>
<td>Wet Tropical Forest</td>
<td>Hendley et al. 1991</td>
</tr>
<tr>
<td>Parasou</td>
<td>French Guiana</td>
<td>5.3°N</td>
<td>52.9°W</td>
<td>Wet Tropical Forest</td>
<td>Simmons and Voss 1998</td>
</tr>
<tr>
<td>Community</td>
<td>Country</td>
<td>Latitude</td>
<td>Longitude</td>
<td>Habitat</td>
<td>Reference</td>
</tr>
<tr>
<td>------------</td>
<td>-----------</td>
<td>----------</td>
<td>-----------</td>
<td>-----------------------------</td>
<td>---------------------</td>
</tr>
<tr>
<td>Zabelitas</td>
<td>Colombia</td>
<td>4.0°S</td>
<td>76.5°W</td>
<td>Wet Tropical Forest</td>
<td>Thomas 1972</td>
</tr>
<tr>
<td>Macarena</td>
<td>Colombia</td>
<td>3.3°N</td>
<td>73.9°W</td>
<td>Wet Tropical Forest</td>
<td>Sanchez-Palomino et al. 1993</td>
</tr>
<tr>
<td>Pace</td>
<td>Colombia</td>
<td>3.0°N</td>
<td>76.0°W</td>
<td>Montane Tropical Forest</td>
<td>Thomas 1972</td>
</tr>
<tr>
<td>Hoemiguer</td>
<td>Colombia</td>
<td>3.0°N</td>
<td>76.0°W</td>
<td>Montane Tropical Forest</td>
<td>Thomas 1972</td>
</tr>
<tr>
<td>Manaas</td>
<td>Brazil</td>
<td>3.0°S</td>
<td>60.0°W</td>
<td>Wet Tropical Forest</td>
<td>Duarte 1984</td>
</tr>
<tr>
<td>Edaphic Cerrado</td>
<td>Brazil</td>
<td>7.2°S</td>
<td>39.4°W</td>
<td>Tropical Woodland-Savannah</td>
<td>Willig 1982</td>
</tr>
<tr>
<td>Caratinga</td>
<td>Brazil</td>
<td>7.6°S</td>
<td>39.7°W</td>
<td>Dry Tropical Forest</td>
<td>Willig 1982</td>
</tr>
<tr>
<td>Limares</td>
<td>Brazil</td>
<td>19.0°S</td>
<td>40.3°W</td>
<td>Wet Semi-Tropical Forest</td>
<td>Percacci and Albuquerque 1993</td>
</tr>
<tr>
<td>Panga</td>
<td>Brazil</td>
<td>19.3°S</td>
<td>48.4°W</td>
<td>Wet Semi-Tropical Forest</td>
<td>Pedro and Taddei 1997</td>
</tr>
<tr>
<td>Minas Gerais</td>
<td>Brazil</td>
<td>19.8°S</td>
<td>41.8°W</td>
<td>Wet Semi-Tropical Forest</td>
<td>Moara de Souza Aguiar 1994</td>
</tr>
<tr>
<td>Jango Herrera</td>
<td>Peru</td>
<td>4.9°S</td>
<td>73.8°W</td>
<td>Wet Tropical Forest</td>
<td>Gorchov and Ascorna in litt.</td>
</tr>
<tr>
<td>Manu</td>
<td>Peru</td>
<td>11.9°S</td>
<td>71.3°W</td>
<td>Wet Tropical Forest</td>
<td>Ascorna et al. 1996</td>
</tr>
<tr>
<td>Mbaracayu</td>
<td>Paraguay</td>
<td>24.1°S</td>
<td>55.5°W</td>
<td>Wet Semi-Tropical Forest</td>
<td>Stevens and Willig in litt.</td>
</tr>
<tr>
<td>Rio Verde</td>
<td>Paraguay</td>
<td>23.5°S</td>
<td>56.1°W</td>
<td>Dry Semi-Tropical Forest</td>
<td>Stevens and Willig in litt.</td>
</tr>
</tbody>
</table>
Table 3.2. Latitude and functional diversity for each of 32 bat communities in the New World. Functional group richness corresponds to the number of feeding guilds. Diversity, evenness, and dominance correspond to Shannon’s diversity, Camargo’s evenness, and Berger-Parker’s dominance indices, respectively (see text for additional details).

<table>
<thead>
<tr>
<th>Community</th>
<th>Latitude</th>
<th>Richness</th>
<th>Evenness</th>
<th>Diversity</th>
<th>Dominance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Iowa</td>
<td>42.25°</td>
<td>1</td>
<td>1.00</td>
<td>0.00</td>
<td>1.00</td>
</tr>
<tr>
<td>California</td>
<td>36.50°</td>
<td>3</td>
<td>0.53</td>
<td>0.64</td>
<td>1.25</td>
</tr>
<tr>
<td>Nevada</td>
<td>36.20°</td>
<td>3</td>
<td>0.58</td>
<td>0.74</td>
<td>1.33</td>
</tr>
<tr>
<td>New Mexico</td>
<td>33.87°</td>
<td>3</td>
<td>0.46</td>
<td>0.46</td>
<td>1.14</td>
</tr>
<tr>
<td>Big Bend Ranch</td>
<td>29.75°</td>
<td>3</td>
<td>0.52</td>
<td>0.66</td>
<td>1.27</td>
</tr>
<tr>
<td>Querétaro</td>
<td>21.12°</td>
<td>6</td>
<td>0.60</td>
<td>1.52</td>
<td>2.33</td>
</tr>
<tr>
<td>Manantlan</td>
<td>19.33°</td>
<td>6</td>
<td>0.56</td>
<td>1.46</td>
<td>2.55</td>
</tr>
<tr>
<td>Ixtapan del Oro</td>
<td>19.25°</td>
<td>5</td>
<td>0.62</td>
<td>1.36</td>
<td>2.27</td>
</tr>
<tr>
<td>Los Tuxtlas</td>
<td>18.42°</td>
<td>5</td>
<td>0.61</td>
<td>1.35</td>
<td>2.19</td>
</tr>
<tr>
<td>Chiapas</td>
<td>16.10°</td>
<td>7</td>
<td>0.58</td>
<td>1.61</td>
<td>3.57</td>
</tr>
<tr>
<td>Guanacaste¹</td>
<td>9.47°</td>
<td>6</td>
<td>0.67</td>
<td>1.60</td>
<td>3.00</td>
</tr>
<tr>
<td>Guanacaste²</td>
<td>9.47°</td>
<td>6</td>
<td>0.61</td>
<td>1.45</td>
<td>3.33</td>
</tr>
<tr>
<td>Puntarenas</td>
<td>10.00°</td>
<td>4</td>
<td>0.73</td>
<td>1.21</td>
<td>2.67</td>
</tr>
<tr>
<td>Heredia</td>
<td>10.50°</td>
<td>6</td>
<td>0.61</td>
<td>1.49</td>
<td>3.17</td>
</tr>
<tr>
<td>Sherman</td>
<td>9.33°</td>
<td>7</td>
<td>0.49</td>
<td>1.47</td>
<td>2.38</td>
</tr>
<tr>
<td>Rodman</td>
<td>8.95°</td>
<td>7</td>
<td>0.52</td>
<td>1.55</td>
<td>2.55</td>
</tr>
<tr>
<td>Community</td>
<td>Latitude</td>
<td>Richness</td>
<td>Evenness</td>
<td>Diversity</td>
<td>Dominance</td>
</tr>
<tr>
<td>------------------</td>
<td>----------</td>
<td>----------</td>
<td>----------</td>
<td>-----------</td>
<td>-----------</td>
</tr>
<tr>
<td>BCI</td>
<td>9.17°</td>
<td>5</td>
<td>0.58</td>
<td>1.29</td>
<td>2.44</td>
</tr>
<tr>
<td>Paracou</td>
<td>5.27°</td>
<td></td>
<td></td>
<td>1.62</td>
<td>3.12</td>
</tr>
<tr>
<td>Zabelitas</td>
<td>4.00°</td>
<td></td>
<td>0.57</td>
<td>1.26</td>
<td>1.84</td>
</tr>
<tr>
<td>Marcarena</td>
<td>3.25°</td>
<td></td>
<td>0.58</td>
<td>1.30</td>
<td>2.05</td>
</tr>
<tr>
<td>Pance</td>
<td>3.00°</td>
<td></td>
<td>0.51</td>
<td>0.92</td>
<td>1.42</td>
</tr>
<tr>
<td>Hormiguero</td>
<td>3.00°</td>
<td></td>
<td>0.60</td>
<td>1.47</td>
<td>2.00</td>
</tr>
<tr>
<td>Manaus</td>
<td>3.00°</td>
<td></td>
<td>0.57</td>
<td>1.62</td>
<td>3.25</td>
</tr>
<tr>
<td>Edaphic Cerrado</td>
<td>7.23°</td>
<td></td>
<td>0.63</td>
<td>1.72</td>
<td>3.57</td>
</tr>
<tr>
<td>Caatinga</td>
<td>7.58°</td>
<td></td>
<td>0.68</td>
<td>1.77</td>
<td>3.78</td>
</tr>
<tr>
<td>Linhares</td>
<td>19.01°</td>
<td></td>
<td>0.54</td>
<td>1.42</td>
<td>2.31</td>
</tr>
<tr>
<td>Panga</td>
<td>19.25°</td>
<td></td>
<td>0.72</td>
<td>1.65</td>
<td>2.83</td>
</tr>
<tr>
<td>Minas Gerias</td>
<td>19.83°</td>
<td></td>
<td>0.63</td>
<td>1.54</td>
<td>2.22</td>
</tr>
<tr>
<td>Jarino Herrera</td>
<td>4.92°</td>
<td></td>
<td>0.55</td>
<td>1.44</td>
<td>2.46</td>
</tr>
<tr>
<td>Manu</td>
<td>11.93°</td>
<td></td>
<td>0.49</td>
<td>1.47</td>
<td>2.27</td>
</tr>
<tr>
<td>Mbarancayu</td>
<td>24.12°</td>
<td></td>
<td>0.57</td>
<td>1.26</td>
<td>2.14</td>
</tr>
<tr>
<td>Rio Verde</td>
<td>23.49°</td>
<td></td>
<td>0.63</td>
<td>1.53</td>
<td>3.22</td>
</tr>
<tr>
<td>Mean</td>
<td>15.58</td>
<td>5.41</td>
<td>0.60</td>
<td>1.31</td>
<td>2.41</td>
</tr>
<tr>
<td>Standard Deviation</td>
<td>10.98</td>
<td>1.52</td>
<td>0.10</td>
<td>0.40</td>
<td>0.76</td>
</tr>
<tr>
<td>CV</td>
<td>70.48</td>
<td>28.10</td>
<td>16.67</td>
<td>30.53</td>
<td>31.54</td>
</tr>
</tbody>
</table>
Table 3.3. Results from orthogonal polynomial regression analyses (Dutka and Ewens 1971) estimating relationships of local functional diversity with species richness and latitude. $b_0$, $b_1$, and $b_2$ correspond to regression coefficients. $r$-square refers to the coefficient of determination for the simple linear component of a particular model whereas $R$-square refers to the coefficient of determination of the non-linear model. $P$ corresponds to the probability that the observed latitudinal gradient comes from a population of gradients that exhibit no relationship with latitude. Measures of diversity that are bold-faced exhibit significant latitudinal gradients after maintaining experiment-wise error rate at 0.05 using a Bonferroni sequential adjustment (Rice 1989).

<table>
<thead>
<tr>
<th>Independent Variable</th>
<th>Measure of Functional Diversity</th>
<th>$b_0$</th>
<th>$b_1$</th>
<th>$b_2$</th>
<th>Linear $r$-square</th>
<th>$P$</th>
<th>Quadratic $R$-square</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species Richness</td>
<td>Richness</td>
<td>5.406</td>
<td>0.058</td>
<td>-0.002</td>
<td>0.365</td>
<td>&lt; 0.001</td>
<td>0.484</td>
<td>0.009</td>
</tr>
<tr>
<td></td>
<td>Diversity</td>
<td>1.308</td>
<td>0.014</td>
<td>-0.001</td>
<td>0.286</td>
<td>&lt; 0.001</td>
<td>0.452</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td>Evenness</td>
<td>0.597</td>
<td>-0.001</td>
<td>0.000</td>
<td>0.018</td>
<td>0.226</td>
<td>&lt; 0.001</td>
<td>0.494</td>
</tr>
<tr>
<td></td>
<td>Dominance</td>
<td>2.405</td>
<td>0.026</td>
<td>-0.001</td>
<td>0.304</td>
<td>&lt; 0.001</td>
<td>0.395</td>
<td>0.026</td>
</tr>
<tr>
<td>Latitude</td>
<td>Richness</td>
<td>5.406</td>
<td>-0.096</td>
<td>-0.006</td>
<td>0.463</td>
<td>&lt; 0.001</td>
<td>0.669</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Diversity</td>
<td>1.308</td>
<td>-0.026</td>
<td>-0.002</td>
<td>0.486</td>
<td>&lt; 0.001</td>
<td>0.783</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>Evenness</td>
<td>0.597</td>
<td>0.002</td>
<td>0.001</td>
<td>0.027</td>
<td>0.176</td>
<td>0.062</td>
<td>0.156</td>
</tr>
<tr>
<td></td>
<td>Dominance</td>
<td>2.405</td>
<td>-0.039</td>
<td>-0.002</td>
<td>0.294</td>
<td>&lt; 0.001</td>
<td>0.445</td>
<td>0.005</td>
</tr>
</tbody>
</table>
Table 3.4. Comparisons of aspects of functional diversity among tropical, subtropical, and temperate communities. Means for each measure of diversity for latitudinal regions that share an alphabetic subscript are statistically indistinguishable (Student-Newman-Keuls tests, comparison-wise error rate held constant at 5 percent).

<table>
<thead>
<tr>
<th>Measure of Functional Diversity</th>
<th>ANOVA F</th>
<th>P</th>
<th>Mean Temperate</th>
<th>Mean Subtropical</th>
<th>Mean Tropical</th>
</tr>
</thead>
<tbody>
<tr>
<td>Richness</td>
<td>17.56</td>
<td>&lt; 0.001</td>
<td>3.429&lt;sup&gt;a&lt;/sup&gt;</td>
<td>5.875&lt;sup&gt;b&lt;/sup&gt;</td>
<td>6.000&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Diversity</td>
<td>17.18</td>
<td>&lt; 0.001</td>
<td>0.756&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.489&lt;sup&gt;b&lt;/sup&gt;</td>
<td>1.450&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td>Evenness</td>
<td>0.24</td>
<td>0.786</td>
<td>0.613&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.608&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.586&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Dominance</td>
<td>6.65</td>
<td>0.004</td>
<td>1.621&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2.534&lt;sup&gt;b&lt;/sup&gt;</td>
<td>2.668&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
Table 3.5. Results from simulation analyses (mean parameter estimates and the probability that the empirical estimated is different from those generated by simulation) determining the degree to which latitudinal gradients in functional diversity could be produced by a latitudinal gradient in species richness. Pools for the entire New World involved simulations in which all continental New World bat species formed the group of species from which to assemble each local community. In regionally constrained simulations, only those species whose range included each community formed the species pool. $X_{50}$, $X_{50}$, and $X_{52}$ refer to the average parameter estimate (subscripts identify the particular parameter) for all simulations; corresponding P-values indicate the probability that a particular parameter estimate came from the random distribution generated from simulation.

