5-1-2013

Integrating, Developing, and Testing Methods to Generate More Cohesive Approaches to Biogeographic Inference

Mallory Elizabeth Eckstut
University of Nevada, Las Vegas, eckstutm@unlv.nevada.edu

INTEGRATING, DEVELOPING, AND TESTING METHODS TO GENERATE MORE COHESIVE
APPROACHES TO BIOGEOGRAPHIC INFERENCE

By

Mallory Elizabeth Eckstut

Bachelor of Arts
Simon's Rock College of Bard
2006

Master of Science
Southeastern Louisiana University
2008

A dissertation submitted in partial fulfillment of
the requirements for the

Doctor of Philosophy in Biological Sciences

School of Life Sciences
College of Sciences
The Graduate College

University of Nevada, Las Vegas
May 2013

THE GRADUATE COLLEGE

We recommend the dissertation prepared under our supervision by

Mallory Elizabeth Eckstut

entitled

Integrating, Developing, and Testing Methods to Generate More Cohesive Approaches to Biogeographic Inference

be accepted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy in Biological Sciences
School of Life Sciences

Brett Riddle, Ph.D., Committee Chair

Javier Rodriguez, Ph.D., Committee Member

Daniel Thompson, Ph.D., Committee Member

Brian Crother, Ph.D., Committee Member

Matthew Lachniet, Ph.D., Graduate College Representative

Tom Piechota, Ph.D., Interim Vice President for Research &
Dean of the Graduate College

May 2013

ABSTRACT

Integrating, Developing, and Testing Methods to Generate More Cohesive Approaches

to Biogeographic Inference

by

Mallory E. Eckstut

Dr. Brett R. Riddle, Examination Committee Chair
Professor of Biological Sciences
University of Nevada, Las Vegas

As a fundamental component of the developing discipline of conservation

biogeography, broadscale analyses of biotic assembly and disassembly across multiple

temporal and spatial scales provide an enhanced understanding of how geologic

transformations and climate oscillations have shaped extant patterns of biodiversity. As

with any scientific field, there are limitations in the case of biogeographic historical

reconstructions. Historical reconstructions are only as robust as the theoretical

underpinnings of the methods of reconstruction (including data collection, quality,

analysis, and interpretation). Nevertheless, historical reconstructions of species

distributions can help inform our understanding of how species respond to

environmental change.

My dissertation takes a critical look at the current state of biotic-level

biogeographic analyses across an array of spatio-temporal scales and I use the North

American warm deserts as a model system to both develop and test biogeographic

methods. In particular, I address the biogeographic issue of pseudo-congruence (similar

biogeographic patterns produced by historically dissimilar events) and develop potential

approaches to reduce the issue of pseudo-congruence in biotic-level analyses. I review

potential confounding issues that could produce pseudo-congruence in climate change-

based biogeographic analyses and I incorporate temporal components into complex

biogeographic theories and methods to reduce pseudo-congruence in biogeographic

analysis. My dissertation goals and approaches are described in Chapter 1, which serves

as an introduction.

In Chapter 2, I provide a summary of paleoclimatic patterns and processes in the

North American deserts. A refined understanding of paleoclimatic pattern and process

can facilitate the generation of enhanced hypotheses about how biotas are altered by

climate change events, particularly in cases where climate change events occurring at

different times and scales could produce pseudo-congruent biogeographic patterns.

In Chapter 3, I propose a modification to the Phylogenetic Analysis for

Comparing Trees (PACT) multi-clade biogeographic analysis, in order to facilitate a

modern, integrative biotic-level analysis. I developed a modified PACT (mPACT) protocol

that incorporates a temporal component (to reduce pseudo-congruence) and facilitates

likelihood-based phylogenetic ancestral area reconstruction. To test the performance of

my modification, I conducted modified and standard PACT (mPACT and PACT,

respectively) analyses on data previously generated for the North American warm

deserts and compared these results to those of a prior analysis that uses Secondary

Brooks Parsimony Analysis (Secondary BPA), which is a binary-coded pre-cursor method

to PACT. This analysis showed that results from mPACT revealed more diversification

compared to Secondary BPA and PACT analyses and that pseudo-congruent patterns were rampant in this dataset.

Finally, in Chapter 4, I developed and tested a novel operational approach to exploring evolutionary dynamics of areas of endemism (areas thought by some biogeographers to generate and maintain unique lineages through time). My procedure implements mPACT analyses as well as paleoclimatic and geologic information and I tested my analysis by conducting an analysis on the North American warm deserts. The results of my analysis were congruent with the pre-existing biogeographic hypotheses of the North American warm deserts but also showed that there were more pseudo-congruent events than previously recognized, which may alter the understanding of areas of endemism on a temporal scale. Moreover, I provide novel insights into the potential for areas of endemism to act as both areas of persistence (or stability) as well as areas of transition (ephemeral areas) for biodiversity and I address the issue that diagnosed areas of endemism may not all be equal with respect to biodiversity production and stability through time.

ACKNOWLEDGMENTS

Many people contributed to the completion of this dissertation. First and

foremost, I thank my committee for their continued support and helpful ideas that

contributed to my own intellectual development and the execution of this dissertation.

Dr. Brett Riddle, my committee chair and co-mentor on my EPSCoR fellowship, has been

extremely helpful and supportive with project development and was always available to

troubleshoot any issues I had. His suggestions and comments on these projects and my

ideas regarding biogeography have been invaluable for completion of this dissertation.

Dr. Matthew Lachniet, my co-Mentor on the EPSCoR fellowship, has been enthusiastic

and patient while helping me develop a better understanding of climatology,

paleoclimatology, and geological processes. Dr. Daniel Thompson has been incredibly

helpful for brainstorming complex methological ideas in my project and helped me gain

a foundation in evolutionary ecology and population biology. Dr. Javier Rodríguez has

been invaluable for assisting me in harnessing skills in logical, practical project idea

development, coherent scientific writing, and logical, effective, and visually appealing

scientific presentations. Last but not least, I am greatly indebted to Dr. Brian Crother,

who has served on both my Master's and Ph.D. committees and has been an excellent

mentor who has helped me develop confidence in my own research abilities and

provided constructive criticisms, conversations, and suggestions that helped guide my

interests in evolutionary ecology and biogeography.

I sincerely thank the following School of Life Science ecology and evolution

members (past and present) for conversations and critiques that have contributed to my

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1:

INTRODUCTION

Accelerated rates of environmental disturbance, such as exacerbated rates of climate change and habitat fragmentation, have made it vital to understand how environmental factors alter regional floral and faunal distributions and biogeographic patterns in order to prescribe effective conservation strategies (Whittaker et al., 2005). As a fundamental component of the developing discipline of conservation biogeography, broadscale analyses of biotic assembly and disassembly across multiple temporal and spatial scales provide an enhanced understanding of how geologic transformations and climate oscillations have shaped extant patterns of biodiversity (Morrone, 2009).