<table>
<thead>
<tr>
<th>Pool</th>
<th>Measure</th>
<th>Mean</th>
<th>P</th>
<th>Intercept</th>
<th>Linear</th>
<th>Quadratic</th>
<th>$R^2$</th>
<th>Mean</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Entire New World</td>
<td>5.319</td>
<td>0.376</td>
<td>-0.035</td>
<td>&lt; 0.001</td>
<td>-0.002</td>
<td>&lt; 0.001</td>
<td>0.235</td>
<td>0.004</td>
<td></td>
</tr>
<tr>
<td>Diversity</td>
<td>1.454</td>
<td>&lt; 0.001</td>
<td>0.005</td>
<td>&lt; 0.001</td>
<td>-0.001</td>
<td>&lt; 0.001</td>
<td>0.196</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>Evenness</td>
<td>0.675</td>
<td>&lt; 0.001</td>
<td>0.002</td>
<td>0.960</td>
<td>0.001</td>
<td>0.418</td>
<td>0.093</td>
<td>0.980</td>
<td></td>
</tr>
<tr>
<td>Dominance</td>
<td>2.684</td>
<td>&lt; 0.001</td>
<td>-0.006</td>
<td>&lt; 0.001</td>
<td>-0.001</td>
<td>&lt; 0.001</td>
<td>0.035</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>Regional Constraint</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Richness</td>
<td>5.361</td>
<td>0.624</td>
<td>-0.101</td>
<td>0.550</td>
<td>-0.006</td>
<td>0.914</td>
<td>0.732</td>
<td>0.226</td>
<td></td>
</tr>
<tr>
<td>Diversity</td>
<td>1.388</td>
<td>&lt; 0.001</td>
<td>-0.030</td>
<td>0.122</td>
<td>-0.002</td>
<td>0.492</td>
<td>0.875</td>
<td>0.040</td>
<td></td>
</tr>
<tr>
<td>Evenness</td>
<td>0.665</td>
<td>&lt; 0.001</td>
<td>0.001</td>
<td>0.434</td>
<td>0.001</td>
<td>0.330</td>
<td>0.117</td>
<td>0.664</td>
<td></td>
</tr>
<tr>
<td>Dominance</td>
<td>2.728</td>
<td>&lt; 0.001</td>
<td>-0.054</td>
<td>0.006</td>
<td>-0.002</td>
<td>0.264</td>
<td>0.576</td>
<td>0.944</td>
<td></td>
</tr>
</tbody>
</table>
Figure 3.1. Location of 32 New World bat communities (solid dots) used to evaluate geographic patterns of diversity. The letters a, b, and c denote temperate, subtropical and tropical latitudinal zones, respectively.
Figure 3.2. Gradients in four components of functional diversity of New World bat communities with respect to latitude (left column) and species richness (right column). Regression lines indicate significant relationships after maintaining experiment-wise error rate at 5 percent.
CHAPTER IV
LATITUDINAL GRADIENTS IN THE PHENETIC
DIVERSITY OF NEW WORLD BAT COMMUNITIES

Abstract
Although the examination of latitudinal gradients of biodiversity from a
taxonomic perspective is common, hardly any attention has been devoted to latitudinal
gradients in phenetic diversity. Because the phenotype reflects aspects of an organism’s
environment, ecological relationships, and evolutionary history, measures of phenetic
diversity likely provide complimentary information to that of taxonomic diversity and
may be valuable for understanding patterns of biodiversity. Herein, I evaluate latitudinal
gradients in the phenetic diversity of 32 New World bat communities. Seven
morphological characters were used to estimate phenotypic variation among bat species
within local communities. Principal component analysis decomposed this variation into
axes of size and shape. Three measures of phenetic diversity were calculated for both
size and shape axes. The range of species scores on a particular axis described the
amount of phenetic variation encompassed by species in a community. The standard
deviation of minimum spanning-tree segment lengths connecting all species in a
community on a particular axis described the uniformity of species in phenetic space.
Average nearest-neighbor distances for species within a community provided information
regarding the local packing of species and the potential intensity of competitive
interactions. I separately regressed each of these six measures of phenetic diversity on
local species richness and latitude. Variation in species richness accounted for a significant amount of variation in all measures of phenetic diversity. Moreover, significant differences among temperate, subtropical, and tropical zones existed regarding measures of phenetic diversity characterizing the range of phenotypes. Latitude accounted for significant variation in measures of phenetic diversity except measures of the standard deviation of minimum-spanning tree segment lengths and for average nearest-neighbor distance on the shape axis. Gradients in phenetic diversity were significantly different than would be expected as a consequence of latitudinal gradients in species richness (range of species phenotypes on both the size and shape axis and measures of variability on the shape axis). When variation among communities regarding the richness and composition of their regional faunas was taken into consideration, differences between empirical and simulated gradients remained regarding variability on the shape axis, but disappeared regarding the range of phenotypes on both the size and shape axes. Thus, those factors that determine the composition of regional fauna have a great impact on the phenetic diversity of communities and suggest that better understanding of latitudinal gradients in biodiversity may come from considerations of both local and regional processes on the structure of local communities.

Introduction

The latitudinal gradient in species diversity is one of the most frequently described biogeographic patterns characterizing the distribution of numerous taxa across space and time (Willig 2001). Moreover, latitudinal effects on mammalian species
diversity manifest at a number of levels in the taxonomic hierarchy (Kaufman 1995), at multiple spatial extents (Lyons and Willig 1999, 2001), and at different ecological scales (Stevens and Willig 2002). Although latitudinal gradients in diversity have represented important foci in the development of ecological theory, the empirical characterization of variation among communities has been limited primarily to the richness and at times relative abundances of co-existing species. Nonetheless, taxonomic diversity is not the only aspect of biodiversity that may be affected by latitude. Different components of biodiversity (e.g., functional, genetic, or interaction diversity) may or may not exhibit similar geographic gradients. Moreover, it is uncertain whether these basic constituents of biodiversity respond in an independent fashion along environmental gradients, or whether they co-vary spatially.

Phenotypic attributes of species have a profound impact on their ecology and provide an “integrated” view of ecological relationships over space and time (Wainright and Reilly 1994). For example, to the degree that morphology determines the ecological range of a phenotype, it may limit the geographical distribution of individuals, thereby affecting the coexistence of populations in local communities (Ricklefs and Miles 1994). Moreover, morphology is a useful predictor of species-specific characteristics such as metabolic rate, energy use, home range-size, population density, population growth rate, and food particle size (Brown 1995). Despite these characteristics, measures of phenotypic variation among species represent a much less understood component of biodiversity. Moreover, this component may provide complementary insights into
patterns of biodiversity not attainable by examining other components such as taxonomic diversity or functional diversity (Findley 1973).

Morphological measures prove to be excellent descriptors of the trophic position of bat species in the New World (Stevens and Willig 1999). Nonetheless, to be useful as a descriptor of biodiversity, phenotypic variation must characterize the relationships among species in order to describe their organization within communities. Measures of phenetic diversity describe the variety of phenotypes inhabiting a particular community as well as the distribution of species within a phenotypic space (Findley 1973). Two components of phenetic variation are the size of the phenetic volume and the distribution of species within that volume. Communities can have high phenetic diversity relative to other communities if they occupy a larger phenetic volume due to the presence of species that are phenotypically novel. Similarly, communities can have relatively high phenetic diversity if they possess species that are more evenly distributed within a particular phenotypic volume. Because phenetic and taxonomic diversity measure different aspects of the structure of communities, geographic patterns in phenetic diversity provide alternative perspectives regarding patterns of biodiversity that cannot be obtained by examination of taxonomic diversity alone.

Herein, I describe the phenetic diversity of 32 New World bat communities and evaluate latitudinal gradients regarding this component of biodiversity. I evaluate the strength of the association between phenetic diversity and species richness and determine the degree to which latitudinal gradients in phenetic diversity can be explained solely by latitudinal changes in the number of species or the composition of regional species pools.
Materials and Methods

Species composition of 32 New World bat communities (Figure 4.1, Table 4.1) were derived from the literature (see Stevens and Willig 2002, Chapters II and III). For each species, I obtained measurements for seven morphological characteristics. These characters reflect variation in body-size (i.e., forearm length and greatest length of skull), as well as cranial geometry and associated trophic structures (i.e., greatest length of skull, condylar length, length of maxillary toothrow, breadth across upper molars, width across post-orbital constriction, breadth of braincase). In most cases, means were determined from a sample of at least four males and four females of each species. For most members of the family Phyllostomidae, these measurements came from Swaine and Genoways (1979). For other taxa, measurements either came directly from the description of the actual community, from other literature sources, or from museum specimens. Morphological variables were log-transformed prior to analyses to enhance the likelihood of fulfilling assumptions of multivariate analyses (Marcus 1990).

I used principal components analysis (PCA) to create composite morphological axes that reflect the salient features of body-size and shape variation expressed by continental New World bats. PCA creates sets of linear combinations of the original variables (loadings) that define orthogonal axes in multivariate space that maximally account for variation among observations (Manley 1986). Correlation analyses were used to interpret principal components (PCs). Morphological characters with high correlations to a particular PC reflect the type of variation accounted for by that derived
axis. Principal components based on morphological data which have loadings that are all positive and relatively uniform in magnitude represent variation in body size, whereas PCs with loadings that are variable in magnitude and sign represent shape variation (Marcus 1990, Klingenberg 1996). Only the first two PCs were retained for further analyses. In this particular analysis, these two components characterized the major axes of variation in size and shape.

The phenetic diversity of species within communities was estimated in three ways on the size and on the shape axis (Figure 4.2). To estimate the extent and uniformity of the distribution of species on a particular axis, I calculated the range of PC scores and the standard deviation of minimum spanning-tree segment lengths that connected all species in the community on that PC axis (Ricklefs and Travis 1980). I also used the average euclidean distance between species and their nearest morphological neighbor to estimate “species packing” or the degree of crowding in morphological space (Findley 1976, Ricklefs and Travis 1980, Schum 1984, Shepherd 1998).

Latitudinal variation in phenetic diversity may not be represented by a continuous linear function. Accordingly, I assigned communities to three geographic zones [tropical (12° N to 12° S), subtropical (13° N to 23.45° N and 13° S to 23.45° S), or temperate (> 23.45° N or >23.45° S)] and evaluated differences among zones regarding average measures of phenetic diversity using a multivariate analysis of variance (MANOVA). Univariate analyses of variance (ANOVAs) were used to infer significant differences among zones regarding each of the six measures of phenetic diversity. Experiment-wise error rate was held at 5 percent for each morphological component (i.e., size or shape) by
application of a Bonferroni sequential adjustment (Rice 1989). Finally, Student-Newman-Keuls tests (Sokal and Rohlf 1995) conducted on each of the measures of phenetic diversity identified the location of significant latitudinal differences. All analyses regarding zonal differences were performed using SPSS (SPSS Inc 1990).

I used orthogonal polynomial regression analysis to determine the relationship between each measure of phenetic diversity and species richness or latitude. The advantage of orthogonal polynomial regression analysis is that linear, quadratic, and higher order regression coefficients are independent of each other thereby allowing the decomposition of relationships into their linear and nonlinear components (Sokal and Rohlf 1995). Because values of the independent variable (latitude) were not uniformly spaced, the calculation of regression coefficients is quantitatively lengthy. I used a function written in Matlab (Math Works 1995) to conduct the procedure described in Dutka and Ewens (1971) for determining orthogonal polynomial regressions when values of the independent variable are not evenly spaced. Again, experiment-wise error rate was held at 5 percent for each morphological component (i.e., size or shape) by application of a Bonferroni sequential adjustment (Rice 1989).

Latitudinal gradients in phenetic diversity could result primarily from latitudinal gradients in species richness because the morphological volume of a community is likely to increase by chance alone with increases in the number of species. To determine if observed gradients in phenetic diversity could be generated by latitudinal increases in species richness, I conducted two suites of simulation analyses. In the first, species were drawn randomly from a pool comprising all continental New World bat species. I
followed Koopman (1993) for a comprehensive list of extant continental New World
bats. For each community, a simulated community was assembled by randomly
selecting from the pool the same number of species as occurred in an actual community.
Measures of phenetic diversity were then calculated for each simulated community and
then regressed on latitude using orthogonal polynomial regression analysis. This process
was then iterated 1000 times to create a distribution of gradients in phenetic diversity that
could be produced by the empirical latitudinal gradient in species richness. Parameter
estimates ($b_0$, $b_1$, $b_2$, and coefficient of determination) characterizing the latitudinal
gradient in phenetic diversity from actual communities were then compared with the
distribution of like values from the simulated gradients to determine significance. The
position of the observed parameter estimate relative to the distribution of simulated
values describes the probability that the observed value was randomly obtained from the
simulated distribution. Parameter estimates were deemed significantly different when
they were not among the rarest of values in either tail of the simulated distribution.
Alpha levels for each morphological component (i.e., size or shape) were determined by a
Bonferroni sequential adjustment (Rice 1989).

A second suite of analyses was constrained to account for differences among
communities in the richness and composition of their associated regional faunas. In these
analyses, simulated communities were assembled as before, except that species were
drawn from a taxonomically restricted pool (i.e., regional fauna) comprising only those
species whose geographic distributions encompassed the location of a particular
community. This provided a more restrictive constraint in that only those species with
the dispersal potential to be part of a particular community were included in analyses. Distribution maps for each species were modified from Willig and Selcer (1989) and Willig and Sandlin (1991) based on information in Hall (1981) and Koopman (1982), and updated by Lyons and Willig (1999) based on Eisenberg (1989) and Redford and Eisenberg (1992). All simulation analyses were performed using Matlab (Math Works 1995).

Results

Characterization of Phenetic Diversity

The first two principal components accounted for approximately 87% of the variation among continental New World bat species regarding the seven morphological characters. The first PC was positively and significantly (P < 0.05) correlated with each of these morphological characters and represents the principal axis of size variation among species (Figure 4.3). Correlations of the second PC with the seven morphological measures were variable in magnitude, positive for measures of width, and negative for measures of length. All cranial measures were significantly (P < 0.05) correlated with the second PC whereas forearm length was not significantly correlated with this axis. Consequently, this shape axis is one that reflects the degree of cranial roundness (Figure 4.3). Large, positive values on the second principal component indicate species with a short and round cranium (i.e., frugivores), whereas large negative values indicate species with a long and narrow cranium (i.e., nectarivores). In addition, characters that reflect variation in tooth area (i.e., breadth across the upper molar and length of maxillary
toothrow) were strongly correlated with this axis whereas characters that reflect cranial features that facilitate muscle attachment (i.e., breadth of braincase and width of the post-orbital constriction) were more weakly correlated with this axis.

Measures of phenetic diversity were variable among the 32 bat communities (Table 4.2). In general, indices derived from nearest-neighbor distances were most variable among sites based on relative measures of dispersion (CV). The range of phenotypes on the size axis exhibited the least relative variation among sites (CV = 27) whereas the average nearest-neighbor distance on the size axis exhibited the most relative variation among sites (CV = 47).

**Empirical Patterns**

Phenetic diversity continuously varied with changes in species richness (Table 4.3, Figure 4.4). Statistically significant coefficients of determination ranged from 0.67 (range of species scores on size axis versus species richness) to 0.30 (standard deviation of minimum spanning tree segment lengths on the shape axis versus species richness). In all significant cases, the ranges of species phenotypes was related positively to increases in species richness, whereas variability of minimum-spanning tree segment lengths and averages of nearest-neighbor distances were related negatively to increases in species richness.

Significant differences regarding phenetic diversity existed among temperate, subtropical, and tropical sites (MANOVA; F_{12,48} = 4.09, P < 0.001). Univariate analyses (ANOVA) indicated that the range of PC scores rather than variation in minimum...
spanning-tree segment lengths or nearest-neighbor distances contributed to differences among latitudinal zones (Table 4.4). *A posteriori* tests revealed that significant differences among latitudinal zones are the result of differences between the temperate zone and both the tropical and subtropical zones (Table 4.4). No significant difference between zones existed regarding the variability of minimum spanning-tree segment lengths or average nearest-neighbor distance on either size or shape axes.

Significant latitudinal gradients in phenetic diversity exist on size and shape axes (Table 4.3, Figure 4.5). Statistically significant coefficients of determination ranged from 0.67 between latitude and the range of species scores on the size axis, to 0.14 between latitude and the average nearest-neighbor distance among species on the size axis. In all significant cases, increases in the range of species scores were associated with decreases in latitude, whereas the increase in phenetic diversity involving nearest-neighbors was associated with an increase in latitude.

**Empirical Versus Simulated Gradients**

Simulation analyses in which the species pool for each community was the continental New World bat fauna indicated that significant latitudinal gradients in a number of measures of phenetic diversity could not be solely a consequence of latitudinal increases in species richness (Table 4.5). Significant differences existed for both size- and shape-related measures. On the size axis, the linear rate of change in the range of species phenotypes was greater than expected given observed changes in species richness. A significantly greater coefficient of determination for this relationship
indicated that latitude accounted for significantly more of the variation in phenetic ranges of species in the empirical communities than in those that were assembled randomly from the faunal pool. Significant differences between real and simulated gradients existed on the shape axis as well. On average, the range of species phenotypes and the amount of variability in minimum spanning tree segment lengths was smaller than in communities created by simulation. The linear rate of increase with latitude in the standard deviation of minimum spanning-tree segments lengths on the shape axis was greater in the observed communities than in simulated ones, and this relationship was stronger (higher $R^2$) than expected based on simulation. Quadratic components of observed relationships were never significantly different from those produced by simulation when communities were assembled from faunas of the entire continental New World.

Regionally constrained models further illustrate how biogeographic processes determining the composition of regional faunal pools in conjunction with local processes affecting species richness influence local gradients in phenetic diversity (Table 4.5). Significant differences between observed and simulated latitudinal gradients existed only with respect to the variability of minimum spanning-tree segment lengths on the shape axis. In all other cases, the effects of latitude on the composition of regional faunas were sufficient to account for latitudinal gradients in the phenetic diversity of bat communities.

**Discussion**

The phenetic diversity of bat communities varies considerably throughout the New World. As with other measures of biodiversity, phenetic diversity is greatest toward
the equator and least toward the poles. Moreover, latitudinal increases in phenetic diversity are not solely the product of latitudinal changes in taxonomic diversity. Although phenetic and taxonomic gradients are inter-related, they each provide unique insights regarding variation in biodiversity. The composition of regional faunas has an important influence on the phenetic diversity of local communities. Indeed, much of the latitudinal variation in phenetic diversity of local communities can be accounted for by variation in local species richness and changes in the composition of regional faunas. To this end, local processes that determine species richness, acting in concert with regional processes determining the types of species from which communities can be assembled, determines much of the variation among sites regarding phenetic diversity. Considerations of the interplay between local and regional processes in determining local species composition will enhance not only our understanding of community ecology, but also the understanding of the multifaceted gradients of biodiversity.