As with any scientific field, there are limitations in the case of biogeography. Historical reconstructions are only as robust as the theoretical underpinnings of the methods of reconstruction (including data collection, quality, analysis, and interpretation). Nevertheless, historical reconstructions of species distributions can help inform our understanding of how species respond to environmental change. My dissertation takes a critical look at the current state of biotic-level biogeographic analyses across an array of spatio-temporal scales and addresses potential approaches to enhancing the quality and integration of complex biogeographic theories and methods, particularly to reduce the issue of pseudo-congruence in biotic-level biogeographic analyses (similar biogeographic patterns from dissimilar historical events;

1

Cunningham & Collins, 1994; Fig. 1.1), and I use the North American deserts as a model

system to both develop and test biogeographic methods.

REVEALING BIOTIC RESPONSES TO HISTORICAL EVENTS

There has been substantial debate among biogeographers about which processes (e.g.,

vicariance or dispersal, ecological or historical) and spatio-temporal scales (e.g.,

populations or species) to emphasize, but an emerging consensus recognizes the

importance of integrating information from each of these perspectives. However, the

inherent complexity of biodiversity has made it difficult to develop a single method to

address an admittedly large array of biogeographic patterns and processes;

consequently, a variety of methods have been developed, each optimizing a different

aspect of the interaction of biotic processes with a dynamic abiotic history (Brooks &

McLennan, 2002; Wiens & Donoghue, 2004; Morrone, 2009).

Moreover, the field of biogeography has gone through substantial paradigm

shifts and produced several subdisciplines, and recently, the overarching theoretical

viewpoint has shifted from exclusively area-based biogeography (e.g., cladistic

biogeography) to a more taxon-based biogeography (e.g., phylogeography and event-

based methods). Throughout this process, the production of numerous techniques has

been perceived as both beneficial and detrimental to the field of biogeography –

beneficial because it is a sign that the field is expanding, but detrimental because it

demonstrates the divisive nature of biogeography as a discipline (as reviewed in

Morrone, 2009). In recognition of the validity of each of these perspectives, the need

has been expressed to develop integrative methodological frameworks to illuminate the reciprocity of perspectives (Haydon et al., 1994; Donoghue & Moore, 2003; Riddle & Hafner, 2006).

Even though it may be difficult to develop one technique to address all sub-disciplines and approaches in biogeography, practitioners acknowledge that a rich and robust understanding of the formation of biodiversity will require development of a more integrative biogeography (Pyron & Burbrink, 2010). Early cladistic biogeographers (e.g., Rosen, 1978; Nelson & Platnick, 1981) incorporated a variety of types of data in their analyses, but did not have access to the molecular data that comprise much of modern historical biogeography. A problem that cladistic biogeographers, and in particular tests of the vicariance hypothesis, have suffered from is the issue of pseudo-congruence (similar biogeographic patterns from dissimilar historical events; Cunningham & Collins, 1994; Fig. 1.1). Pseudo-congruent patterns can be produced by either i) vicariant events at one point in time (e.g., as the result of tectonic uplift) and dispersal events at a different point in time (e.g., resulting from climate change), or ii) repeated dispersal of different taxa across the same barrier at different times, perhaps as a result of different climate oscillations, and thus at different points in time. Pseudo-congruent diversification patterns can be misleading in analyses of numerous taxa (Donoghue & Moore, 2003; Ree & San Martín, 2008; Eckstut et al., 2011), but can be addressed by identifying divergence timing, which can be estimated using techniques such as molecular dating (Mantooth & Riddle, 2011). Consequently, the use of molecular data has revealed numerous instances of previously unrecognized pseudo-

3

congruence (e.g., Upchurch, 2008; Marko & Moran, 2009; McGovern et al., 2010; Folinsbee & Evans, 2012; Garrick et al., 2012).

As biogeographers endeavor to reveal the history of biotas, in particular trying to alleviate issues such as pseudo-congruence, new analytical approaches in historical biogeography appear regularly (e.g., Phylogenetic Analysis for Comparing Trees, Wojcicki & Brooks, 2004, 2005; Approximate Bayesian Estimation, Hickerson et al., 2006; Dispersal-Extinction-Cladogenesis model, Ree & Smith, 2008). A combination of cladistic frameworks, molecular data, species distribution modeling, and improved methods promises to offer a format for development of highly integrative historical biogeographic approaches that can reduce the impact of issues such as pseudo-congruence (Donoghue & Moore, 2003; Riddle et al., 2008).

THE NORTH AMERICAN WARM DESERTS AS A MODEL SYSTEM

The North American deserts (Fig. 1.2) are subject to extreme temperature and precipitation variability and a large number of biotic, geologic, and climatological datasets and hypotheses have been generated and tested for this region. The North American deserts thus represent an ideal system within which to employ theoretical tests that are designed to evaluate methods using well-corroborated hypotheses of biotic distribution and diversification (Grant, 2002; Riddle & Hafner, 2006). However, the northern, cold Great Basin desert is comprised of a greater proportion of lineages that have a distinctly different origin than those of the more southern warm deserts (i.e., Arcto-tertiary and Madro-tertiary compared to Neotropical-tertiary and Madro-

tertiary; Axelrod, 1958, 1972, 1985). Consequently, for method testing, using only the North American warm deserts reduces error resulting from phylogenetic independence (i.e., biogeographic patterns and dynamics resulting from evolutionary constraints and not necessarily environmental influence). These deserts have co-occurring lineages with sister taxa in the adjacent deserts. For example, a biotic-level analysis with wide-ranging lineages, such as co-occurring lizards, snakes, and rats that occur in the Mojave and Sonoran deserts, would facilitate comparison of the environmental impacts while still controlling for any evolutionary patterns that may be due to evolutionary constraints within either the lizard, snake, or rat lineages.

The North American warm deserts span a broad latitudinal and elevational gradient – from the southern, low elevation warm deserts (the Peninsular, Chihuahuan, and Sonoran deserts) to the more northern, higher elevation moderately warm Mojave Desert (Fig. 1.2; Table 1.1). Additionally, although each of these regional deserts have distinct arid-adapted biotic assemblages, many taxa have sister lineages in adjacent deserts. Comparing the evolutionary dynamics of taxa that are broadly co-distributed but ecologically occupy different habitats (e.g., sand vs. rock specialists) can reveal how environmentally dissimilar aridland communities respond to large-scale historical perturbations (Hafner & Riddle, 2011). The biotas of these regions are primarily proposed to have diversified in response to two sets of historical events that may have produced many pseudo-congruent diversification events: i) fragmentation created by Neogene (primarily Miocene and Pliocene) geologic activity that resulted in the rapid uplifting of mountains and plateaus and associated habitat modifications, and ii)

Pleistocene climate oscillations that promoted diversification by producing isolated refugia of arid-adapted terrestrial lineages during glacial periods and expansion during interglacial cycles (e.g., Thompson, 1990; Jezkovaet al., 2009; Waltari & Guralnick, 2009).