Differences Between Bats and Terrestrial Mammals

Latitudinal gradients in phenetic diversity also characterize local assemblages of terrestrial mammals ranging from Alaska to Costa Rica (Shepherd 1998). Both bats (this work) and terrestrial mammals (Shepherd 1998) exhibit strong latitudinal gradients in phenetic diversity (Figure 4.6). In addition to the average nearest-neighbor distance among species in a community, Shepherd (1998) used the average distance among all species as a measure of the amount of morphological variation, and this is comparable to the range of scores on a particular PC as used in my study. In comparison to what
happened to the phenetic diversity of bat communities, for terrestrial mammals, nearest-neighbor distances increased with latitude for size and decreased with latitude for shape. Moreover, the amount of phenetic variation within terrestrial mammal communities increased on the size axis and decreased on the shape axis with increases in latitude. Thus, bats and terrestrial mammals were similar in that communities exhibited greatest shape variation at the equator. Nonetheless, terrestrial mammals and bats differ in the direction of change in size variation with latitude. Although differences in "shape" could arise because of either biological differences or differences in the actual characters used, differences in "size" likely are more comparable among groups when using different morphological characters. This is because the particular linear combinations that are used to construct a size axis reflect the allometric relationships that define size variation (Marcus 1990). Thus, I will restrict the remainder of my comparison between terrestrial mammals and bats to what transpires on the size axis.

For bats, mean nearest-neighbor distances increase and the amount of phenetic variation decreases with latitude on the size axis, whereas for terrestrial mammals both measures increase with latitude. Moreover, the amount of phenetic variation and nearest-neighbor distances are correlated positively for terrestrial mammals but are correlated negatively for bats. Bats attain phenetic diversity on the size axis in a manner different from that of terrestrial mammals. These differences likely result because bat communities are derived from a single mammalian order, whereas terrestrial mammal assemblages are derived from multiple orders representing a paraphyletic group. Increases in species richness for bats transpire within a space defined by their particular
body plan, in particular one that is constrained on the small end by the ability of
thermoregulate and on the large end by the ability to fly. In contrast, latitudinal increases
in the species richness of terrestrial mammals involve the addition of new body plans as
well as diversification within existing body plans. This variation in body plans
corresponds to much variation in the masses of terrestrial mammals. Thus, from the
perspective of body size, terrestrial mammal communities experience much less species
packing than do bat communities. Because terrestrial mammal communities can differ in
the number and identity of body plans, as well as in the number and identity of species
within those body plans, their communities are likely assembled in much different ways
than those of bats, from a phenetic perspective. Paraphyletic groups such as "terrestrial
mammals" that entail quantitative as well as qualitative morphological variation may not
experience the same kind of species packing as do natural groups that vary in only a
quantitative manner.

Bats and terrestrial mammals also differ in the geographic distribution of their
average body-sizes. Body-size increases with latitude for terrestrial mammals (Zevaloff
and Boyce 1988), whereas it decreases with latitude for bats (Willig and Green,
unpublished data). Moreover, in the New World, extreme northern and southern latitudes
are characterized by the least amount of size variation for bats and the greatest amount of
size variation for terrestrial mammals. In northern North America, bat communities
comprise only species from the family Vespertilionidae, generally species from the genus
Myotis (Findley 1993). In contrast, terrestrial mammal assemblages from the same
northern sites comprise orders of mammals that represent large amounts of size variation

103
(i.e., differences among insectivores, rodents, carnivores, and ungulates). As latitude increases, the mean and variability of sizes of terrestrial mammal species increases, whereas the mean and variability of sizes of volant mammals decreases. Although patterns of taxonomic diversity for terrestrial and volant mammals are quite similar at broad spatial scales and for large foci (Kaufman 1995) and likely result from similar mechanisms, differences in gradients of phenetic diversity likely result from differences between these two groups regarding their particular biogeographic history and body plan evolution. Moreover, differences between taxonomic and phenetic diversity patterns highlight the multifaceted nature of biodiversity, suggesting that comprehensive approaches are necessary to completely understand its spatial dynamics.

Nearest-Neighbor and Community-Wide Perspectives

Findley (1973, 1976) and Schum (1984) investigated extensively the relationship between species richness and species packing (measured by average nearest-neighbor distance) in bat faunas. Although Schum (1984) found that average nearest-neighbor distances increased with decreases in species richness, Findley (1976) failed to find major differences between tropical and temperate faunas regarding the same measure. A similar situation exists for the local communities in this study; average nearest-neighbor distances decreased with increases in species richness, yet this association translated into a significant latitudinal gradient on only the size axis and not the shape axis. Although species richness always accounted for significant variation in mean nearest-neighbor distances, there was considerable residual variation in these relationships. The same is
true regarding the relationship between species richness and latitude (i.e., a significant yet variable association, see Chapter II). Thus, although nearest-neighbor distances are significantly related to variation in species richness and species richness is significantly related to latitude, these two relationships are not sufficiently strong so as to derive a latitudinal gradient in nearest-neighbor distances on the shape axis.

Patterns regarding nearest-neighbors have traditionally been interpreted in light of the effects of competitive interactions within a particular functional group (Findley 1973, Ricklefs and Travis 1980). Nonetheless, most New World bat communities include more than one functional group, and hence comprise different suites of species each likely experiencing different competitive interactions. Moreover, latitudinal changes in the composition of bat communities entails changes in the number of functional groups as well as changes in the number of species per functional group. All of this variation likely obscures any sign of the effects of competition within functional groups and suggests that when communities represent a functionally diverse group of species, nearest-neighbor distances may not be the best perspective from which to evaluate patterns of phenetic diversity.

Latitudinal gradients in phenetic diversity were detected consistently for indices measuring the range of species in morphological space, and this likely is related to the way in which bat species are assembled into communities. As indicated in Chapter III, latitudinal increases in biodiversity are associated with increases in the functional diversity of bat communities. Decreases in latitude are accompanied by increases in the richness and diversity of functional groups and decreases in the dominance of those
groups. Because structure and function are so highly related in bats (Findley 1993, Stevens and Willig 1999), latitudinal changes in the phenetic diversity of entire communities likely are more reflective of latitudinal changes in the number of functional groups than to changes in the number of species in each functional group. Winemiller (1991) suggested that increases in the volume of morphological spaces in the absence of increases in nearest-neighbor distances are indicative of niche diversification due to resource expansion. Variation along the shape axis suggests that this transpires across New World bat communities. The two extreme ends of the shape axis are inhabited exclusively by phyllostomids (stenodermatines on one end and glossophagines on the other end). The Phyllostomidae is highly diverse taxonomically, ecologically, and morphologically, is primarily tropical in distribution, and exhibits a marked latitudinal gradient of species density (Willig and Selcer 1989, Willig and Sandlin 1991). Moreover, the biogeographic termini of subfamilies of the Phyllostomidae coincide with increases in phenetic diversity on the shape axis and this reflects the niche expansion of New World bats that transpires while moving from the temperate to tropical regions.

Whereas niche expansion characterizes the latitudinal increase in phenetic diversity on the shape axis, species packing characterizes the increase on the size axis. This is indicated by increases in the ranges of sizes and simultaneous decreases in nearest-neighbor distances. As the range of sizes expands within a community, constituent species also become more tightly packed within local phenetic space. The number of species from all bat families increases toward the equator and this results in an increase in the range of sizes found in communities. Niche expansion likely contributes
to increases in phenetic diversity on the size axis. Nonetheless, once in the subtropics, most families of bats are represented in communities and niche expansion diminishes. Once this has transpired, latitudinal increases in species richness are facilitated by adding species within the same range of sizes as opposed to adding larger or smaller sizes and increasing the range. This causes an increase in species packing within body plans and the resultant decrease in nearest-neighbor distances.

Latitudinal gradients in the phenetic diversity of New World bats provide complimentary perspectives on patterns of biodiversity to those generated from the examination of patterns of taxonomic or functional diversity. Increases in biodiversity toward the equator are facilitated by increases in the number of species, increases in the number of functional groups, and by a non random assembly of species into communities based on morphology. Phenetic diversity gradients primarily reflect variation in the range of morphologies that New World bats can attain at a particular place in time. The nonrandom geographic distribution of families and subfamilies of bats in the New World greatly influences the morphological diversity of communities. Nonetheless, the close association between taxonomy and ecological function obscures the mechanisms underlying phenetic diversity gradients. Future research should decouple the influences of ecology and phylogeny on patterns of phenetic diversity, as well as address the contribution that historical phylogenetic radiation has made to contemporary patterns of biodiversity.
References


SPSS, Inc. 1990. The SPSS base system user's guide. SPSS, Inc., Chicago, Illinois, USA.


Yancey, F. D. 1996. The mammals of Big Bend Ranch State Park. Dissertation, Texas Tech University, Lubbock, Texas, USA.

Table 4.1. Geographic and environmental characteristics of each of 32 bat communities used to evaluate patterns of phenetic diversity in the New World.

<table>
<thead>
<tr>
<th>Community</th>
<th>Country</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Habitat</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Iowa</td>
<td>USA</td>
<td>42.3°N</td>
<td>93.0°W</td>
<td>Riparian</td>
<td>Kunz 1973</td>
</tr>
<tr>
<td>California</td>
<td>USA</td>
<td>36.5°N</td>
<td>117.3°W</td>
<td>Desert</td>
<td>Suprenant 1977</td>
</tr>
<tr>
<td>Nevada</td>
<td>USA</td>
<td>36.2°N</td>
<td>115.2°W</td>
<td>Desert</td>
<td>O'Farrell and Bradley 1970</td>
</tr>
<tr>
<td>New Mexico</td>
<td>USA</td>
<td>33.9°N</td>
<td>107.4°W</td>
<td>Desert</td>
<td>Black 1974</td>
</tr>
<tr>
<td>Big Bend Ranch</td>
<td>USA</td>
<td>29.8°N</td>
<td>103.8°W</td>
<td>Desert</td>
<td>Yancey 1996</td>
</tr>
<tr>
<td>Queretaro</td>
<td>Mexico</td>
<td>21.1°N</td>
<td>99.3°W</td>
<td>Montane Tropical Forest</td>
<td>Navarro L. and Leon-Panagni 1995</td>
</tr>
<tr>
<td>Manantlan</td>
<td>Mexico</td>
<td>19.3°N</td>
<td>104.0°W</td>
<td>Montane Tropical Forest</td>
<td>Iniguez Davalos 1993</td>
</tr>
<tr>
<td>Etapaz del Oro</td>
<td>Mexico</td>
<td>19.3°N</td>
<td>100.2°W</td>
<td>Montane Tropical Forest</td>
<td>Alvarez and Alvarez-Castaneda 1996</td>
</tr>
<tr>
<td>Los Tuxtlas</td>
<td>Mexico</td>
<td>18.4°N</td>
<td>95.0°W</td>
<td>Wet Tropical Forest</td>
<td>Estrada et al. 1993</td>
</tr>
<tr>
<td>Chiapas</td>
<td>Mexico</td>
<td>16.1°N</td>
<td>91.0°W</td>
<td>Wet Tropical Forest</td>
<td>Medellin 1993</td>
</tr>
<tr>
<td>Guanacaste-1</td>
<td>Costa Rica</td>
<td>9.5°N</td>
<td>85.2°W</td>
<td>Wet Tropical Forest</td>
<td>LaVal and Fitch 1977</td>
</tr>
<tr>
<td>Guanacaste-2</td>
<td>Costa Rica</td>
<td>9.5°N</td>
<td>85.2°W</td>
<td>Wet Tropical Forest</td>
<td>Fleming et al. 1972</td>
</tr>
<tr>
<td>Puntarenas</td>
<td>Costa Rica</td>
<td>10.0°N</td>
<td>64.8°W</td>
<td>Montane Tropical Forest</td>
<td>LaVal and Fitch 1977</td>
</tr>
<tr>
<td>Heredia</td>
<td>Costa Rica</td>
<td>10.5°N</td>
<td>83.8°W</td>
<td>Wet Tropical Forest</td>
<td>LaVal and Fitch 1977</td>
</tr>
<tr>
<td>Sherman</td>
<td>Panama</td>
<td>9.3°N</td>
<td>80.0°W</td>
<td>Wet Tropical Forest</td>
<td>Fleming et al. 1972</td>
</tr>
<tr>
<td>Redman</td>
<td>Panama</td>
<td>9.0°N</td>
<td>79.6°W</td>
<td>Dry Tropical Forest</td>
<td>Fleming et al. 1972</td>
</tr>
<tr>
<td>BCI</td>
<td>Panama</td>
<td>9.2°N</td>
<td>79.8°W</td>
<td>Wet Tropical Forest</td>
<td>Handley et al. 1991</td>
</tr>
<tr>
<td>Panama</td>
<td>French Guiana</td>
<td>5.3°N</td>
<td>52.9°W</td>
<td>Wet Tropical Forest</td>
<td>Simmons and Voss 1998</td>
</tr>
<tr>
<td>Community</td>
<td>Country</td>
<td>Latitude</td>
<td>Longitude</td>
<td>Habitat</td>
<td>Reference</td>
</tr>
<tr>
<td>--------------------</td>
<td>---------------</td>
<td>----------</td>
<td>-----------</td>
<td>-----------------</td>
<td>--------------------</td>
</tr>
<tr>
<td>Zebidua</td>
<td>Colombia</td>
<td>4°6'N</td>
<td>76°8'W</td>
<td>Wet Tropical Forest</td>
<td>Thomas 1972</td>
</tr>
<tr>
<td>Mariposa</td>
<td>Colombia</td>
<td>3°48'N</td>
<td>72°46'W</td>
<td>Wet Tropical Forest</td>
<td>Schnetger-Palmieri et al. 1993</td>
</tr>
<tr>
<td>Porte</td>
<td>Colombia</td>
<td>3°6'N</td>
<td>76°6'W</td>
<td>Monsoon-Tropical Forest</td>
<td>Thomas 1972</td>
</tr>
<tr>
<td>Paramo</td>
<td>Colombia</td>
<td>3°0'N</td>
<td>76°0'W</td>
<td>Monsoon-Tropical Forest</td>
<td>Thomas 1972</td>
</tr>
<tr>
<td>Paramo</td>
<td>Colombia</td>
<td>3°0'N</td>
<td>60°0'W</td>
<td>Wet Tropical Forest</td>
<td>Thomas 1972</td>
</tr>
<tr>
<td>Manaus</td>
<td>Brazil</td>
<td>3°18'N</td>
<td>59°41'W</td>
<td>Tropical Woodland-Savannah</td>
<td>Doo 1984</td>
</tr>
<tr>
<td>Edithia Carinosa</td>
<td>Brazil</td>
<td>7°48'S</td>
<td>39°41'W</td>
<td>Dry Tropical Forest</td>
<td>Wille 1982</td>
</tr>
<tr>
<td>Carating</td>
<td>Brazil</td>
<td>18°53'S</td>
<td>46°23'W</td>
<td>Wet Sem-Tropical Forest</td>
<td>Francisco and Albuquerque 1993</td>
</tr>
<tr>
<td>Libranes</td>
<td>Brazil</td>
<td>13°58'S</td>
<td>48°41'W</td>
<td>Wet Sem-Tropical Forest</td>
<td>Francisco and Albuquerque 1993</td>
</tr>
<tr>
<td>Panga</td>
<td>Brazil</td>
<td>10°58'S</td>
<td>41°8'W</td>
<td>Wet Sem-Tropical Forest</td>
<td>Francisco and Albuquerque 1993</td>
</tr>
<tr>
<td>Malac Manu</td>
<td>Peru</td>
<td>15°58'S</td>
<td>72°6'W</td>
<td>Wet Tropical Forest</td>
<td>Garcia and Gomez 1964</td>
</tr>
<tr>
<td>Guatamala</td>
<td>Peru</td>
<td>13°0'S</td>
<td>72°3'W</td>
<td>Wet Tropical Forest</td>
<td>Azcuna et al. 1986</td>
</tr>
<tr>
<td>Montes-Arrechea</td>
<td>Peru</td>
<td>24°17'S</td>
<td>55°5'W</td>
<td>Wet Sem-Tropical Forest</td>
<td>Stevens and Willig in litt.</td>
</tr>
<tr>
<td>Río Verde</td>
<td>Paraguay</td>
<td>23°58'S</td>
<td>50°17'W</td>
<td>Dry Semi-Tropical Forest</td>
<td>Stevens and Willig in litt.</td>
</tr>
</tbody>
</table>
Table 4.2. Measures of pheretic diversity for each of 32 New World bat communities. Size and Shape refer to the
size and shape axis, respectively, derived from a principal components analysis of seven morphological variables.
Range refers to the range between the two most disparate species within a community on a particular morphological
axis. STD refers to the standard deviation of the lengths of a minimum spanning-tree connecting all taxa in a
community on a particular morphological axis. Nearest-Neighbor refers to the average distance between
morphologically nearest-neighbors in a community on a particular morphological axis.

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude</th>
<th>Species Richness</th>
<th>Range</th>
<th>Std</th>
<th>Nearest-Neighbor</th>
</tr>
</thead>
<tbody>
<tr>
<td>Iowa</td>
<td>42.25</td>
<td>8</td>
<td>3.77</td>
<td>1.37</td>
<td>0.38 0.21</td>
</tr>
<tr>
<td>California</td>
<td>36.50</td>
<td>10</td>
<td>4.97</td>
<td>1.62</td>
<td>0.25 0.28</td>
</tr>
<tr>
<td>Nevada</td>
<td>36.20</td>
<td>8</td>
<td>4.97</td>
<td>0.72</td>
<td>0.71 0.15</td>
</tr>
<tr>
<td>New Mexico</td>
<td>33.87</td>
<td>16</td>
<td>4.97</td>
<td>1.62</td>
<td>0.25 0.20</td>
</tr>
<tr>
<td>Big Bend Ranch</td>
<td>29.75</td>
<td>14</td>
<td>6.13</td>
<td>2.22</td>
<td>0.43 0.22</td>
</tr>
<tr>
<td>Queretaro</td>
<td>21.12</td>
<td>28</td>
<td>9.37</td>
<td>3.88</td>
<td>0.43 0.23</td>
</tr>
<tr>
<td>Manantlan</td>
<td>19.33</td>
<td>28</td>
<td>8.76</td>
<td>4.00</td>
<td>0.34 0.20</td>
</tr>
<tr>
<td>Ixtapan del Oro</td>
<td>19.25</td>
<td>25</td>
<td>9.37</td>
<td>2.71</td>
<td>0.34 0.12</td>
</tr>
<tr>
<td>Los Tuxtlas</td>
<td>18.42</td>
<td>35</td>
<td>11.42</td>
<td>4.92</td>
<td>0.59 0.22</td>
</tr>
<tr>
<td>Chiapas</td>
<td>16.10</td>
<td>50</td>
<td>10.35</td>
<td>3.26</td>
<td>0.23 0.09</td>
</tr>
<tr>
<td>Guanacaste1</td>
<td>9.47</td>
<td>36</td>
<td>12.93</td>
<td>3.85</td>
<td>0.51 0.16</td>
</tr>
<tr>
<td>Guanacaste2</td>
<td>9.47</td>
<td>27</td>
<td>10.35</td>
<td>2.82</td>
<td>0.30 0.13</td>
</tr>
<tr>
<td>Puntarenas</td>
<td>10.00</td>
<td>24</td>
<td>8.29</td>
<td>3.20</td>
<td>0.62 0.13</td>
</tr>
<tr>
<td>Heredia</td>
<td>10.50</td>
<td>57</td>
<td>12.93</td>
<td>3.30</td>
<td>0.35 0.09</td>
</tr>
<tr>
<td>Sherman</td>
<td>9.33</td>
<td>31</td>
<td>10.20</td>
<td>2.82</td>
<td>0.30 0.14</td>
</tr>
<tr>
<td>Rodman</td>
<td>8.95</td>
<td>28</td>
<td>11.47</td>
<td>2.82</td>
<td>0.49 0.15</td>
</tr>
<tr>
<td>BCI</td>
<td>9.17</td>
<td>39</td>
<td>12.11</td>
<td>3.50</td>
<td>0.42 0.18</td>
</tr>
<tr>
<td>Paracou</td>
<td>5.27</td>
<td>78</td>
<td>12.93</td>
<td>3.98</td>
<td>0.27 0.10</td>
</tr>
<tr>
<td>Zabelitas</td>
<td>4.00</td>
<td>35</td>
<td>11.02</td>
<td>3.58</td>
<td>0.36 0.18</td>
</tr>
</tbody>
</table>
Table 4.2 Continued

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude</th>
<th>Species</th>
<th>Range</th>
<th>STD</th>
<th>Nearest-Neighbor</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Richness</td>
<td>Size</td>
<td>Shape</td>
<td>Size</td>
</tr>
<tr>
<td>Macarena</td>
<td>3.25</td>
<td>39</td>
<td>10.20</td>
<td>2.37</td>
<td>0.32</td>
</tr>
<tr>
<td>Pance</td>
<td>3.00</td>
<td>17</td>
<td>6.69</td>
<td>2.26</td>
<td>0.41</td>
</tr>
<tr>
<td>Hormiguero</td>
<td>3.00</td>
<td>14</td>
<td>9.55</td>
<td>2.12</td>
<td>0.56</td>
</tr>
<tr>
<td>Manaus</td>
<td>3.00</td>
<td>52</td>
<td>12.93</td>
<td>3.98</td>
<td>0.35</td>
</tr>
<tr>
<td>Edaphic Cerrado</td>
<td>7.23</td>
<td>25</td>
<td>9.68</td>
<td>3.13</td>
<td>0.40</td>
</tr>
<tr>
<td>Caatingas</td>
<td>7.58</td>
<td>34</td>
<td>10.82</td>
<td>3.49</td>
<td>0.35</td>
</tr>
<tr>
<td>Linhares</td>
<td>19.01</td>
<td>37</td>
<td>11.02</td>
<td>3.29</td>
<td>0.35</td>
</tr>
<tr>
<td>Panga</td>
<td>19.25</td>
<td>17</td>
<td>8.46</td>
<td>2.63</td>
<td>0.40</td>
</tr>
<tr>
<td>Minas Gerais</td>
<td>19.83</td>
<td>20</td>
<td>8.08</td>
<td>3.63</td>
<td>0.35</td>
</tr>
<tr>
<td>Peru</td>
<td>4.92</td>
<td>59</td>
<td>12.73</td>
<td>3.39</td>
<td>0.32</td>
</tr>
<tr>
<td>Maru</td>
<td>11.93</td>
<td>50</td>
<td>11.02</td>
<td>3.98</td>
<td>0.24</td>
</tr>
<tr>
<td>Mbaracayu</td>
<td>24.12</td>
<td>15</td>
<td>8.58</td>
<td>2.37</td>
<td>0.62</td>
</tr>
<tr>
<td>Rio Verde</td>
<td>23.49</td>
<td>29</td>
<td>8.58</td>
<td>2.37</td>
<td>0.31</td>
</tr>
<tr>
<td>Mean</td>
<td>15.58</td>
<td>30.78</td>
<td>9.52</td>
<td>2.96</td>
<td>0.39</td>
</tr>
<tr>
<td>STD</td>
<td>10.98</td>
<td>16.36</td>
<td>2.56</td>
<td>0.88</td>
<td>0.12</td>
</tr>
<tr>
<td>CV</td>
<td>70.48</td>
<td>53.16</td>
<td>26.91</td>
<td>29.65</td>
<td>30.96</td>
</tr>
<tr>
<td>Independent Variable</td>
<td>Morphological Axis</td>
<td>Measure of Diversity</td>
<td>b₀</td>
<td>b₁</td>
<td>b₂</td>
</tr>
<tr>
<td>----------------------</td>
<td>--------------------</td>
<td>----------------------</td>
<td>-----</td>
<td>-------</td>
<td>-------</td>
</tr>
<tr>
<td><strong>Richness</strong></td>
<td>Size</td>
<td>Range</td>
<td>9.519</td>
<td>0.129</td>
<td>-0.003</td>
</tr>
<tr>
<td></td>
<td></td>
<td>STD</td>
<td>0.393</td>
<td>-0.003</td>
<td>-0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nearest-Neighbor</td>
<td>0.244</td>
<td>-0.004</td>
<td>-0.001</td>
</tr>
<tr>
<td><strong>Richness</strong></td>
<td>Shape</td>
<td>Range</td>
<td>2.956</td>
<td>0.037</td>
<td>-0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>STD</td>
<td>0.160</td>
<td>-0.002</td>
<td>-0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nearest-Neighbor</td>
<td>0.079</td>
<td>-0.001</td>
<td>-0.000</td>
</tr>
<tr>
<td><strong>Latitude</strong></td>
<td>Size</td>
<td>Range</td>
<td>9.519</td>
<td>-0.183</td>
<td>-0.006</td>
</tr>
<tr>
<td></td>
<td></td>
<td>STD</td>
<td>0.393</td>
<td>0.001</td>
<td>-0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nearest-Neighbor</td>
<td>0.244</td>
<td>0.004</td>
<td>-0.001</td>
</tr>
<tr>
<td><strong>Latitude</strong></td>
<td>Shape</td>
<td>Range</td>
<td>2.956</td>
<td>-0.047</td>
<td>-0.003</td>
</tr>
<tr>
<td></td>
<td></td>
<td>STD</td>
<td>0.160</td>
<td>0.002</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nearest-Neighbor</td>
<td>0.078</td>
<td>0.001</td>
<td>-0.000</td>
</tr>
</tbody>
</table>

Table 4.3. Results from regression analyses estimating relationships of local phenetic diversity with species richness and latitude. b₀, b₁, and b₂ correspond to regression coefficients. r-square refers to the coefficient of determination for the simple linear component of a particular model, whereas R-square refers to the non-linear component of the model. P correspond to the p-value associated with a particular parameter estimate. Measures of diversity that are bold-faced exhibit significant relationships after maintaining experiment-wise error rate at 5 percent using a Bonferroni sequential adjustment (Rice 1989).
Table 4.4. Comparisons of aspects of phenetic diversity among tropical, subtropical, and temperate zones (Figure 1). Means for latitudinal zones that share an alphabetic subscript are statistically indistinguishable (Student-Newman-Keuls tests, comparison-wise error rate held constant at five percent).

<table>
<thead>
<tr>
<th>Axis</th>
<th>Measure of Phenetic Diversity</th>
<th>ANOVA</th>
<th>Means</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Size</td>
<td>Range</td>
<td>21.23</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td>STD</td>
<td>0.260</td>
<td>0.773</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nearest Neighbor Distance</td>
<td>Range</td>
<td>2.44</td>
<td>0.105</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shape</td>
<td>Range</td>
<td>18.24</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>STD</td>
<td>1.42</td>
<td>0.259</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nearest-Neighbor Distance</td>
<td>Range</td>
<td>2.64</td>
<td>0.088</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 4.5. Results from simulation analyses determining the degree to which latitudinal gradients in phenetic diversity could be produced by the empirical latitudinal gradient in species richness. Pools for the New World involved simulations in which all continental New World bat species formed the group from which each community was assembled randomly. Regional pools involved only those species whose geographic distribution overlapped each community. $b_0$, $b_1$, and $b_2$ refer to parameter estimates generated from 1000 simulated latitudinal gradients. Corresponding P-values indicate the probability that a parameter estimate characterizing the actual community came from the random distribution generated from simulation. Bold values indicate significance after a Bonferroni sequential adjustment (see text, Rice 1989) in which experiment-wise error rate was equal to 5 percent.

<table>
<thead>
<tr>
<th>Pool</th>
<th>Morphological Axis</th>
<th>Measure of Diversity</th>
<th>$b_0$ Mean</th>
<th>$b_0$ P</th>
<th>$b_1$ Mean</th>
<th>$b_1$ P</th>
<th>$b_2$ Mean</th>
<th>$b_2$ P</th>
<th>CD Mean</th>
<th>CD P</th>
</tr>
</thead>
<tbody>
<tr>
<td>New World</td>
<td>Size</td>
<td>Range</td>
<td>9.146</td>
<td>0.178</td>
<td>-0.071</td>
<td>&lt; 0.001</td>
<td>-0.003</td>
<td>0.284</td>
<td>0.174</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>STD</td>
<td>3.258</td>
<td>0.030</td>
<td>-0.002</td>
<td>0.012</td>
<td>-0.001</td>
<td>0.496</td>
<td>0.042</td>
<td>0.020</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nearest-Neighbor</td>
<td>0.260</td>
<td>0.358</td>
<td>0.010</td>
<td>0.030</td>
<td>0.001</td>
<td>0.324</td>
<td>0.520</td>
<td>0.086</td>
</tr>
<tr>
<td>New World</td>
<td>Shape</td>
<td>Range</td>
<td>3.341</td>
<td>0.006</td>
<td>-0.034</td>
<td>0.310</td>
<td>-0.001</td>
<td>0.066</td>
<td>0.174</td>
<td>0.014</td>
</tr>
<tr>
<td></td>
<td></td>
<td>STD</td>
<td>1.059</td>
<td>&lt; 0.001</td>
<td>-0.001</td>
<td>&lt; 0.001</td>
<td>-0.001</td>
<td>0.022</td>
<td>0.058</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nearest-Neighbor</td>
<td>0.098</td>
<td>0.010</td>
<td>0.003</td>
<td>0.036</td>
<td>-0.001</td>
<td>0.060</td>
<td>0.406</td>
<td>0.084</td>
</tr>
<tr>
<td>Region</td>
<td>Size</td>
<td>Range</td>
<td>9.383</td>
<td>0.588</td>
<td>-0.129</td>
<td>0.030</td>
<td>-0.005</td>
<td>0.672</td>
<td>0.437</td>
<td>0.030</td>
</tr>
<tr>
<td></td>
<td></td>
<td>STD</td>
<td>3.224</td>
<td>0.010</td>
<td>-0.021</td>
<td>0.210</td>
<td>-0.002</td>
<td>0.412</td>
<td>0.232</td>
<td>0.452</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nearest-Neighbor</td>
<td>0.256</td>
<td>0.458</td>
<td>0.007</td>
<td>0.326</td>
<td>-0.001</td>
<td>0.938</td>
<td>0.283</td>
<td>0.518</td>
</tr>
<tr>
<td>Region</td>
<td>Shape</td>
<td>Range</td>
<td>3.041</td>
<td>0.366</td>
<td>-0.039</td>
<td>0.388</td>
<td>-0.002</td>
<td>0.200</td>
<td>0.358</td>
<td>0.086</td>
</tr>
<tr>
<td></td>
<td></td>
<td>STD</td>
<td>0.947</td>
<td>0.014</td>
<td>-0.006</td>
<td>&lt; 0.001</td>
<td>-0.001</td>
<td>0.646</td>
<td>0.181</td>
<td>0.004</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Nearest-Neighbor</td>
<td>0.084</td>
<td>0.340</td>
<td>0.002</td>
<td>0.014</td>
<td>-0.001</td>
<td>0.316</td>
<td>0.216</td>
<td>0.320</td>
</tr>
</tbody>
</table>
Figure 4.1. Location of 32 New World bat communities (solid dots) used to evaluate geographic patterns of diversity. The letters a, b, and c denote temperate, subtropical and tropical latitudinal zones, respectively.
Figure 4.2. Diagramatic representation of variation in phenetic diversity. A through D represent the dispersion of species (grey dots) in four different communities on a hypothetical phenetic axis. Range refers to the amount of space on a phenetic axis that is represented by species in a local community. STD represents the standard deviation of segment lengths of a minimum spanning-tree connecting all species in a community. NND represents the average nearest-neighbor distance and is a measure of the degree of species packing or crowding in phenetic space. Numbers next to Range, STD or NND correspond to their rank value for the four communities. Low values represent high phenetic diversity. When species comprise a relatively small space (A) or are unevenly distributed in phenetic space (B) they exhibit low phenetic diversity. When species are more evenly distributed within a large space (C and D), they exhibit high phenetic diversity.
Figure 4.3. Correlogram depicting the magnitude and direction of correlations of the original morphological variables with the first two axes from principal components analysis. Black arrows represent dental attributes (breadth across upper molars [BUM] and length of maxillary tooththrow [LMT]). Grey arrows represent cranial attributes (width of post-orbital constriction [POC], breadth of braincase [BOB], greatest length of skull [GLS], and condylobasal length [CBL]). The hatched arrow represents forearm length (FA).
Figure 4.4. Relationships between aspects of phenetic diversity and species richness. Range refers to the range of species. STD refers to the standard deviation of minimum spanning-tree segment lengths connecting species. Solid lines indicate situations in which variation in species richness of communities accounted for a significant amount of the variation in a measure of phenetic diversity and was determined by orthogonal polynomial regression analysis. Experiment-wise error rate was held constant at five percent for measures of size separately from measures of shape by imposing a Bonferroni sequential adjustment (Rice 1989).
Figure 4.5. Latitudinal gradients in phenetic diversity with regard to both size (left column) and shape (right column). Range refers to the range of species. STD refers to the standard deviation of minimum spanning-tree segment lengths connecting species. Solid lines indicate situations in which variation in latitude accounted for a significant amount of the variation in a particular measure of phenetic diversity and was determined by orthogonal polynomial regression analysis. Experiment-wise error rate was held constant at five percent for measures of size separately from measures of shape by imposing a Bonferroni sequential adjustment (Rice 1989).
Figure 4.6. Latitudinal gradients in phenetic diversity of terrestrial mammals (redrawn from Shepherd 1998). The volume assumed by species on the both the size and shape axes was estimated by the average distance among all species within a community and is denoted by Average Distance. The level of species packing was estimated by average nearest-neighbor distance.
CHAPTER V
INTERACTIONS AMONG TAXONOMIC,
FUNCTIONAL, AND PHENETIC COMPONENTS OF
BIODIVERSITY AND THE CORRESPONDENCE OF
THEIR LATITUDINAL GRADIENTS

Abstract
I explored the associations among taxonomic, functional, and phenetic components of biodiversity in New World bat communities and compared the strength of their latitudinal gradients. Components of taxonomic and functional diversity were estimated using indices of richness, diversity, evenness, and dominance. Phenetic diversity was characterized by the size of the morphological volume as well as the variability of phenotypes within that volume. Components of biodiversity were related strongly. Taxonomic and phenetic diversity exhibited the strongest relationships with each other, whereas taxonomic and functional diversity exhibited the weakest relationships. Moreover, phenetic diversity exhibited a significantly stronger latitudinal gradient than did either taxonomic or functional diversity, which exhibited statistically indistinguishable latitudinal gradients. The strong latitudinal gradient in phenetic diversity is likely enhanced by the synergistic effects of variation in both taxonomic and functional diversity on phenetic diversity. Nonetheless, variation in these three components of biodiversity is not coincident. While much variation in overall biodiversity may be captured by the examination of single components, future
conservation efforts should embrace its multifaceted nature. In particular, they should explicitly incorporate them into contemporary conservation strategies in order to enhance the likelihood of conserving all forms of the earth's biological capital.