These sets of temporally divergent earth history events also make the warm deserts an ideal region to test hypotheses of pseudo-congruence in biogeographic datasets. Pseudo-congruent events would not occur if every vicariant and dispersal event through time happened in a different place. Instead, warm desert biogeographic biodiversity has been shaped by an overlay of diversification events across similar geographic locations at different points in time – from older tectonic uplift events to younger climate change events. As a consequence, this region is ideal for testing the ability of methods to detect pseudo-congruence among diverse biogeographic datasets.

CHAPTER 2

In Chapter 2, I provide a summary of paleoclimatic patterns and processes that have shaped the environment of the North American deserts. In this review, I address why i) biologists should consider embedded details of paleoclimatic processes (e.g., "long vs. short," "gradual vs. abrupt" periods of climate change) in addition to general patterns (e.g., "cold vs. warm," "dry vs. wet") and ii) potential errors that can occur from excluding these processes. A refined understanding of paleoclimatic pattern and process can facilitate the generation of enhanced hypotheses about biodiversity response to climate change events and better integration of climatic or paleoclimatic data into

biogeographic analyses, particularly in cases where climate change events occurring at different times could produce pseudo-congruent biogeographic patterns.

CHAPTER 3

In Chapter 3, I propose a modification to the Phylogenetic Analysis for Comparing Trees (PACT; Wojcicki & Brooks, 2004, 2005) multi-clade biogeographic analysis in order to produce a modern, integrative biogeographic approach. PACT can be used to reveal patterns such as the taxon pulse, Hennig's progression rule, and species-area relationships (Halas et al., 2005). However, this algorithm is conducted without a temporal component, which can be problematic when temporally and spatially discordant events result in identical cladogram patterns (pseudo-congruence; Eckstut et al., 2011). Additionally, there is currently no way to distinguish unique from general diversification events, and only parsimony-based optimization can be implemented for ancestral area reconstruction (Eckstut et al., 2011). To alleviate these issues, I developed a modified PACT protocol that incorporates a temporal component and phylogenetic branch lengths based on the number of lineages representing each diversification event. To test the performance of my modification, I conducted modified and standard PACT analyses on data previously generated for the North American warm deserts and compared these results to those of a prior analysis that uses Secondary Brooks Parsimony Analysis (Secondary BPA), which is a binary-coded pre-cursor method to PACT.

CHAPTER 4

In Chapter 4, I address the philosophical and operational approaches to diagnosing areas of endemism (areas that generate and maintain unique lineages through time). An area of endemism is a scale-specific, spatio-temporally bounded area with unique species or combinations of species, and can be eradicated, shrink, or expand over time (Crother & Murray, 2011). However, operational approaches to exploring endemism are limited and mostly restricted to how to diagnose an area of endemism as a fundamental unit of biogeography, rather than focusing on how these units may form, change, and dissolve through time. I propose an approach to inferring the dynamic nature of areas of endemism by conducting an mPACT analysis as well as paleoclimatic and geologic information. I tested my approach using data from the North American warm deserts and hypothesized that my results would be congruent with the pre-existing biogeographic data and I address issues of pseudo-congruence and the notion that diagnosed areas of endemism may not all be equal with regard to biodiversity production and stability.

DISSERTATION GOALS

My dissertation goals include integration and enhancement of biotic-level biogeographic methods and theory, particularly by revealing and reducing the role of pseudo-congruence in older analyses by using novel approaches. I employ approaches including areas of endemism and general area cladograms (area-based biogeography) to phylogeographic data and molecular clocks (taxon-based biogeography). This research

will ideally benefit the field of biogeography by demonstrating, for example, how

integrated approaches to historical biogeography can be used by conservation biologists

to reveal regions that are biologically most vulnerable and valuable for the future

retention of biodiversity. For instance, regions between areas of endemism tend to have

the highest species richness, but may not be a top priority for conservation because

these regions can be highly transitory and only ephemerally species rich during events

such as glacial or interglacial cycles (Hafner & Riddle, 2011). The successful development

of rigorous and integrative methods and approaches will ideally benefit both regional

conservation efforts in the North American deserts and provide case studies for

reference by biogeographers whose interest lie in other threatened regions.

Table 1.1. Comparison of North American desert characteristics. Comparative information gleaned from World Wildlife Fund (WWF)'s "Desert and xeric shrublands: Nearctic" ecoregions (WWF, 2013). * indicates that, despite the average elevations listed, the Mojave Desert is the location of Badwater Basin, Death Valley, which is -146 m below sea level.