Introduction

Worldwide, interest in environmental issues has proliferated at an amplified rate in the final decade of the twentieth century. The view that human activities are driving erosion of the world's biological capital and are increasingly endangering the current sustainability of the biosphere has been the primary impetus behind this interest (Heywood and Watson 1995). Nonetheless, our current understanding of the richness and complexity of life is superficial, thereby limiting efforts to set and implement strategies of management, conservation, and restoration of the world's biota (Heywood and Watson 1995).

Although "biodiversity" has been used regularly and often since its inception more than twenty years ago (Swingland 2001), its definitions are quite variable. This in part stems from its similarity to "diversity," which historically has referred to the richness and evenness of species (Pielou 1975, Magurran 1988, Cornell 2001). Often used as a synonym of diversity, biodiversity has developed into a concept that embraces multiple forms of biological variation such as those involving genetic differentiation and biotic interactions within communities, as well as production, nutrient cycling, decomposition, and energy flow within ecosystems (Tilman 2001). Currently, biodiversity may be defined as the totality of variation in living things, and refers to variation with respect to
taxonomic diversity, all of the phenotypic and genetic variation that species possess, as well as all of the variation among the communities and ecosystems that they form (Tilman 2001).

Indeed, such a broad definition has compromised the tangibility of the concept and made the very measurement of biodiversity problematic. In fact, due to the multifaceted nature of biodiversity, it may not be readily measurable given our current understanding and technological abilities (Swingland 2001). At present, the best understanding of the concept may come from the decomposition of biodiversity into its more measurable components and to comparatively evaluate patterns based on the similarities and differences among them (Swingland 2001). Understanding the degree to which various components are related to each other, as well as how similarly they exhibit variation across environmental gradients remains a significant challenge to contemporary biology.

Components of Biodiversity

Historically, ecologists and biogeographers alike have evaluated variation in a number of individual components of biodiversity along environmental gradients. In particular, these include components of taxonomic, phenetic, genetic, functional, phylogenetic, and interaction diversity. In this chapter, I will focus on components of taxonomic, functional, and phenetic diversity. Taxonomic diversity reflects the number of species as well as the distribution of abundances among species in local communities or assemblages, and its measurement has been addressed comprehensively by Peet
(1974), Magurran (1988), Smith and Wilson (1996), Hubalek (2000), and Stevens and Willig (2002). Functional Diversity represents the variety of ways that species perform ecological functions within a community. Function refers to the ecological processes associated with living organisms (Noss 1990, Martinez 1996). Moreover, the variety of ways that species of a particular taxon perform trophic functions (e.g., transfer of energy, nutrient cycling, seed dissemination, flower pollination, control of insect populations) can be used to characterize patterns of functional diversity among communities. Phenetic diversity measures phenotypic dispersion within a community. Investigation of patterns regarding morphological attributes may provide unique insights not captured by functional or taxonomic diversity. As with measures of functional diversity, patterns of phenetic diversity are sensitive to changes in the number of species in an assemblage.

Nonetheless, phenetic approaches differentially weight the contribution of species to biodiversity by considering their phenotypic attributes and consequently integrate rich information regarding the systematic, ecological, and functional attributes of species that may be highly informative when comparing communities across extensive environmental gradients (Wainwright and Rielly 1994).

As with all components of biodiversity, taxonomic, functional, and phenetic diversity can be characterized by a number of descriptors. Components of taxonomic and functional diversity include measures of richness, evenness, diversity and dominance. The phenetic component of biodiversity is described by a number of measures that reflect the size of and the dispersion of species within morphological space. A number of measures characterizing each of these three components of biodiversity are related
significantly to latitude (see previous chapters). Herein, I more precisely define the latitudinal gradient in each component of biodiversity (i.e., that combination of variables comprising a particular component of biodiversity that is most correlated with latitude), as well as determine whether significant differences exist in the degree to which components are related to latitude. Finally, I will investigate the associations among taxonomic, functional, and phenetic components of biodiversity by determining the interrelationships of the various indices that characterize them.

Materials and Methods

Data on the species composition of 32 New World bat communities (Figure 5.1, Table 5.1) come from the literature (see Stevens and Willig 2002, Chapters II, III, and IV).

Components of Biodiversity

Taxonomic Diversity. Four measures of diversity were calculated using a program written in Matlab (The Math Works 1995). These measures reflect species richness, evenness, dominance, and diversity. Species richness was estimated by the number of species sampled from a particular community. The equability of species abundances (evenness) was estimated using the Camargo index (CE, Camargo 1993). Simultaneous variation in richness and evenness was estimated by Shannon's diversity index (SHD, Pielou 1975). Finally, the degree to which community composition was dominated by the most abundant species (dominance) was estimated using the Berger-Parker index (BP,
Berger and Parker 1970). Following Magurran (1988), BP was scaled so that a large index represents low dominance and high diversity.

**Functional Diversity.** Feeding guilds represent discrete trophic strategies that reflect a variety of ecosystem functions. I identified species of bats to one of seven functional groups (e.g., aerial insectivorans, frugivores, gleaning animalivorans, high-flying insectivorans, nectarivorans, piscivorans, sanguinivorans) that represent distinct foraging strategies (sensu Stevens and Willig 1999, 2001).

The number of functional groups and their relative contribution to total species richness (i.e., proportional species richness) can be used to estimate the functional diversity of a particular community. The richness of functional groups represents the number of functional groups in a local community. The diversity of functional groups reflects the number of groups and equability of the number of species among groups, and was quantified using the Shannon’s index (Pielou 1975). The evenness of functional groups reflects equability in the distribution of species among functional groups and was calculated using the Camargo evenness index (Camargo 1993). The dominance of functional groups describes the degree to which the most species-rich functional group dominates the composition of a community in terms of species richness; it was quantified using the Berger-Parker index (Berger and Parker 1970). Following Magurran (1988), dominance was scaled so that a large index represents low dominance and high diversity.

**Phenetic Diversity.** For each species, I obtained measurements for seven morphological characteristics. These characteristics reflect variation in body-size (i.e., forearm length and greatest length of skull), as well as the geometry of the cranium and
associated trophic structures (i.e., greatest length of skull, condylobasal length, length of 
maxillary toothrow, breadth across upper molars, width across post-orbital constriction, 
breadth of braincase). In most cases, means were determined from at least four males 
and four females of each species. For most members of the family Phyllostomidae, these 
measures came from Swanepoel and Genoways (1979). For other taxa, measures either 
came directly from the description of the actual community, other literature sources, or 
from museum specimens. Morphological variables were log-transformed prior to 
analyses to enhance the matching of assumptions of multivariate analyses (Marcus 1990).

I used principal components analysis (PCA) to create composite morphological 
axes that reflected the salient features of body-size and shape variation in New World 
bats. PCA is a multivariate technique that creates sets of linear combinations (loadings) 
of the original variables that define orthogonal axes in multivariate space that maximally 
account for variation among observations (Manley 1986). Correlation analyses were 
used to interpret principal components (PCs). Morphological measures with high 
correlations to a particular PC reflect the type of variation accounted for by that derived 
axis. Principal components based on morphological data that have loadings that are all 
positive and relatively uniform in magnitude reflect variation in body size, whereas PCs 
with loadings that are variable in magnitude and sign represent morphological tradeoffs 
characteristic of shape variation (Marcus 1990, Klingenberg 1996). Only the first two 
PCs were retained in analyses of phenetic diversity. In this particular investigation, these 
two components characterized the major axes of size and shape in continental New 
World bats.
The phenetic diversity of species within communities was estimated in six ways. The range of species scores on either PC1 or PC2 described the amount of morphological variation assumed by species in a community. The standard deviation of minimum spanning-tree segment lengths between all species in a community on either PC1 or PC2 described the regularity of species dispersion. Finally, the average of the euclidean distance between each species and its nearest morphological neighbor was used as a measure of "species packing" or the degree of crowding in morphological space (Findley 1976, Ricklefs and Travis 1980, Schum 1984, Shepherd 1998).

Relationships between Components of Biodiversity

I used canonical correlation analysis (CCA) to describe the magnitude of correlation between components of biodiversity. CCA is a multivariate technique that selects a series (either equal to the number of variables or equal to the number of observations, whichever is smaller) of sets of linear combinations (canonical variates) of the original variables characterizing two data sets that are maximally correlated with each other (Digby and Kempton 1987). Each series is orthogonal to all others, and as a result, the first canonical correlation is of the highest magnitude and all subsequent canonical correlations are of decreasingly lower magnitude. Correlations of the original variables back to the canonical variates (loadings) can be used to interpret canonical correlations (CCs). Variables with high loadings on a particular canonical variate contribute relatively more to the identity of that canonical variate compared to variables with low loadings.
The interpretation of significance of CCs is not as straightforward as with simple correlations (Tabachnick and Fidell 1996). The degree of correlation between components of biodiversity, the number of variables comprising each component, and the number of variables relative to the number of observations in each matrix affect the magnitude of CCs. Components of biodiversity that include more variables will yield higher CCs than will components with fewer variables because there are more ways to combine variables and achieve a high correlation. As the number of variables approaches the number of observations, the number of possible solutions to derive the CC is constrained, thereby inflating the magnitude of CCs.

Although the behavior of CCs complicates the interpretation of their magnitude, this can be alleviated with randomization. I compared each CC to a distribution of simulated CCs that were produced after randomizing data matrices characterizing components of biodiversity. To produce a simulated CC, the order of the rows of each (two) data matrix was randomized, a CCA was performed, and the resultant CCs were quantified. This was done one thousand times to yield a random distribution of correlation coefficients. The actual canonical correlation coefficients were then compared to corresponding random distributions. If the actual canonical correlation coefficient was greater than alpha percent of the distribution, I concluded that it was significantly different from a population where the canonical correlation is zero.

I conducted three canonical correlation analyses (i.e., taxonomic diversity and functional diversity, taxonomic diversity and phenetic diversity, functional diversity and phenetic diversity). I held experiment wise error rate at five percent by adjusting alpha
via a Bonferroni sequential adjustment (Rice 1989). In this particular suite of analyses, the Iowa community was an outlying observation when CCA was performed on taxonomic and functional components of biodiversity. Although the low diversity of the Iowa community is biologically real, its inclusion could have created a situation in which canonical variates primarily represented a polarization between the Iowa community and all other communities. For this reason, two sets of analyses were performed, one including and one excluding the Iowa community.

Characterization of Latitudinal Gradients

Because CCA constructs a linear combination of one set of data that is maximally correlated with a linear combination of a second set of data, it is ideally suited to define latitudinal gradients in the different components of biodiversity. Thus, CCA can be used to define the linear combination of indices for a particular component of biodiversity that is maximally correlated with latitude. The magnitude of the CC coefficient defines the degree to which latitude affects a particular component of biodiversity. Randomization was performed to facilitate interpretation of the significance of canonical correlations. Experiment-wise error rate was maintained at five percent by adjusting alpha according to a Bonferroni sequential adjustment (Rice 1989).

Differences in the Strength of Latitudinal Gradients Among Components of Biodiversity

Differences among components of biodiversity regarding the magnitude of their association with latitude were evaluated by another randomization technique.
Components of biodiversity characterized by a larger number of indices will naturally exhibit stronger latitudinal gradients than those characterized by a smaller number of indices when evaluated using CCA. Thus, I determined differences regarding latitudinal gradients by comparing distributions of canonical correlations that were derived from each component of biodiversity using the same number of indices. In the original data, functional and taxonomic components of diversity were each characterized by four indices, whereas phenetic diversity was characterized by six indices. In order to calculate canonical correlations between phenetic diversity and latitude using the same number of indices as those involving taxonomic and functional diversity, I randomly selected a subset of four of the indices of phenetic diversity. I then independently bootstrapped all three components of biodiversity, conducted a CCA between a component of biodiversity and latitude, and saved the canonical correlation coefficient. This process was done 1000 times to yield three distributions of canonical correlation coefficients. The distribution for each component of biodiversity characterizes the sampling error inherent to that particular latitudinal gradients and can be used to evaluate significant differences among components of biodiversity regarding their latitudinal gradients. To enhance the normality of distributions of canonical correlations, I conducted a z-transformation (Sokal and Rohlf 1995). Then, I calculated pair-wise studentized t-values (Sokal and Rohlf 1995) between pairs of distributions, and used t-tests (Sokal and Rohlf 1995) with 62 degrees of freedom each to determine the significance of pair-wise differences.
Results

Relationships between Components of Biodiversity

Significant canonical correlations existed between components of biodiversity in all three analyses: (1) taxonomic and phenetic diversity, (2) taxonomic and functional diversity, and (3) functional and phenetic diversity (Table 5.2). Moreover, analyses that excluded and included the Iowa community were similar. Significant canonical correlations ranged from 0.98 between taxonomic and phenetic components to 0.48 between functional and phenetic components of biodiversity.

**Taxonomic versus Functional Diversity.** A single significant canonical correlation existed between taxonomic and functional components of biodiversity ($r = 0.80$). Based on correlations of the original variables to the canonical axes (Figure 5.2), this canonical correlation primarily reflects variation in the richness and diversity of species as well as the richness, diversity, and dominance of functional groups. Measures of evenness were not highly correlated with either canonical axes.

**Taxonomic versus Phenetic Diversity.** A single significant CC existed between taxonomic and phenetic diversity ($r = 0.98$). Inspection of variable loadings indicated that measures of species richness and diversity exhibited the highest correlations with the first canonical axis of taxonomic diversity (Figure 5.3). The range of species on both the size and shape axes were correlated most highly, average nearest-neighbor distances intermediately, and measures of the variability minimum spanning tree segment lengths least highly with the first canonical axis of phenetic diversity (Figure 5.3). Thus, changes
in species richness and species diversity are primarily associated with changes in the size of phenetic space, but also influence the dispersion of species within that space but to a lesser degree.

**Functional versus Phenetic Diversity.** The three significant canonical correlations between functional and phenetic diversity ranged from 0.48 to 0.88 (Table 5.2). The first canonical axis of functional diversity was most highly correlated with the richness, diversity, and dominance of functional groups, whereas the first canonical axis of phenetic diversity was moderately to highly correlated with all measures of phenetic diversity (Figure 5.4). Measures of the size of the morphological axis were correlated positively whereas measures of the variability of minimum spanning-tree segment lengths and nearest-neighbor distances were correlated negatively with the first canonical axis of phenetic diversity. Thus, increases in the richness, diversity, and dominance of functional groups correspond to changes in phenetic diversity via increases in the size of the phenetic space as well as by decreases in the variability of species and the degree of species packing.

Although the second canonical correlation between functional and morphological components of biodiversity was significant, it was only moderate in magnitude ($r = 0.51$). Moreover, correlations of the original variables with the canonical axes were low and not easily interpretable (Figure 5.5). The second canonical axis of functional diversity was correlated most highly with the evenness of functional groups but this was not consistent across analyses that included the Iowa community and those that did not. The second canonical axis of phenetic diversity was consistently correlated most highly and
positively with the variability of species on the shape axis as well as positively with the magnitude of nearest-neighbor distances on both the size and the shape axis. High variability of species with respect to shape possibly reflects the clumped nature of species on the shape axis when species are evenly distributed among functional groups. When this transpires, distances among functional groups should be greater than the distances among species within groups, and the mix of small and large distances will produce greater variance along the shape axis. Thus, the third canonical correlation possibly reflects the effects of increases in functional evenness on the distribution of species in morphological space.

The third canonical correlation between functional and phenetic diversity was significant but low in magnitude ($r \sim 0.39$). Again, interpretation was difficult and tentative due to low correlations of the original variables with the canonical axes. The evenness and dominance of functional groups exhibited the highest correlations with the third canonical axis of functional diversity. Moreover, the mean nearest-neighbor distances on the size axis and the variability of species on the shape axis exhibited the greatest correlations with the third canonical axis of phenetic diversity (Figure 5.6). The correlation of these variables was low and different depending on the inclusion of the Iowa community. Nonetheless, the third canonical correlation characterizes changes on the size axis that are due to changes in the equability of species within functional groups.
Characterization of Latitudinal Gradients

Canonical correlations between latitude and taxonomic, functional and phenetic components of biodiversity were 0.68, 0.72, and 0.83, respectively (Table 5.3). All three latitudinal gradients were highly significant. Latitudinal gradients in taxonomic and functional diversity primarily involved indices of richness and diversity, and to a lesser degree measures of dominance and evenness (Figure 5.7). Latitude was most highly correlated to measures of phenetic diversity that involved the range of species and only moderately correlated with variability on the size and shape axes and nearest-neighbor distances (Figure 5.7).

Differences in the Strength of Latitudinal Gradients among Components of Biodiversity

The central tendency of canonical correlations between latitude and taxonomic, functional, and morphological components of biodiversity produced by bootstrapping were left skewed and moderate to high in magnitude (Figure 5.8). Z-transformations yielded distributions that were more symmetrical and better suited for parametric analyses of significant differences (Figure 5.8). t-tests indicated that significant pair-wise differences in the magnitude of canonical correlations exist between taxonomic and phenetic diversity as well as between functional and phenetic diversity, but no significant difference existed between taxonomic and functional diversity (Table 5.4). Phenetic diversity exhibited the strongest latitudinal gradient, whereas functional and taxonomic
diversity exhibited weaker gradients that are statistically indistinguishable from each other.

Discussion

Taxonomic, functional, and phenetic components of biodiversity are clearly related in New World bat communities. Functional and taxonomic components are associated primarily because increases in species richness involve increases in community complexity derived from simultaneous increases in the number of species per functional groups as well as the number of functional groups. The morphological volume occupied by bats concomitantly increases as a consequence of increases in species and functional richness. Indeed, all components of biodiversity exhibited qualitatively similar latitudinal gradients in which diversity increases toward the equator. Nonetheless, the degree to which phenetic diversity is related to latitude is significantly greater than that of either taxonomic or functional components of biodiversity. This suggests that variation in biodiversity of New World bat communities is complex and the consequence of the interaction of a number of distinct components.

Not only is spatial variation in evenness of functional groups and species independent of latitude, but spatial variation in evenness of these two units exhibited no covariation either. As a consequence, measures of evenness at one level of biological organization may provide little information regarding the magnitude of evenness at other levels of organization. The lack of a relationship between the evenness of species and the evenness of functional groups likely has to do with a lack of correspondence in the
community attributes they characterize. Changes in species evenness involve variation in the number of individuals per species and likely coincides with changes in the abundance of resources within particular resource classes (i.e., fruit, fish, grasses, etc.; Pielou 1975). In contrast, changes in the evenness of functional groups involves variation in the number of species allocated to functional groups that coincides with the number of resource classes and the abundance of resources within those classes. To this end, evenness of species and the evenness of functional groups may respond to quite different environmental gradients or at least respond to similar gradients in quite different ways.

The greatest association between taxonomic and functional components of biodiversity involved indices that are sensitive to changes in richness. This suggests that environmental gradients underlying the spatial distribution of these communities are primarily ones that affect the number and kinds of species within communities. Latitudinal changes in the number and kinds of species inhabiting communities may be particularly related to the nonrandom distribution of higher taxonomic categories of New World bats, especially the geographic distributions of the subfamilies of the Phyllostomidae. These subfamilies have a strong correspondence to the functional groupings used in this study. Moreover, these subfamilies have distinct biogeographic termini (Willig and Sandlin 1991) as well as exhibit increases in species richness from their termini to the equator. Similarly, the other 8 families of New World bats also exhibit distinctive latitudinal termini and increases in species richness toward the equator within their biogeographic range (Willig and Selcer 1989). The distinct latitudinal gradient of all of these New World groups of bats facilitates a latitudinal gradient in the
complexity of communities derived from increases in the number of functional roles that bats employ as well as the proliferation of species within each functional group.

The biogeographic radiation of families and subfamilies of New World bats also can explain what happens to phenetic diversity and explains why taxonomic and functional diversity were related to phenetic diversity in similar ways. Variation in phenetic diversity primarily was related to aspects of the richness of species and the richness of functional groups. Radiations of the families and subfamilies of New World bats causes an empirical increase in species richness with latitude. This coincides with an increase in the number of functional groups as well as the number of species per functional group. This in turn expands the morphological volume by increasing the range while decreasing average nearest-neighbor distances and variability of phenotypes. Thus, decreases in latitude involve not only nonrandom variation in species richness, but also nonrandom variation in species composition associated with variation in functional diversity. This in turn drives latitudinal gradients in phenetic diversity.

Gradients in taxonomic and functional components of biodiversity likely contribute substantially to much of the variation in phenetic diversity. Although each component affects phenetic diversity in a similar way, cumulative effects likely are positive and synergistic. Because form and function are related strongly regarding New World bats (Stevens and Willig 1999), changes in the functional composition of species within communities enhance variation in phenetic diversity. Nonetheless, all functional groups are present at relatively high latitudes in the sub tropics and further increases toward the equator in phenetic diversity due to increases in the number of functional
groups are not possible. Nonetheless, increases in species richness within functional
groups allow further increases in phenetic diversity towards the equator and provide for a
stronger gradient in phenetic diversity than would be possible by increases solely in the
number of functional groups or the number of species regardless of their functional role.
Consequently, gradients of phenetic diversity may represent an emergent property
resulting from the positively synergistic influences of variation in taxonomic and
functional diversity. This also explains why latitudinal gradients in phenetic diversity are
significantly stronger than either gradients of taxonomic or functional diversity alone.

Indeed, variation in biodiversity in the New World is complex and multifaceted.
Although the three components that I examined exhibited qualitatively similar spatial
variation in North and South America, there variation was not coincident. Thus, from a
conservation perspective, aiming efforts at maximizing a single component of
biodiversity across a number of sites cannot ensure the simultaneous conservation of
other components of biodiversity. Conserving the world’s biota is not only complicated
by the variable costs (money or space) associated with conservation efforts, but also by
what aspects of biodiversity a particular conservation scheme is designed to protect.
Indeed, a wide variety of protocols have been developed to optimally conserve
biodiversity given the amount of money or space that is necessary (Kershaw et al. 1995,
Nonetheless, these protocols have primarily been developed to maximize the
conservation of species richness and not other attributes of biodiversity. Nonetheless,
maximizing species richness may not maximally conserve phenotypic or functional
diversity or any other component of biodiversity. Future conservation efforts should attempt to simultaneously conserve a number of components of biodiversity in order to more comprehensively protect the world’s rich biota.
References


Yancey, F. D. 1996. The mammals of Big Bend Ranch State Park. Dissertation, Texas Tech University, Lubbock, Texas, USA.
Table 5.1. Geographic and environmental characteristics of each of 32 bat communities used to evaluate patterns of diversity in the New World.

<table>
<thead>
<tr>
<th>Community</th>
<th>Country</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Habitat</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Iowa</td>
<td>USA</td>
<td>42.3° N</td>
<td>93.0° W</td>
<td>Riparian</td>
<td>Kunz 1973</td>
</tr>
<tr>
<td>California</td>
<td>USA</td>
<td>36.5° N</td>
<td>117.3° W</td>
<td>Desert</td>
<td>Suprenant 1977</td>
</tr>
<tr>
<td>Nevada</td>
<td>USA</td>
<td>36.2° N</td>
<td>115.2° W</td>
<td>Desert</td>
<td>O’Farrell and Bradley 1970</td>
</tr>
<tr>
<td>New Mexico</td>
<td>USA</td>
<td>33.9° N</td>
<td>107.4° W</td>
<td>Desert</td>
<td>Black 1974</td>
</tr>
<tr>
<td>Big Bend Ranch</td>
<td>USA</td>
<td>29.8° N</td>
<td>103.8° W</td>
<td>Desert</td>
<td>Yancey 1996</td>
</tr>
<tr>
<td>Queretaro</td>
<td>Mexico</td>
<td>21.1° N</td>
<td>99.3° W</td>
<td>Montane Tropical Forest</td>
<td>Navarro L. and Leon-Paniagua 1995</td>
</tr>
<tr>
<td>Manantlan</td>
<td>Mexico</td>
<td>19.5° N</td>
<td>104.0° W</td>
<td>Montane Tropical Forest</td>
<td>Iniguez Davales 1993</td>
</tr>
<tr>
<td>Ixtapan del Oro</td>
<td>Mexico</td>
<td>19.3° N</td>
<td>100.2° W</td>
<td>Montane Tropical Forest</td>
<td>Alvarez and Alvarez-Castaneda 1996</td>
</tr>
<tr>
<td>Los Tuxtlas</td>
<td>Mexico</td>
<td>18.4° N</td>
<td>95.0° W</td>
<td>Wet Tropical Forest</td>
<td>Estrada et al. 1993</td>
</tr>
<tr>
<td>Chiapas</td>
<td>Mexico</td>
<td>16.1° N</td>
<td>91.0° W</td>
<td>Wet Tropical Forest</td>
<td>Medellin 1993</td>
</tr>
<tr>
<td>Guanacaste-1</td>
<td>Costa Rica</td>
<td>9.5° N</td>
<td>85.2° W</td>
<td>Wet Tropical Forest</td>
<td>LaVal and Fitch 1977</td>
</tr>
<tr>
<td>Guanacaste-2</td>
<td>Costa Rica</td>
<td>9.5° N</td>
<td>85.2° W</td>
<td>Wet Tropical Forest</td>
<td>Fleming et al. 1972</td>
</tr>
<tr>
<td>Puntarenas</td>
<td>Costa Rica</td>
<td>10.0° N</td>
<td>84.8° W</td>
<td>Montane Tropical Forest</td>
<td>LaVal and Fitch 1977</td>
</tr>
<tr>
<td>Community</td>
<td>Country</td>
<td>Latitude</td>
<td>Longitude</td>
<td>Habitat</td>
<td>Reference</td>
</tr>
<tr>
<td>------------</td>
<td>----------------</td>
<td>----------</td>
<td>-----------</td>
<td>-----------------------------</td>
<td>----------------------------</td>
</tr>
<tr>
<td>Heredia</td>
<td>Costa Rica</td>
<td>10.5°N</td>
<td>83.8°W</td>
<td>Wet Tropical Forest</td>
<td>LaVal and Fitch 1977</td>
</tr>
<tr>
<td>Sherman</td>
<td>Panama</td>
<td>9.3°N</td>
<td>80.0°W</td>
<td>Wet Tropical Forest</td>
<td>Fleming et al. 1972</td>
</tr>
<tr>
<td>Rodman</td>
<td>Panama</td>
<td>9.0°N</td>
<td>79.6°W</td>
<td>Dry Tropical Forest</td>
<td>Fleming et al. 1972</td>
</tr>
<tr>
<td>BCI</td>
<td>Panama</td>
<td>9.2°N</td>
<td>79.8°W</td>
<td>Wet Tropical Forest</td>
<td>Handley et al. 1991</td>
</tr>
<tr>
<td>Paroucou</td>
<td>French Guiana</td>
<td>5.3°N</td>
<td>52.9°W</td>
<td>Wet Tropical Forest</td>
<td>Simmons and Voss 1998</td>
</tr>
<tr>
<td>Zabelitas</td>
<td>Colombia</td>
<td>4.0°N</td>
<td>76.5°W</td>
<td>Wet Tropical Forest</td>
<td>Thomas 1972</td>
</tr>
<tr>
<td>Marcarena</td>
<td>Colombia</td>
<td>3.3°N</td>
<td>73.9°W</td>
<td>Wet Tropical Forest</td>
<td>Sanchez-Palomino et al. 1993</td>
</tr>
<tr>
<td>Panče</td>
<td>Colombia</td>
<td>3.0°N</td>
<td>76.0°W</td>
<td>Montane Tropical Forest</td>
<td>Thomas 1972</td>
</tr>
<tr>
<td>Hormiguero</td>
<td>Colombia</td>
<td>3.0°N</td>
<td>76.0°W</td>
<td>Montane Tropical Forest</td>
<td>Thomas 1972</td>
</tr>
<tr>
<td>Manaus</td>
<td>Brazil</td>
<td>3.0°S</td>
<td>60.0°W</td>
<td>Wet Tropical Forest</td>
<td>Dos Reis 1984</td>
</tr>
<tr>
<td>Edaphic Cerrado</td>
<td>Brazil</td>
<td>7.2°S</td>
<td>39.4°W Tropical Woodland-Savannah</td>
<td>Willig 1982</td>
<td></td>
</tr>
<tr>
<td>Caatinga</td>
<td>Brazil</td>
<td>7.6°S</td>
<td>39.7°W</td>
<td>Dry Tropical Forest</td>
<td>Willig 1982</td>
</tr>
<tr>
<td>Linhares</td>
<td>Brazil</td>
<td>19.0°S</td>
<td>40.3°W</td>
<td>Wet Semi-Tropical Forest</td>
<td>Peracchi and Albuquerque 1993</td>
</tr>
<tr>
<td>Panga</td>
<td>Brazil</td>
<td>19.3°S</td>
<td>48.4°W</td>
<td>Wet Semi-Tropical Forest</td>
<td>Pedro and Taddei 1997</td>
</tr>
<tr>
<td>Community</td>
<td>Country</td>
<td>Latitude</td>
<td>Longitude</td>
<td>Habitat</td>
<td>Reference</td>
</tr>
<tr>
<td>---------------</td>
<td>-----------</td>
<td>-----------</td>
<td>-----------</td>
<td>-----------------------------</td>
<td>----------------------------</td>
</tr>
<tr>
<td>Minas Gerais</td>
<td>Brazil</td>
<td>19.8° S</td>
<td>41.8° W</td>
<td>Wet Semi-Tropical Forest</td>
<td>Moura de Souza Aguiar 1994</td>
</tr>
<tr>
<td>Jeparo Herrera</td>
<td>Peru</td>
<td>4.9° S</td>
<td>73.8° W</td>
<td>Wet Tropical Forest</td>
<td>Gorchov and Ascorra in litt.</td>
</tr>
<tr>
<td>Manu</td>
<td>Peru</td>
<td>11.9° S</td>
<td>71.3° W</td>
<td>Wet Tropical Forest</td>
<td>Ascorra et al. 1996</td>
</tr>
<tr>
<td>Mbaracru</td>
<td>Paraguay</td>
<td>24.1° S</td>
<td>55.5° W</td>
<td>Wet Semi-Tropical Forest</td>
<td>Stevens and Willig in litt.</td>
</tr>
<tr>
<td>Rio Verde</td>
<td>Paraguay</td>
<td>23.5° S</td>
<td>56.1° W</td>
<td>Dry Semi-Tropical Forest</td>
<td>Stevens and Willig in litt.</td>
</tr>
</tbody>
</table>
Table 5.2. Results of canonical correlation analyses between taxonomic, functional, or phenetic components of biodiversity. "Outlier Removed" refers to analyses that excluded the Iowawa community, whereas "All Data" refers to analyses involving all communities including that from Iowawa. To maintain experiment-wise error rate at 5 percent across the three canonical correlation analyses, I adjusted comparison-wise error rate using a Bonferroni sequential adjustment (Rice 1989).

<table>
<thead>
<tr>
<th>Canonical Correlation</th>
<th>First Canonical Axis</th>
<th>Second Canonical Axis</th>
<th>r</th>
<th>P</th>
<th>r</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Taxonomic Diversity</td>
<td>Functional Diversity</td>
<td>0.802</td>
<td>0.004*</td>
<td>0.839</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td>2</td>
<td>Taxonomic Diversity</td>
<td>Functional Diversity</td>
<td>0.329</td>
<td>0.714</td>
<td>0.399</td>
<td>0.345</td>
</tr>
<tr>
<td>3</td>
<td>Taxonomic Diversity</td>
<td>Functional Diversity</td>
<td>0.161</td>
<td>0.744</td>
<td>0.300</td>
<td>0.115</td>
</tr>
<tr>
<td>4</td>
<td>Taxonomic Diversity</td>
<td>Functional Diversity</td>
<td>0.095</td>
<td>0.268</td>
<td>0.129</td>
<td>0.130</td>
</tr>
<tr>
<td>5</td>
<td>Taxonomic Diversity</td>
<td>Phenetic Diversity</td>
<td>0.976</td>
<td>&lt;0.001*</td>
<td>0.976</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td>6</td>
<td>Taxonomic Diversity</td>
<td>Phenetic Diversity</td>
<td>0.586</td>
<td>0.085</td>
<td>0.583</td>
<td>0.095</td>
</tr>
<tr>
<td>7</td>
<td>Taxonomic Diversity</td>
<td>Phenetic Diversity</td>
<td>0.432</td>
<td>0.097</td>
<td>0.467</td>
<td>0.025</td>
</tr>
<tr>
<td>8</td>
<td>Taxonomic Diversity</td>
<td>Phenetic Diversity</td>
<td>0.127</td>
<td>0.704</td>
<td>0.132</td>
<td>0.693</td>
</tr>
</tbody>
</table>
Table 5.2. Continued

<table>
<thead>
<tr>
<th>Correlation</th>
<th>First Canonical Axis</th>
<th>Second Canonical Axis</th>
<th>Outlier Removed</th>
<th>All Data</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Functional Diversity</td>
<td>Phenetic Diversity</td>
<td><em>0.881 &lt; 0.001</em></td>
<td>0.577 &lt; 0.001*</td>
</tr>
<tr>
<td>2</td>
<td>Functional Diversity</td>
<td>Phenetic Diversity</td>
<td>0.600 0.057</td>
<td>0.607 0.068</td>
</tr>
<tr>
<td>3</td>
<td>Functional Diversity</td>
<td>Phenetic Diversity</td>
<td>0.505 0.012*</td>
<td>0.504 0.015*</td>
</tr>
<tr>
<td>4</td>
<td>Functional Diversity</td>
<td>Phenetic Diversity</td>
<td><em>0.479 &lt; 0.001</em></td>
<td>0.311 0.029</td>
</tr>
</tbody>
</table>
Table 5.3. Results of canonical correlation analyses between latitude and taxonomic, functional, and phenetic components of biodiversity. $r$ refers to the canonical correlation coefficient whereas $P$ refers to the probability of a type-1 error.