Desert	Average Elevation (m)	Climate	Annual Rainfall (mm)	Dominant Plantlife
Chihuahuan	1,100 – 1,500	Subtropical/Tropical Dry	150 – 400	Creosote, tarbush, yucca, saltbrush, mesquite
Sonoran	Sea level – 2,000	Subtropical/Tropical Dry	< 90	Saguaro, creosote, cholla, cacti, bursage, mesquite
Peninsular	200 – 1,000	Subtropical Dry	< 100	Creosote, desert burrsage, xeric scrubs
Mojave	610 – 1,220*	Warm Temperate Dry	65 – 190	Joshua trees, creosote bush, all-scale, desert holly, white burrobush
Great Basin	4,000 – 6,500	Cold Temperate Dry	< 250	Sagebrush, saltbrush, winterfat
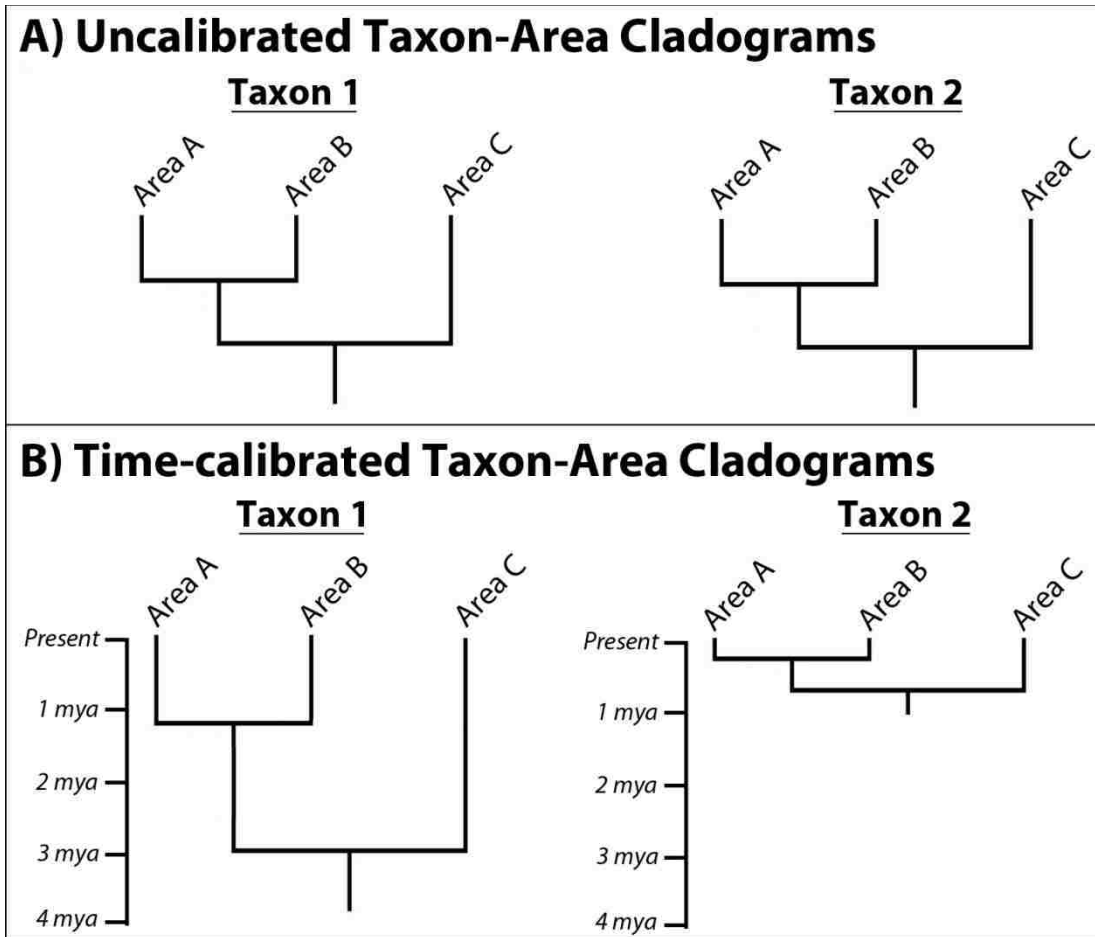
Figure 1.1. Pseudo-congruence in two hypothetical taxa (Taxa 1 and 2) that are found in three areas (Areas A, B, and C). A) Uncalibrated taxon-area cladograms in Taxa 1 and 2 appear identical. B) Time-calibrated taxon-area cladograms reveal that divergences in Taxon 1 are older than divergences in Taxon 2.
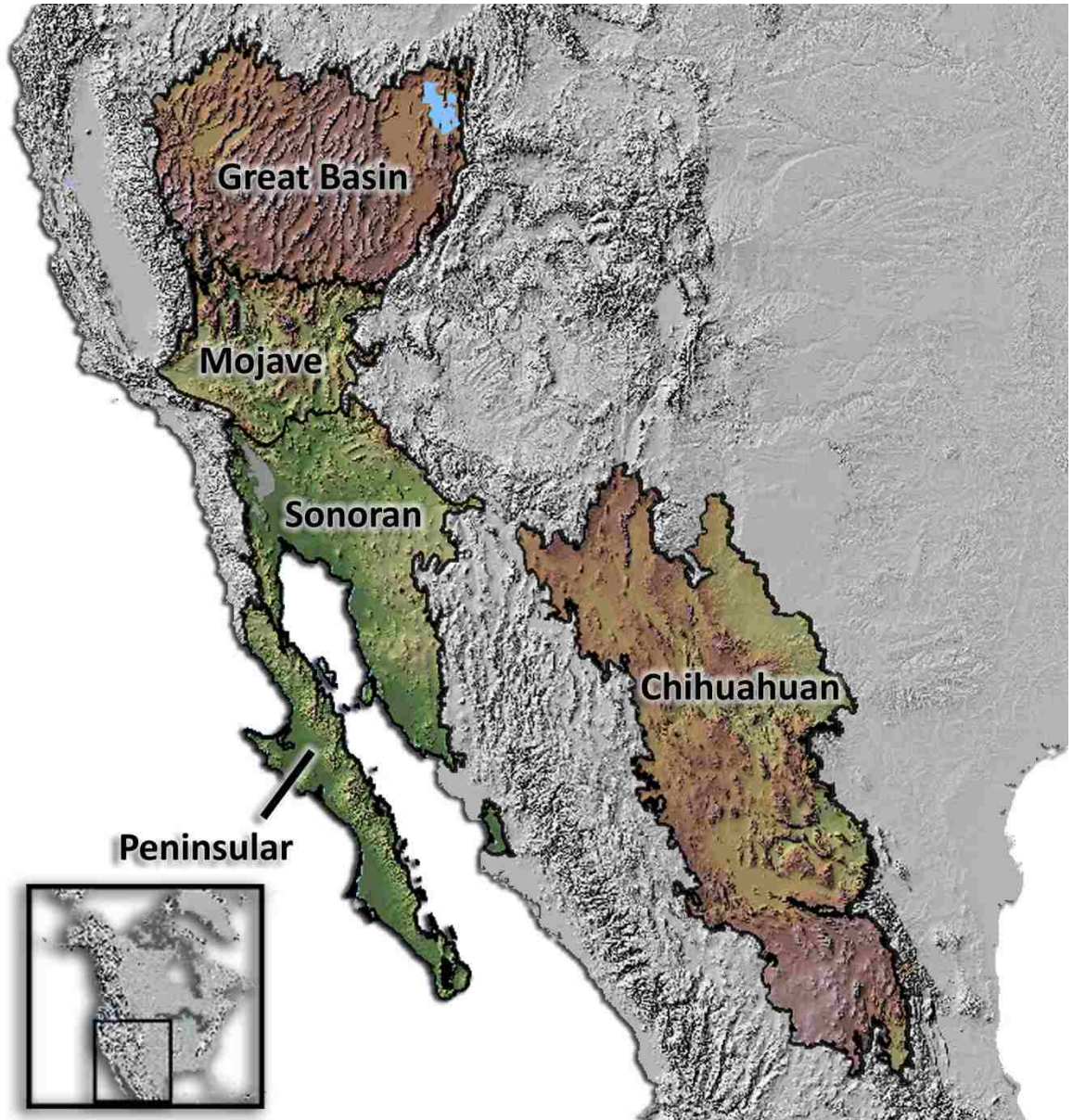
Figure 1.2. The North American deserts. Red-green shading indicates elevation, with dark red indicating higher elevations and dark green indicating lower elevations. The Peninsular Desert is recognized as a separate desert based on Hafner & Riddle (1997).

CHAPTER 2:

AN ARGUMENT FOR BETTER INTEGRATION OF PALEOCLIMATIC INFERENCE INTO NORTH

AMERICAN DESERT BIOGEOGRAPHIC RESEARCH

ABSTRACT

Both geoscientists and biologists strive to understand how the Earth's environments and

biodiversity will be altered by the release of greenhouse gases such as carbon dioxide

(CO_2) and methane (CH_4) – i.e., anthropogenically-driven climate change. Investigators

often use organismal responses to paleoclimatic change as a metric for estimating the

future distributions of Earth's biodiversity under various climate change scenarios.

However, biologists traditionally rely on general patterns of climate change ("cold vs.

warm," "dry vs. wet") rather than the processes that drive those patterns. Additionally,

other paleoclimatic factors (e.g., "long vs. short," "gradual vs. abrupt" periods of climate

change) may be equally as important for production and retention of biodiversity. An

improved understanding of paleoclimatic history would provide a foundation for

refining hypotheses about how organisms respond to climate change (such as

evolutionary diversification or range shifting, contraction, or expansion). I herein

describe several regional and global paleoclimatic forcings that have shaped the biotic

history of the North American deserts, which have been subject to complex topographic

and climatic changes across different timescales and for which extensive geologic,

climatic, and biotic datasets exist. First, I discuss several methods used to estimate and

reconstruct paleoclimates. Second, I describe how tectonic forcing altered regional

climate as i) the uplift of the North American Cordillera contributed to the full formation of the deserts, and ii) inter-continental plateau uplifts promoted global cooling by chemical weathering. Third, I explain how orbital forcing and atmospheric CO_2 maintained Northern Hemisphere glaciation and altered the frequency and strength of the El Niño / Southern Oscillation (ENSO). Finally, I discuss the implementation of future climate models into biogeographic models and I provide examples of how these events may have differentially affected North American desert biodiversity. This review demonstrates the importance of incorporating models of past temperature and precipitation change, as constrained by paleoclimatic proxy reconstructions, into historical biogeographic research to reduce the impact of issues such as pseudo-congruence (similar diversification patterns produced by dissimilar historical events) and improving species distribution model construction.

INTRODUCTION

Concentrations of greenhouse gases such as carbon dioxide (CO_2) and methane (CH_4) in Earth's atmosphere are increasing because of fossil fuel consumption (e.g., Meehl et al., 2007; Solomon et al., 2007; Hansen et al., 2008; Zachos et al., 2008). In order to prescribe effective conservation strategies, it is therefore vital to understand how regional environments respond to such atmospheric changes, including alterations in regional floral and faunal distributions and biogeographic patterns (Whittaker et al., 2005). Biogeographers aim to identify patterns and processes that shape biotic diversity, such as demographic responses (e.g., physical isolation or population

expansion/contraction to track suitable habitat) to historical events, and sometimes cast

models of future responses (e.g., Jezkova et al., 2009; Waltari and Guralnick, 2009;

Wiens et al., 2009). Biogeographers often try to identify specific environmental forcing

factors that govern paleoclimatic patterns because climate is a strong regulator of

species' ranges (Whittaker et al., 2005). If the magnitudes and modes of past range

expansion, contraction, or persistence of organisms, populations, and species in

response to historical warming and cooling trends can be used to model future

responses, biogeographers can provide us with a novel way to prioritize protected areas

(Araújo & Williams, 2000; Williams & Araújo, 2000; Franklin, 2010). For example, these

data can i) be used as a metric to predict future distributions based on climate change

trends, and/or ii) identify areas where organisms might be predicted to persist in the

face of future climate change (Guisan & Thuiller, 2005; Ackerly et al., 2010).

An aspect of biogeography that has recently gained popularity is comparison of

current species distributions or species distribution models (SDMs) with paleoclimatic

SDMs from the last glacial maximum (LGM) and mid-Holocene optimum. SDMs correlate

species collection locality data and climate layers to infer species' climatic

preferences/tolerances and, in turn, the possible extent of species' ranges under

different climate regimes (e.g., Carstens & Richards, 2007; Elith & Leathwick, 2009;

Jezkova et al., 2009; Graham et al., 2010; Brown & Knowles, 2012; Graham et al., 2013).

Robust SDMs can be informative for predicting how ranges change or persist under

changing climate, but there are several potential confounding issues with SDMs,

including lack of consideration for biotic interactions, community ecology, realized

versus fundamental niches, and the scale of climate models (Pearson & Dawson, 2003;

Guisan & Thuiller, 2005). General Circulation Models (GCMs) are often coarse in scale

and cannot capture microclimatic differences (Guisan & Thuiller, 2005) and climate

models can also be misleading in biogeography because they portray estimates of

climate at specific points in time (e.g., comparison of "cold vs. warm" or "wet vs. dry" at

two points in time) and do not account for the potential influence of climate change

progression (e.g., "gradual vs. abrupt" or "long-term vs. short-term" climate change) .

Attributes such as the rate and frequency of climate change may be more

informative for biogeographic inference - are organisms diversifying or shifting ranges in

response long- or short-term climate change; or gradual or abrupt climate change?

Organisms experience different adaptation rates in response to changing climate, and

adaptation rates can be constrained by dispersal rates, phenotypic plasticity, or genetic

change via microevolution (e.g., Visser, 2008). Although some species may experience

plastic responses and rapid microevolutionary adaptation (Hill et al., 2011), such as

exacerbated microevolutionary adaptation rates in Great Tits (*Parus major*) that are

correlated with strong annual selection and warmer temperatures (Husby et al., 2011),

many species cannot respond so rapidly.

Metapopulation dynamics influence the persistence of species' distributions in

part because population densities across a species's range vary based on climatic and

habitat suitability and fragmentation. Commonly, the edges of species' ranges have

lower densities and connectivity, making them more susceptible to local extinction (e.g.,

Davis et al., 1998; Opdam & Wascher, 2004; Gienapp et al., 2008; Anderson et al., 2009;

Hill et al., 2011; Fig. 2.1). Populations or species, particularly at the edge of ranges, may be able to genetically adapt to extreme temperatures if the temperature change is gradual through time, but they may not be able to adapt to temperatures if changes are rapid or abrupt (Alley et al., 2003; Parmesan, 2006), and in many cases, regardless of metapopulation density and connectivity, species may be more likely to go extinct (). In paleo-records, there is also evidence of numerous large North American mammal extinctions as well as local extinctions and ecosystem disruptions in the Appalachians following the Younger Dryas, which was a brief but abrupt cold period, ca. 10,800-10,000 years ago (Peteet, 2000; Alley et al., 2003; Muscheler et al., 2008). As a result, caution should be taken when using general qualitative estimates of earth history in biogeographic research and other aspects, such as rate of climate change, should be taken into consideration.

Further complicating climate change-related biogeographic inference is the concept of pseudo-congruence (similar biogeographic patterns from dissimilar historical events; Cunningham & Collins, 2004; Fig. 1.1). Dispersal and vicariant events may be difficult to tease apart in cases of climate change because climate change events can occur on different scales. For example, similar distribution patterns may be produced by vicariant events produced by older climate change events resulting from tectonic changes such as mountain uplift and dispersal events may be produced by younger climate change events such as orbital forcing that produces glacial-interglacial cycles (e.g., Thompson, 1990; Riddle & Hafner, 2006; Jezkova et al., 2009; Waltari & Guralnick, 2009; Hafner & Riddle, 2011).