<table>
<thead>
<tr>
<th>First Canonical Axis</th>
<th>Second Canonical Axis</th>
<th>$r$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Taxonomic Diversity</td>
<td>Latitude</td>
<td>0.68</td>
<td>0.002</td>
</tr>
<tr>
<td>Functional Diversity</td>
<td>Latitude</td>
<td>0.72</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Phenetic Diversity</td>
<td>Latitude</td>
<td>0.83</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Table 5.4. Results from t-tests evaluating significant differences regarding the correlation of taxonomic, functional, and taxonomic diversity with latitude. Experiment-wise error rate was held at 5 percent via a Bonferroni sequential adjustment (Rice 1989).

<table>
<thead>
<tr>
<th>Component of Biodiversity</th>
<th>Mean</th>
<th>Standard Deviation</th>
<th>T-Values</th>
<th>P-Values</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Taxonomic</td>
<td>Functional</td>
</tr>
<tr>
<td>Taxonomic</td>
<td>0.955</td>
<td>0.255</td>
<td>0</td>
<td>0.41</td>
</tr>
<tr>
<td>Functional</td>
<td>0.979</td>
<td>0.219</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Phenetic</td>
<td>1.150</td>
<td>0.316</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
Figure 5.1. Location of 32 New World bat communities (solid dots) used to evaluate geographic patterns of diversity. The letters a, b, and c denote temperate, subtropical and tropical latitudinal regions, respectively.
Figure 5.2. Correlations of original measures of taxonomic (upper) and functional (lower) diversity to the first set of canonical variates derived from canonical correlation analysis. Left column (outlier removed) refers to analyses that excluded the Iowa community whereas the right column (all sites) refers to analyses involving all 32 communities. The length of an arrow represents the magnitude of the correlation between the original variable and the canonical variate.
Figure 5.3. Correlations of original measures of taxonomic (upper) and phenetic (lower) diversity to the first set of canonical variates derived from canonical correlation analysis. Left column (outlier removed) refers to analyses that excluded the Iowa community whereas the right column (all sites) refers to analyses involving all 32 communities. The length of an arrow represents the magnitude of the correlation between the original variable and the canonical variate.
Figure 5.4. Correlations of original measures of functional (upper) and phenetic (lower) diversity to the first set of canonical variates derived from canonical correlation analysis. Left column (outlier removed) refers to analyses that excluded the Iowa community whereas the right column (all sites) refers to analyses involving all 32 communities. The length of an arrow represents the magnitude of the correlation between the original variable and the canonical variate.
Figure 5.5. Correlations of original measures of functional (upper) and phenetic (lower) diversity to the second set of canonical variates derived from canonical correlation analysis. Left column (outlier removed) refers to analyses that excluded the Iowa community whereas the right column (all sites) refers to analyses involving all 32 communities. The length of an arrow represents the magnitude of the correlation between the original variable and the canonical variate.
Figure 5.6. Correlations of original measures of functional (upper) and phenetic (lower) diversity to the third set of canonical variates derived from canonical correlation analysis. Left column (outlier removed) refers to analyses that excluded the Iowa community whereas the right column (all sites) refers to analyses involving all 32 communities. The length of an arrow represents the magnitude of the correlation between the original variable and the canonical variate.
Figure 5.7. Correlations of original measures of taxonomic (upper), functional (middle), and phenetic (lower) diversity with canonical variates derived from canonical correlation analyses between latitude and each of the three components of biodiversity. Long arrows represent high correlations between a particular index and latitude.
Figure 5.8. Frequency distributions characterizing bootstrapped canonical correlation coefficients between latitude and taxonomic (hatched), functional (grey) and phenetic (black) components of biodiversity. Upper distribution characterizes raw coefficients whereas the lower distribution characterizes standardized coefficients.
CHAPTER VI
SYNTHESIS

Variation in biodiversity embodies the community-level impression of the multifaceted ways in which organisms have diversified through space and time. The complexity of this variation is highlighted by a lack of direct correspondence among the three components that I evaluated in this dissertation. Components of taxonomic, functional, and phenetic diversity exhibit qualitative and quantitative differences regarding their latitudinal gradients as well as their relationships with each other. Taxonomic and functional diversity uniquely contribute to variation in phenetic diversity and additive effects likely contribute to the significantly stronger latitudinal gradient in phenetic diversity.

All components of biodiversity exhibited strong, complementary latitudinal gradients. Nonetheless, gradients in taxonomic diversity were linear whereas gradients in functional and phenetic diversity were most often quadratic. Thus, in the subtropics and sub tropics, increases in biodiversity toward the equator involve primarily increases in taxonomic diversity and to a lesser degree increases in functional and phenetic diversity. Relationships among components of biodiversity derive primarily from variation in the number of things that comprise a community such as species, functional groups, and body plans. Because morphology and function are species-specific attributes, increases in species richness are strongly associated with increases in the number of functional groups, and ultimately the range of morphologies found at a particular site.
Latinulina patterns regarding evenness do not exist as measured from perspectives of the allocation of individuals to species, the allocation of species to functional groups, or the dispersion of species in pheretic space. This is true not only when examining relationships of these three components of biodiversity with latitude, but also when examining their relationships to each other. One thing appears certain; the spatial variation among the 32 sites that I examined primarily involves changes in the magnitude of biodiversity, whether it be the number of species, the number of functional groups, or the size of the pheretic space encompassed by communities and does not involve changes in the evenness of these components. The action of those processes that affect evenness likely are specific to a particular level of biological organization such as species or functional groups and this may explain only weak relationships among components of biodiversity regarding their evenness. For example, the evenness of species is determined by processes that affect the allocation of individuals to species such as the amount of available resources (Pielou 1975), whereas the differences in abundance and heterogeneity of prey influences evenness of functional groups. Different individual-level and species-level processes likely cause the evenness of species and functional groups to vary in quite different ways in the New World.

Reductionist approaches, such as the use of species richness as a surrogate of biodiversity, used to capture the essence of its variation, have vastly improved our understanding of the diversification of organisms across space and time, particularly with respect to latitude (Willig 2001). Equally important, variation in biodiversity is much more complex than intimated by consideration of variation in species richness. Variation in taxonomic diversity provides only limited information regarding pheretic and
functional diversity. Indeed, variation in species richness cannot account for gradients in these two components of biodiversity in the New World. Unfortunately, historical concentration on species richness alone may have stymied the growth of our understanding of biodiversity. Accordingly, future efforts should focus on aspects other than species richness in order to better understand the richness and complexity of variation in biodiversity.

Much of the recent popularity regarding the concept of biodiversity stems from the realization that mankind is rapidly eroding the world’s biotic capitol, and is doing so at an increasing rate (Heywood and Watson 1995). This has led to a large body of research that has greatly enhanced our understanding of biodiversity and made us realize how multifaceted the diversification of organisms has been (Swingle 2001). The cost of failing to adequately assess biodiversity, forecast its loss, and expeditiously strive to conserve it may be one which society will consider the most grave mistake of the 21st century.
References


APPENDIX A
MATLAB FUNCTION TO CALCULATE MEASURES
OF TAXONOMIC DIVERSITY
function [divs]=diversities(x)

[chec,chec]=size(x);
if chec >= 2
  x=x';
end;

p=sort(x);
c=p==0; %Sorts the types in ascending order

zero=sum(c);
chec=chec+length(x);

size=length(x);
totaux=sum(x);
p=(x)/totaux; %Determines species richness
preH=p.*(log(p)); %Determines log proportion times proportion

% DIVERSITIES: Calculates the fourteen taxonomic diversity measures found in
% Chapter 2.
% Usage: divs=diversities(x)
% where: x= vector of species abundances
% divs= vector of 14 diversity measures:
% divs=[size;Margalef;Menrich;ShannonD;ShannonE;Simpson;BP;McD;A;
% HB;PIE;EPrime;DPrime;O];
% Margalef= Margalef richness index
% Menrich= Menhinick richness index
% ShannonD= Shannon diversity index
% ShannonE= Shannon evenness index
% Simpson= Simpson dominance index
% BP= Berger-Parker dominance index
% McD= McIntosh dominance index
% A= Fisher log series alpha diversity index
% HB= Bellouin diversity index
% PIE= PIE evenness index
% Eprime= Camargo evenness index
% Dprime= Camargo diversity index
% O= Pielou evenness index

171
ShannonD=(sum(preH));  % Determines sums and resultant Shannon-Weaver index
ShannonE=ShannonD/log(size);  % Determines Shannon evenness
p2=p.*2;
sump2=sum(p2);  % Determines proportion squared
Simpson=1/sump2;  % Determines Simpson index

sorted=sort(x);  % Sorts vector
largest=sorted(size);  % Chooses the species with highest abundance
bp=largest/totaln;  % Determines the proportion of most abundant species
BP=1/bp;  % Berger-Parker index
U=sqrt(sum((x).^2));  % Determines U for McIntosh indices
McD=(totaln-U)/(totaln-sqrt(totaln));  % McIntosh D

Margarich=(size-1)/log(totaln);  % Margalef index of richness
Menrich=size/sqrt(totaln);  % Menhinick index of richness

for i=1:size
    y=sum(log(1:x(i)));
    z=[i;y];
end;
sumz=sum(z);
lnNfact=sum(log(1:totaln));
HB=(lnNfact-sumz)/totaln;  % First half of numerator of Brillouin Index
z=sort(x);
R1=ceil(size.*.25);
R2=ceil(size.*.75);
half1=R2(R1);

rindex=size/totaln;
if totaln/size>20
    ex=0.99000;
else
    ex=0.80000;
end;
msgr='because of the iterative process of log-series alpha, this will take a long time';
end;
sindex=((1-ex)*(-log(1-ex)));

while sindex>rindex
    if sindex>rindex
        ex=(ex+.000001);
sindex=((1-ex)*(-log(1-ex)));
    end;
end;
alpha=(totaln.*(1-ex))/ex);  %Fisher's log-series alpha

firstsum=sum((x./totaln).^2);  %PIE index
PIE=(totaln/(totaln-1))*(1-firstsum);

dp=[];
m1=p*ones(1,length(p));
m2=ones(length(p),1)*p;
d=m1-m2;
dabs=abs(d);
dprime=sum(sum(tril(dabs)))/size;
EPrime=1-dprime;
DPrime=size*EPrime;  %Camargo Diversity

xz=(1/size)*ones(1,length(p));  %Pielou Index
p;
xz';
yz=abs(p-xz');
O=1-(0.5*sum(yz));

divs=[size;Margarith;Menrich;ShannonD;ShannonE;Simpson;BP;McD:A;HB;PIE;...EPrime;DPrime;O];

end;
return;
APPENDIX B
MATLAB FUNCTION TO CALCULATE MEASURES
OF FUNCTIONAL DIVERSITY
%FUNCDIVS: Calculates measures of functional diversity found in Chapter 3.
% Usage: funcdivs=funcdiv(x)
% x = vector of number of species per functional group
% funcdivs = vector of 4 functional diversity measures:
% funcdivs=[length(x);ShannonD;BP;Eprime]
% where: length(x) = richness of functional groups
% ShannonD = diversity of functional groups measured by the Shannon
% diversity index
% BP = dominance of functional groups measured by the Berger-Parker
% index
% Eprime = evenness of functional groups measured by the Camargo
% evenness index

function [funcdivs]=funcdiv(x)

[cber,chee]=size(x);
if chee >= 2
  x=x';
end;

p=sort(x); %Sorts the types in ascending order
c=p==0; %Determines the number of types that are zero
zero=sum(c);
x=p(zero+1:length(x)); %Removes zeros from vector

size=length(x);
total=sum(x);
p=(x)/total;
preH=p.*log(p)); %Determines richness of functional groups
ShannonD=-sum(preH)); %Determines total number of species
%Determines proportions
%Determines log proportion times proportion
%Determines Shannon index

sorted=sort(x); %Sorts vector
largest=sorted(size);
bp=largest/total;
BP=1/bp;

m1=p*ones(1,length(p)); %Chooses the species with highest abundance
m2=ones(length(p),1).*p; %Determines proportion of most abundant species

175
dabs=abs(d);

dprime=sum(sum(tril(dabs)))/size;
EPrime=1-dprime;
funcdivs=[length(x),ShannonD;BP;EPrime]; % Measures of Functional Diversity
return;
APPENDIX C

MATLAB FUNCTION TO SIMULATE EFFECTS OF CHANGES IN SPECIES RICHNESS ON FUNCTIONAL DIVERSITY GRADIENTS
%FDIVSIMSQ: Performs simulations analyses to evaluate whether the observed gradient in functional diversity could be produced by a latitudinal gradient in species richness.
% Usage: [bouts,R2adj]=fdivsimsq(c1,c2,c3,c4,c5,c6,c7,c8,c9,c10,c11,c12,c13,c14,
  ...c15,c16,c17,c18,
  c19,c20,c21,c22,c23,c24,c25,c26,c27,c28,c29,c30,c31,c32,richs,lats,iter)
% bouts = vector of three parameter estimates of the quadratic relationship
% determined by orthogonal polynomial regression.
% R2adj = vector of three adjusted coefficients of determination describing
% the quadratic relationship determined by orthogonal polynomial regression.
% %
% c1-c32 = vectors of guild identifiers (integers) for each species found in
% the faunal pool for a particular community.
% richs = vector of species richness values for each of the 32 communities
% lats = vector of latitude values for each of the 32 communities
% iter = number of iterations to be performed in analysis

Function [bouts,R2adj]=fdivsimsq(c1,c2,c3,c4,c5,c6,c7,c8,c9,c10,c11,c12,
c13,c14,c15,c16,c17,c18,c19,c20,c21,c22,c23,c24,c25,c26,c27,c28,c29,c30,c31,c32,richs,
lats,iter)

bouts=[];
R2adj=[];

for i=1:iter

  %Begin for loop
  %Counter

divs=[];

  p1 = randperm(length(c1));
  r1 = p1(1:richs(1));
  ndfunct1 = c1(r1);
  [value1,freq1] = uniquef(ndfunct1);
  d1=funcdiv(freq1);

  p2 = randperm(length(c2));
  r2 = p2(1:richs(2));
  ndfunct2 = c2(r2);
  [value2,freq2] = uniquef(ndfunct2);
  d2=funcdiv(freq2);

  %Simulated functional diversity for c1
  %Simulated functional diversity for c2

end
p3 = randperm(length(c3)); % Simulated functional diversity for c3
r3 = p3(1:riches(3));
rdfunc3 = c3(r3, :);
[value3, freq3] = unique(rdfunc3);
d3 = funcdiv(freq3);

p4 = randperm(length(c4)); % Simulated functional diversity for c4
r4 = p4(1:riches(4));
rdfunc4 = c4(r4, :);
[value4, freq4] = unique(rdfunc4);
d4 = funcdiv(freq4);

p5 = randperm(length(c5)); % Simulated functional diversity for c5
r5 = p5(1:riches(5));
rdfunc5 = c5(r5, :);
[value5, freq5] = unique(rdfunc5);
d5 = funcdiv(freq5);

p6 = randperm(length(c6)); % Simulated functional diversity for c6
r6 = p6(1:riches(6));
rdfunc6 = c6(r6, :);
[value6, freq6] = unique(rdfunc6);
d6 = funcdiv(freq6);

p7 = randperm(length(c7)); % Simulated functional diversity for c7
r7 = p7(1:riches(7));
rdfunc7 = c7(r7, :);
[value7, freq7] = unique(rdfunc7);
d7 = funcdiv(freq7);

p8 = randperm(length(c8)); % Simulated functional diversity for c8
r8 = p8(1:riches(8));
rdfunc8 = c8(r8, :);
[value8, freq8] = unique(rdfunc8);
d8 = funcdiv(freq8);

p9 = randperm(length(c9)); % Simulated functional diversity for c9
r9 = p9(1:riches(9));
rdfunc9 = c9(r9, :);
[value9, freq9] = unique(rdfunc9);
d9 = funcdiv(freq9);

p10 = randperm(length(c10)); % Simulated functional diversity for c10
r10 = p10(1:riches(10));
rdfunc10 = c10(r10, :);
\[\text{value10}, \text{freq10} = \text{unique}(\text{ndfuncs}10)\];
\[\text{d10} = \text{funcdiv}(\text{freq10})\];

\[\text{p11} = \text{randperm}(\text{length}(\text{c11}))\];
\[\text{r11} = \text{p11}(1: \text{richs}(\text{c11}))\];
\[\text{ndfuncs}11 = \text{c11}(\text{r11}, :)\];
\[\text{value11}, \text{freq11} = \text{unique}(\text{ndfuncs}11)\];
\[\text{d11} = \text{funcdiv}(\text{freq11})\];

\[\text{p12} = \text{randperm}(\text{length}(\text{c12}))\];
\[\text{r12} = \text{p12}(1: \text{richs}(\text{c12}))\];
\[\text{ndfuncs}12 = \text{c12}(\text{r12}, :)\];
\[\text{value12}, \text{freq12} = \text{unique}(\text{ndfuncs}12)\];
\[\text{d12} = \text{funcdiv}(\text{freq12})\];