To emphasize why caution should be taken and provide biogeographers with useful Earth history information regarding paleoclimate change, I herein provide a review of how paleoclimatic records are generated, how paleoclimatic patterns are used to infer processes, and some potential implications of using this information in biological research. In particular, I focus on the North American desert paleoclimatic patterns and processes and describe potential biological implications using examples within the North American deserts biotas. First, I describe why the North American deserts provide a good model system for exploring the relationship between shifting paleoclimates and biological responses. Second, I review some standard techniques and proxies used to infer paleoclimates. Third, I address two primary processes (tectonic change and orbital forcing) that have influenced climates in the North American deserts and how these processes have driven historical changes in atmospheric CO_2 concentrations and local climate patterns. Finally, I describe the benefits and limitations of how ongoing climate change trends are being used to project future climate change and discuss how improper integration of past and future climate models can lead to erroneous inferences in biogeographic research.

The North American Deserts

The North American deserts (Fig. 1.2) provide a model system in biogeography because they are relatively young arid landscapes (with early development of regional desert formation occurring in the past 2.5 million years) with young arid-adapted biotas (Riddle & Hafner, 2006). These desert regions are subject to extreme temperature and

18

precipitation variability, and they span a broad latitudinal and elevational gradient –

from the southern low elevation warm deserts (the Peninsular, Chihuahuan, and

Sonoran deserts) to the northern, higher elevation deserts (the warm Mojave and cold

Great Basin). These deserts have distinct arid-adapted biotic assemblages, and many

taxa have sister lineages in adjacent deserts, which facilitates comparative analysis

between environmentally similar and dissimilar communities (Hafner & Riddle, 2011).

Axelrod (1983) presented a model of desert formation wherein arid patches

began forming prior to their coalescence into the large regional deserts that exist today.

Subsequently, two kinds of events contributed to the full formation of the North

American regional desert biotas. First, ancestrally widespread biotas were fragmented

as barriers arose through Neogene (primarily Miocene and Pliocene; roughly 10-2.5

mya) geologic activity that resulted in the rapid uplifting of mountains and plateaus.

Climatic alterations, such as modified atmospheric circulation patterns and rain shadow

effects, were associated with these Neogene tectonic events. Second, Quaternary

(Pleistocene and Holocene; 2.5 mya - present) climate oscillations promoted arid habitat

contraction during glacial periods and expansion during interglacial periods (Fig. 2.2;

e.g., Thompson, 1990; Riddle & Hafner, 2006; Jezkova et al., 2009; Waltari & Guralnick,

2009; Hafner & Riddle, 2011).

The complex climatic history of this region make it an ideal system to explore

detailed paleoclimate information. The North American deserts are a region where

there is the potential for substantial amounts of overgeneralization of climate

information that could produce misleading biogeographic inferences, such as misleading

species distribution models and increased amounts of pseudo-congruent biogeographic patterns.

PALEOCLIMATIC INFERENCE METHODS

In science, even if there is a strong hypothesis, results are only as robust as the methods implemented and data analyzed. The appropriateness of methods is an issue that can be problematic for scientific research that involves reconstructing history, such as historical biogeographic distributions in the field of biology. For that reason, it is important to understand the methods and proxies used for estimating paleoclimates when using paleoclimatic information is in turn used for biological analysis (e.g., what information is being used to determine if historical climates were warm or cold; wet or dry?).

When reconstructing paleoclimatic conditions, factors that need to be estimated to infer paleoclimatic processes include incident solar radiation (insolation), temperature, and precipitation. Insolation, the amount of solar energy that strikes the top of Earth's atmosphere at any point in time, is predictable based on the orbital position of Earth, and thus records can be measured using calculations of how solar radiation is distributed with respect to orbital parameter perturbations through time (Laskar et al., 2004). Alternatively, temperature and precipitation paleoclimatic records are inferred using a variety of techniques for generating proxy data. There are numerous paleoclimatic proxies that exist (at least 20; Jones et al., 2001; Henderson, 2002; Jones & Mann, 2004), from documentary-based proxies to natural proxies such as

tree rings and coral data. I herein describe a few commonly used techniques used to infer global patterns of glacial-interglacial cycles, including i) sea data, such as sea surface and deep sea temperatures and stable isotopes in marine foraminferans and ostracods ice cores and sea data, and ii) ice core data, such as dust and gas concentrations as well as stable isotopes in the ice. Discussed methods were chosen because they are frequently used by paleoclimatologists and allow for inferences further back in history than other methods, such as various tree and coral proxy data, and the generated glacial-interglacial patterns have become readily used by evolutionary biologists (Jones et al., 2001; Jones & Mann, 2004).

Some of the most common deep sea climatic proxies include proxies based on marine foraminfera and ostracods. The calcite shells of these organisms can be extracted from dated marine sediment layers and $\delta^{18}O$ and $\delta^{13}C$ isotopic ratios measured. $\delta^{18}O$ is a ratio of ^{18}O to ^{16}O isotopes; because ^{18}O is a heavier isotope, more of it is present in oceans during glacial time periods when ice sheets extract the lighter ^{16}O isotope (Zachos et al., 2001). $\delta^{13}C$, a carbon isotopic ratio of ^{13}C to ^{12}C, is another approach to estimating paleoclimates based on oceanic thermohaline circulation patterns. The ocean's thermohaline circulation influences global heat distribution by warm and cold currents and influences atmospheric CO_2 concentrations by exchanging CO_2 between the deep ocean and atmosphere (Raymo, 1994). The North Atlantic Deep Water (NADW) is a water mass of sinking, highly saline water that forms and strengthens during warmer interglacial cycles. The NADW is correlated with high initial $\delta^{13}C$ levels, and thus marine formaniferan $\delta^{13}C$ analysis can reveal paleorecords of the

NADW and consequently of global climate (Raymo, 1994). In addition, ancient

foraminferans preserved in marine sediments can be used to estimate sea surface and

deep sea temperatures by comparisons of modern species assemblages and their

habitat preferences (Raymo, 1994).

Glacial-interglacial events can also be inferred using proxy data from ice cores,

such as dust content and greenhouse gas concentrations (CO_2 and CH_4) in glacial air

bubbles, and $\delta^{18}O$ and δD (deuterium, or heavy hydrogen) in the ice. Higher dust

concentrations cool temperatures by blocking solar radiation (Raymo, 1994).

Greenhouse gases are strong indicators of global temperature because these molecules

absorb heat, preventing heat from being reflected back to the sun, and the heat is then

re-radiated back toward the surface and lower atmosphere. δD is also a temperature

proxy, and is similar to inferences made with $\delta^{18}O$, because the ratio of deuterium to

hydrogen (^2H to ^1H) is higher in sea water and lower in precipitation. Consequently,

there is a linear and positive correlation between annual surface temperature and δD

(Petit et al., 1999).

Proxies are used under the assumption that historical patterns are the current

patterns we observe today in similar scenarios. For example, biological proxies, such as

species assemblages and isotopic ratios in the calcite shells of foraminfera and ostracods

or pollen grains (see Yasuhara et al., 2012 for a review), are used to infer paleoclimate

records based on current environment-growth relationships in similar, extant

organisms. However, there are possible limitations to these inferences. For example,

biologists might be concerned about the phylogenetic and ecological similarity of the

ancestral organisms to their modern relatives – parameters that will dictate whether the ancestral organisms have the same environmental preferences or environment-growth relationships as their modern relatives.

CLIMATE-INFLUENCING PROCESSES

Neogene Tectonic Activity

In addition to mountain and plateau uplift creating physical barriers (i.e., separation by mountain ranges) for many organisms, uplift can influence both local and global climates by: i) creating rainshadow deserts that are formed by the new mountain or plateau, blocking the transfer of moist air and rain from reaching the other side of the range; ii) altering global circulation patterns in the atmosphere, which in turn alters ocean circulation; and iii) removing CO_2 from the atmosphere by silicate weathering, and thus potentially decreasing global climate temperatures (Raymo & Ruddiman, 1992; Zachos et al., 2001).

Aridland formation in western North America dates back to the Oligocene and mid-Miocene. The Farallon plate was a plate between the Pacific and North American plates that broke apart and subducted below the North American plate between 33-29 mya, and produced an active strike-slip transform fault between the Pacific and North American plates (Atwater, 1970; Blake et al., 1978; Coney, 1987). Global climate cooling post-mid-Miocene Optimum then resulted in less rainfall in western North America between 15-8 mya, creating the origin and expansion of arid shrub and C3 grasslands, and eventually of C4 grasslands (as reviewed in Riddle, 1995; Kohn & Fremd, 2008).

Paleoenvironmental changes and full regional deserts were then formed by rapid

mountain and plateau uplifting in the mid to late Miocene into the early Pliocene (ca. 5 -

2.5 mya) during a "late Cenozoic Cordillerra-wide event," which consisted of uplifting of

the Colorado Plateau, Rocky Mountains, Sierra Nevada, Sierra Madre Occidental, and

Cascade ranges (Unruh, 1991).

This uplift altered local biotic distributions by fracturing the western North

American landscape and creating regional deserts, and impacted global biodiversity by

contributing to the onset of global cooling trends (Ruddiman et al., 1988). Some

researchers have suggested that even a small amount of uplift of the North American

cordillera was likely substantial enough to promote significant cooling in North America

(Foster et al., 2010).

Rainshadow Deserts

As a result of Neogene uplift events, rainshadow deserts were created. The Sonoran and

southern Mojave deserts transformed from semidesert and subtropical thornscrub into

desert scrub, the Chihuahuan Desert from a semi-arid savannah into a desert

scrub/woodland, and the Great Basin and northern Mojave deserts from woodland

savannahs into shrub-steppe/woodlands (Riddle, 1995; Kohn & Fremd, 2008). As the

environment changed, organisms adapted, dispersed, or went extinct (Thompson, 1991;

Riddle, 1995; Kohn & Fremd, 2008). Aridlands are harsh environments, often with

extreme temperatures and scarce precipitation. As a consequence, the formation of the

aridlands produced unique biotas, and potentially very rapid evolution in plants

24

(Stebbins, 1952) and radiations of animals such as rodents (Riddle, 1995; Hafner et al., 2007). These unique biotas were potentially formed by old lineages going extinct and increasing production and selection rates of new lineages that were better adapted to arid environments (e.g., Riddle, 1995; Riddle & Hafner, 2006; Hafner & Riddle, 2011).

Global Atmospheric Circulation Patterns

Aridification and global cooling events were exacerbated between 13 and 8 mya, when there were several plateau uplifts that altered global climate, including the Tibetan, Altiplano, and the Colorado Plateaus (Ruddiman & Kutzbach, 1989; Kohn & Fremd, 2008). The altered global circulation patterns are proposed to have been a significant factor in the onset of the Quaternary climate oscillations that globally altered biotic distributions by changing temperature and precipitation patterns.

All of the plateaus played a role in subsequent global cooling, but the Tibetan Plateau in particular changed the degree of seasonality about 10-8 mya with substantial altitudinal increases, creating a barrier that resulted in stronger Western Pacific westerly winds (Zhisheng et al, 2001). Western Pacific westerly winds are linked to the California Current, and the California Current intensified roughly 10 – 7.6 mya (Barron et al., 2002). California Current intensification then altered western North American climate by creating intensified summer dry seasons and extended winters and snow cover, which increased albedo (the amount of solar radiation reflected from the surface).

The uplift and closure of the Panama Isthmus ca. 4 mya may have also produced further cooling by diverting warm, moist air to the high latitudes that fed the growth of

ice sheets. However, it should also be noted that debate exists regarding whether the Panama Isthmus had the opposite effect on global climate (i.e., substantially warming the Northern Atlantic because of stronger ocean heat transport; Raymo, 1994), because there is disagreement over when the isthmus closed and the relative impact the closure had on global climate (e.g., Duque-Caro, 1990; Coates et al., 1992; Lunt et al., 2008).

Chemical Weathering

In addition to the alteration of atmospheric and oceanic circulation patterns, mountain and plateau uplift has another influence on climate: the removal of CO_2 by increased chemical weathering (Raymo, 1994). Mountain and plateau uplift provides more surface area for erosion, and rain is more often caught by the tops of mountains, which increases weathering rates. Physical weathering increases the amount of silicates, which then results in chemical weathering where CO_2 participates in breaking down silicates, and CO_2 is removed from the atmosphere (Raymo, 1994). With the removal of atmospheric CO_2 came an associated decrease in global temperatures, and in this way, the late Cenozoic Cordillerra-wide event may have contributed to the initiation of Northern Hemisphere glaciation during the Plio-Pleistocene (Raymo, 1994). The participation of the North American cordillera uplift in the onset of North American glaciations altered organismal diversity and distributions across the continent and is one of the most frequently induced geologic explanations of regional biodiversity distributions because it resulted in both geologic barriers and climate changes (the two primary hypotheses of desert biodiversity origins).

Orbital Forcing

The Earth's orbit maintains a constant rhythm and a climatic mean. Nonetheless, orbital

parameters are an important climatic aspect that alters the amount of insolation

received by the Earth. Thus, orbital forcing has global impacts as well as differential

latitudinal impacts that occur on predictable timescales that organisms have been

responding to throughout history. Particularly, orbital parameters often alter Earth's

climate on a shorter timeframe than tectonic forces (10,000 to 1,000,000 years as

opposed to 100,000 to 10,000,000 years) (Zachos et al., 2001), and their role in

influencing the strength and frequency of the El Niño/Southern Oscillation (ENSO) can

occur on the order of decades to centuries (Cane, 2005).