\[\text{p13} = \text{randperm}(\text{length}(\text{c13}))\];
\[\text{r13} = \text{p13}(1: \text{richs}(\text{c13}))\];
\[\text{ndfuncs}13 = \text{c13}(\text{r13}, :)\];
\[\text{value13}, \text{freq13} = \text{unique}(\text{ndfuncs}13)\];
\[\text{d13} = \text{funcdiv}(\text{freq13})\];

\[\text{p14} = \text{randperm}(\text{length}(\text{c14}))\];
\[\text{r14} = \text{p14}(1: \text{richs}(\text{c14}))\];
\[\text{ndfuncs}14 = \text{c14}(\text{r14}, :)\];
\[\text{value14}, \text{freq14} = \text{unique}(\text{ndfuncs}14)\];
\[\text{d14} = \text{funcdiv}(\text{freq14})\];

\[\text{p15} = \text{randperm}(\text{length}(\text{c15}))\];
\[\text{r15} = \text{p15}(1: \text{richs}(\text{c15}))\];
\[\text{ndfuncs}15 = \text{c15}(\text{r15}, :)\];
\[\text{value15}, \text{freq15} = \text{unique}(\text{ndfuncs}15)\];
\[\text{d15} = \text{funcdiv}(\text{freq15})\];

\[\text{p16} = \text{randperm}(\text{length}(\text{c16}))\];
\[\text{r16} = \text{p16}(1: \text{richs}(\text{c16}))\];
\[\text{ndfuncs}16 = \text{c16}(\text{r16}, :)\];
\[\text{value16}, \text{freq16} = \text{unique}(\text{ndfuncs}16)\];
\[\text{d16} = \text{funcdiv}(\text{freq16})\];

\[\text{p17} = \text{randperm}(\text{length}(\text{c17}))\];
\[\text{r17} = \text{p17}(1: \text{richs}(\text{c17}))\];
\[\text{ndfuncs}17 = \text{c17}(\text{r17}, :)\];
\[\text{value17}, \text{freq17} = \text{unique}(\text{ndfuncs}17)\];
\[\text{d17} = \text{funcdiv}(\text{freq17})\];
p18 = randperm(length(c18)); %Simulated functional diversity for c18
r18 = p18(1:richs(18));
randfunsc18 = c18(r18, :);
[value18, freq18] = unique(randfunsc18);
d18 = funcdivv(freq18);

p19 = randperm(length(c19)); %Simulated functional diversity for c19
r19 = p19(1:richs(19));
randfunsc19 = c19(r19, :);
[value19, freq19] = unique(randfunsc19);
d19 = funcdivv(freq19);

p20 = randperm(length(c20)); %Simulated functional diversity for c20
r20 = p20(1:richs(20));
randfunsc20 = c20(r20, :);
[value20, freq20] = unique(randfunsc20);
d20 = funcdivv(freq20);

p21 = randperm(length(c21)); %Simulated functional diversity for c21
r21 = p21(1:richs(21));
randfunsc21 = c21(r21, :);
[value21, freq21] = unique(randfunsc21);
d21 = funcdivv(freq21);

p22 = randperm(length(c22)); %Simulated functional diversity for c22
r22 = p22(1:richs(22));
randfunsc22 = c22(r22, :);
[value22, freq22] = unique(randfunsc22);
d22 = funcdivv(freq22);

p23 = randperm(length(c23)); %Simulated functional diversity for c23
r23 = p23(1:richs(23));
[value23, freq23] = unique(randfunsc23);
d23 = funcdivv(freq23);

p24 = randperm(length(c24)); %Simulated functional diversity for c24
r24 = p24(1:richs(24));
randfunsc24 = c24(r24, :);
[value24, freq24] = unique(randfunsc24);
d24 = funcdivv(freq24);

p25 = randperm(length(c25)); %Simulated functional diversity for c25
r25 = p25(1:richs(25));
randfunsc25 = c25(r25, :);
[value25, freq25] = unique(randfunsc25);
d25=funcdiv(freq25);
p26 = randperm(length(c26));  % Simulated functional diversity for c26
r26 = p26(1:richs(26));
rndfuncs26 = c26(r26,);
[value26, freq26] = unique(rndfuncs26);
d26=funcdiv(freq26);

p27 = randperm(length(c27));  % Simulated functional diversity for c27
r27 = p27(1:richs(27));
rndfuncs27 = c27(r27,);
[value27, freq27] = unique(rndfuncs27);
d27=funcdiv(freq27);

p28 = randperm(length(c28));  % Simulated functional diversity for c28
r28 = p28(1:richs(28));
rndfuncs28 = c28(r28,);
[value28, freq28] = unique(rndfuncs28);
d28=funcdiv(freq28);

p29 = randperm(length(c29));  % Simulated functional diversity for c29
r29 = p29(1:richs(29));
rndfuncs29 = c29(r29,);
[value29, freq29] = unique(rndfuncs29);
d29=funcdiv(freq29);

p30 = randperm(length(c30));  % Simulated functional diversity for c30
r30 = p30(1:richs(30));
rndfuncs30 = c30(r30,);
[value30, freq30] = unique(rndfuncs30);
d30=funcdiv(freq30);

p31 = randperm(length(c31));  % Simulated functional diversity for c31
r31 = p31(1:richs(31));
rndfuncs31 = c31(r31,);
[value31, freq31] = unique(rndfuncs31);
d31=funcdiv(freq31);

p32 = randperm(length(c32));  % Simulated functional diversity for c32
r32 = p32(1:richs(32));
rndfuncs32 = c32(r32,);
[value32, freq32] = unique(rndmorphs32);
d32=funcdiv(freq32);

divs=[d1,d2,d3,d4,d5,d6,d7,d8,d9,d10,d11,d12,d13,d14,d15,d16,d17,d18,d19,
...$d_20, d_21, d_22, d_23, d_24, d_25,$
$d_26, d_27, d_28, d_29, d_30, d_31, d_32$;
div = div$^*$;

regressions = [];
r2adjs = [];
[r,c] = size(div);
for $i = 1 : c$
  regression
  [b,R2a,F,pF,ssr,sse,ssto,dfr,dfe,dfto,mar,mse] = orthopolyregr(lats,div(:,1),2);
  regressions = [regressions,b]';
  r2adjs = [r2adjs,R2a]';
end;
regressions = regressions';
r2adjs = r2adjs';
R2adjs = [R2adjs;r2adjs]';
bouts = [bouts;regressions]';
end;
return;
APPENDIX D
MATLAB FUNCTION TO CALCULATE MEASURES
OF PHENETIC DIVERSITY
function [divstats]=morphdiv(x)

[rich,vars]=size(x);
sizerange=range(x(:,1));
shaperange=range(x(:,2));
y1=sort(x(:,1));
y2=sort(x(:,2));
mvarsiz=std(y1(2:end,1)-y1(1:end-1,1))%std of mt lengths
mvarh=std(y2(2:end,2)-y2(1:end-1,2))%std of mt lengths
sizedists=euc(x(:,1));
shapedists=euc(x(:,2));
sizessort=sort(sizedists);
shapessort=sort(shapedists);
siavendist=mean(sizessort);
shavendist=mean(shapessort);

%Average ndd's on size axis
%Average ndd's on shape axis

divstats=[rich,sizerange,shaperange,mvarsiz,mvarh,siavendist,shavendist];
return;
APPENDIX E
MATLAB FUNCTION TO SIMULATE EFFECTS OF CHANGES IN SPECIES RICHNESS ON PHENOTYPIC DIVERSITY GRADIENTS
%PDIVSIMSQ: Performs simulations analyses to evaluate whether the observed gradient in phenetic diversity could be produced by a latitudinal gradient in species richness.
% Usage: [bouts,R2adjs]=pddivsimsq(c1,c2,c3,c4,c5,c6,c7,c8,c9,c10,c11,c12,c13,
       c14,c15,c16,c17,c18,c19,c20,c21,c22,c23,c24,c25,c26,c27,c28,c29,
       c30,c31,c32,richs,lats,iter)
% bouts = vector of three parameter estimates of the quadratic relationship
determined by orthogonal polynomial regression.
% R2adjs = vector of three adjusted coefficients of determination describing
the quadratic relationship determined by orthogonal polynomial regression.
% %
% c1-c32= vectors of principal component scores for each species found in
% the faunal pool for a particular community.
% richs= vector of species richness values for each of the 32 communities
% lats= vector of latitude values for each of the 32 communities
% iter= number of iterations to be performed in analysis

Function [bouts,R2adjs]=pddivsimsq(c1,c2,c3,c4,c5,c6,c7,c8,c9,c10,c11,c12,
c13,c14,c15,c16,c17,c18,c19,c20,c21,c22,c23,c24,c25,c26,c27,c28,c29,c30,c31,c32,
richs,lats,iter)
bouts=[]; %Initialize vectors
R2adjs=[];
for i=1:iter %Begin for loop
    divs=[]; %Counter
    p1 = randperm(length(c1)); %Simulated phenetic diversity for c1
    r1 = p1(1:richs(1));
    rdmorphs1 = c1(r1);
    d1=morphdiv(freq1);
    p2 = randperm(length(c2)); %Simulated phenetic diversity for c2
    r2 = p2(1:richs(2));
    rdmorphs2 = c2(r2:);
    d2=morphdiv(freq2);
    p3 = randperm(length(c3)); %Simulated phenetic diversity for c3
    % Additional code...

187
r3 = p3(1:richs(3));
rmorphs3 = c3(r3,:);
d3=morphdiv(freq3);

p4 = randperm(length(c4));
r4 = p4(1:richs(4));
rmorphs4 = c4(r4,:);
d4=morphdiv(freq4);

%Simulated phenetic diversity for c4

p5 = randperm(length(c5));
r5 = p5(1:richs(5));
rmorphs5 = c5(r5,:);
d5=morphdiv(freq5);

%Simulated phenetic diversity for c5

p6 = randperm(length(c6));
r6 = p6(1:richs(6));
rmorphs6 = c6(r6,:);
d6=morphdiv(freq6);

%Simulated phenetic diversity for c6

p7 = randperm(length(c7));
r7 = p7(1:richs(7));
rmorphs7 = c7(r7,:);
d7=morphdiv(freq7);

%Simulated phenetic diversity for c7

p8 = randperm(length(c8));
r8 = p8(1:richs(8));
rmorphs8 = c8(r8,:);
d8=morphdiv(freq8);

%Simulated phenetic diversity for c8

p9 = randperm(length(c9));
r9 = p9(1:richs(9));
rmorphs9 = c9(r9,:);
d9=morphdiv(freq9);

%Simulated phenetic diversity for c9

p10 = randperm(length(c10));
r10 = p10(1:richs(10));
rmorphs10 = c10(r10,:);
d10=morphdiv(freq10);

%Simulated phenetic diversity for c10

p11 = randperm(length(c11));
r11 = p11(1:richs(11));
rmorphs11 = c11(r11,:);
d11=morphdiv(freq11);

%Simulated phenetic diversity for c11

188
p12 = randperm(length(c12));
  r12 = p12(1:richs(12));
  rndmorphs12 = c12(r12,:);
  d12 = morphdiv(freq12);
  %Simulated phenetic diversity for c12

p13 = randperm(length(c13));
  r13 = p13(1:richs(13));
  rndmorphs13 = c13(r13,:);
  d13 = morphdiv(freq13);
  %Simulated phenetic diversity for c13

p14 = randperm(length(c14));
  r14 = p14(1:richs(14));
  rndmorphs14 = c14(r14,:);
  d14 = morphdiv(freq14);
  %Simulated phenetic diversity for c14

p15 = randperm(length(c15));
  r15 = p15(1:richs(15));
  rndmorphs15 = c15(r15,:);
  d15 = morphdiv(freq15);
  %Simulated phenetic diversity for c15

p16 = randperm(length(c16));
  r16 = p16(1:richs(16));
  rndmorphs16 = c16(r16,:);
  d16 = morphdiv(freq16);
  %Simulated phenetic diversity for c16

p17 = randperm(length(c17));
  r17 = p17(1:richs(17));
  rndmorphs17 = c17(r17,:);
  d17 = morphdiv(freq17);
  %Simulated phenetic diversity for c17

p18 = randperm(length(c18));
  r18 = p18(1:richs(18));
  rndmorphs18 = c18(r18,:);
  d18 = morphdiv(freq18);
  %Simulated phenetic diversity for c18

p19 = randperm(length(c19));
  r19 = p19(1:richs(19));
  rndmorphs19 = c19(r19,:);
  d19 = morphdiv(freq19);
  %Simulated phenetic diversity for c19

p20 = randperm(length(c20));
  r20 = p20(1:richs(20));
  rndmorphs20 = c20(r20,:);
  d20 = morphdiv(freq20);
  %Simulated phenetic diversity for c20
p21 = randperm(length(c21));
c21 = p21(1:richs(21));
rdmorphs21 = c21(1:21,);
d21=morphdiv(freq21);

%Simulated phenetic diversity for c21

p22 = randperm(length(c22));
r22 = p22(1:richs(22));
rdmorphs22 = c22(22,);
d22=morphdiv(freq22);

%Simulated phenetic diversity for c22

p23 = randperm(length(c23));
r23 = p23(1:richs(23));
d23=morphdiv(freq23);

%Simulated phenetic diversity for c23

p24 = randperm(length(c24));
r24 = p24(1:richs(24));
rdmorphs24 = c24(24,);
d24=morphdiv(freq24);

%Simulated phenetic diversity for c24

p25 = randperm(length(c25));
r25 = p25(1:richs(25));
rdmorphs25 = c25(r25,);
d25=morphdiv(freq25);

%Simulated phenetic diversity for c25

p26 = randperm(length(c26));
r26 = p26(1:richs(26));
rdmorphs26 = c26(r26,);
d26=morphdiv(freq26);

%Simulated phenetic diversity for c26

p27 = randperm(length(c27));
r27 = p27(1:richs(27));
rdmorphs27 = c27(r27,);
d27=morphdiv(freq27);

%Simulated phenetic diversity for c27

p28 = randperm(length(c28));
r28 = p28(1:richs(28));
rdmorphs28 = c28(r28,);
d28=morphdiv(freq28);

%Simulated phenetic diversity for c28

p29 = randperm(length(c29));
r29 = p29(1:richs(29));
rdmorphs29 = c29(r29,);
d29=morphdiv(freq29);

%Simulated phenetic diversity for c29

190
p30 = randperm(length(c30));
r30 = p30(1:richs(30));
rndmorphs30 = c30(r30,:);
d30 = morphdiv(freq30);

p31 = randperm(length(c31));
r31 = p31(1:richs(31));
rndmorphs31 = c31(r31,:);
d31 = morphdiv(freq31);

p32 = randperm(length(c32));
r32 = p32(1:richs(32));
rndmorphs32 = c32(r32,:);
d32 = morphdiv(freq32);

diva = [d1,d2,d3,d4,d5,d6,d7,d8,d9,d10,d11,d12,d13,d14,d15,d16,d17,d18,d19,d...20,d21,d22,d23,d24,d25,d26,d27,d28,d29,d30,d31,d32];
diva = diva;

regressions = [ ];
2adj = [ ];
[r,c] = size(diva);
for l = 1 : c
    %conductor orthogonal polynomial regression
    [b,R2a,F,pF,ssr,sse,ssr,df,ddf,dfb,mse] = ...
    orthopolyregr(lats,diva(:,l));
    regressions = [regressions,b ];
    r2adj = [ r2adj, R2a ];
end;
regressions = regressions;
r2adj = r2adj;
R2adj = [ R2adj ; r2adj ];
bouts = [ bouts ; regressions ];
end;
return;
APPENDIX VI
MATLAB FUNCTION TO CONDUCT CANONICAL CORRELATION ANALYSES
STANDARDIZED TO A PARTICULAR NUMBER OF VARIABLES
CANCORRCOMP: Determines bootstrapped canonical correlation coefficients as % used in Chapter 5.

Usage: [sims] = cancorrcomp(mata, matb, numvara, numvarb, iter)

where: simrs = simulated distribution of canonical correlations

mata = datamatrix a
matb = datamatrix b
numvara = number of permuted variables used to characterize mata
(Latitude Vector)
numvarb = number of permuted variables used to characterize matb
(Diversity Matrix)
iter = number of iterations

function [sims, dwnics, upcis, medians] = cancorrcomp(mata, matb, numvara, numvarb, iter)

mat = [mata, matb]; % Concatinates matrices
rlc = size(mata); % Determines size of Latitude Matrix
rs, cs = size(matb); % Determines size of Diversity Matrix
simrs = []; % Initializes results vector

for i = 1:iter
    bootmat = bootstrapp(mat);
largest = bootmat(:,1:cl);
smallmat = bootmat(:,cl+1:cl+cs);
    if numvara == cl
        largepermmat = largemat;
    else
        permcola = randperm(cl);
        permcolaa = permcola(1:numvara);
        largepermmat = largemat(:,permcola);
    end;
    if numvarb == cs
        smallperm = smallmat;
    else
        permcolb = randperm(cs);
        permcolbb = permcolb(1:numvarb);
        smallperm = smallmat(:,permcolb);
    end;
    [r] = cancorr(largepermmat, smallperm);
    simrs = [sims, r]; % Conducts canonical correlation analysis
end;
sims = simrs'; % Stores output
return;

193