Orbital parameters alter climate on three time scales (together referred to as

Milankovitch cycles): i) precession, which has a full cycle on the order of 21 ky, is the

wobble of the Earth that determines which hemisphere is closest to the sun in which

season, and thus seasonality of the Earth; ii) obliquity, which occurs approximately

every 41 ky and is the change in the degree of Earth's tilt (and thus degree of seasonal

contrast); and iii) eccentricity, the variation in the shape of Earth's orbit, which occurs

on the order of every 100 ky and modulates precession severity (Zachos et al., 2001).

Consequently, orbital forcing participates in climate changes in two distinct ways: i) a

relatively slower, gradual modulation of ice ages, and ii) rapid climatic changes by

altering seasonality, which in turn influences the frequency and amplitude of ENSO

cycles (Overpeck & Webb, 2000; Cane, 2005). These two distinct processes may result in

different effects on biotic distributions. For example, some lineages may be more

affected by overall climate (e.g., an average temperature increase may alter species that have temperature-dependent sex determination, such as desert tortoises in the Mojave and Sonoran deserts; Spotila et al., 1994) whereas other lineages may be more affected by changes in seasonality (e.g., earlier spring migrations from many bird species observed across North America; Walther et al., 2002).

Plio-Pleistocene Glacial-Interglacial Cycles

The Plio-Pleistocene glacial-interglacial cycles are strongly tied to biotic distributions because glacial periods result in colder climates, and specifically in the North American deserts, smaller patches of arid habitat and expansions of montane and aquatic habitats. Moreover, these effects appear to be more extreme in the higher latitude deserts of the Great Basin (a cold desert) and the Mojave (a moderate warm desert) because of the enhanced proximity to ice sheets and more abundant pluvial lakes (Fig. 2.3; Hewitt, 2004). Tectonic events, such as the closure of the Panama Isthmus and the uplift of the North American cordillera, increased rates of chemical weathering and increased the amount of atmospheric dust from volcanism (blocking solar radiation), and are proposed to have initiated the Plio-Pleistocene glacial-interglacial cycles. These tectonic events date to 4.8 mya with long-term cooling trends that resulted in cooler, drier environments in western North America starting 3.2 mya with full glaciation starting 2.4 mya (Thompson, 1991). However, the pacing of the sequence of glacial-interglacial events conform more to the Milankovitch cycles of orbital forcing and

associated positive feedbacks, such as the ice albedo feedback (where increased

amounts of ice promote the growth of more ice by reflecting solar radiation).

Until about 1 mya, glacial-interglacial cycles were dominated by relatively lower

amplitude 41 ky cycles. From 420 kya until present (the Late Pleistocene), 100 ky cycles

with increased amplitude began, and the cycles between 1 mya and 420 kya were

intermediate in frequency and amplitude (Petit et al., 1999; Augustin et al., 2004). These

100 ky cycles are consistent with eccentricity cycles and the amplifications during these

time periods may be the result of precession intensity modulation (Zachos et al., 2001).

However, how eccentricity modulates climate is still unclear because eccentricity cycles

are not reflected in large changes in mean annual insolation cycles (Augustin et al.,

2004). However, Augustin et al. (2004) noted that the switch from 41 ky to 100 ky cycles

are correlated with increased ice volume. Thus, frequency and intensity shifts of glacial-

interglacial cycles may be modulated by the ice albedo feedback, and may also impact

the degree and nature of biotic diversification because of the extent of the ice sheets

and associated changes in air circulation patterns (e.g., increasing or decreasing the

number of pluvial lakes). As a result, biodiversity distributions are likely to be influenced

by alteration of suitable habitats (see Fig. 2.2 for hypothesized habitat alterations).

El Niño / Southern Oscillation

Climatic variance in relation to orbital forcing as well as CO_2 concentrations can occur on

the order of decades to centuries (Cane, 2005). The El Niño / Southern Oscillation

(ENSO) dramatically alters precipitation patterns and results in extreme droughts and

floods, occurs in 2 to 7 year bands, and is observable in paleoclimatic records,

particularly in oxygen isotope $\delta^{18}O$ and sea surface temperature records (Cane, 2005).

The strength of the ENSO is controlled by the contrast in temperatures between the

eastern and western Pacific, where a stark contrast (i.e., colder eastern temperatures

due to equatorial upwelling) results in more extreme pressure differences, producing

stronger easterly winds. Stronger winds then produce a greater pull on the eastern

oceanic thermocline which pulls up more cold water, increasing the pressure differences

between the east and west Pacific (Cane, 2005). Although this is a positive feedback,

runaway effects are mitigated because the thermocline depth (and thus the pull of cold

water) lags with the winds that are driving them, producing the oscillating effect in

changing pressures (the ENSO). Accordingly, the ENSO consists of two extremes: the

warm state (El Niño) and the cold state (La Niña).

The ENSO extremes modify the pattern of the jet stream and greatly alter the

yearly climate in western North America. For instance, the southern warm deserts (the

Peninsular, Chihuahuan, Mojave, and Sonoran deserts) are warmer and drier during the

La Niña events, producing more droughts. However, during the El Niño events, the

southern warm deserts experience wetter, colder winters, and the northern cold desert

(the Great Basin) experiences wetter summers (Ropelewski and Halpert, 1987).

Consequently, frequency and amplitude of ENSOs can drastically affect the population

dynamics of organisms with distributions that are restricted by thermal and

precipitation tolerances. These decadal changes can impact a variety of biogeographic

variables, from soil and vegetation succession to plant/animal diversity, as well as the

frequency and probability of environmental disturbances. The resulting effects increase difficulty of buffering climatic extremes in the American Southwest, where already extreme desert conditions result in slow biotic population growth as well as low soil moisture and organic matter (Swetnam & Betancourt, 2010). In particular, when vegetation is affected by decadal climate variation, vegetative species assemblages may change, and any animals or other vegetation dependent on the pre-existing vegetation will in turn also be altered (e.g., Swetnam & Betancourt, 1998).

Plio-Pleistocene ENSO records using sea surface temperature proxy data suggest that the warmer Pliocene period (5 – 3 mya) had a continual, permanent El Niño-like climate that transitioned to intermittent cycles with the onset of cooler sea surface temperatures and Northern Hemisphere glaciations (Wara et al., 2005; Fedorov et al., 2006). Paleoclimatic records indicate that the frequency and amplitude of ENSO events are strongly tied to Earth's seasonality, which is controlled by the orbital forcings of precession (seasonality timing in each hemisphere) and obliquity (the contrast of seasonality). Analysis of the early and mid-Holocene ENSO records suggests that ENSO amplitudes were reduced or absent (Cane, 2005). Weakened ENSO can result from orbital configuration, particularly the state of precession and obliquity, when the Northern Hemisphere insolation is strongest during the late summer and fall and results in largely warm, stable, and wet conditions in the tropical Pacific (Cane, 2005).

Variance in ENSO frequency is also controlled by the amount of atmospheric heating that is generated by sea surface temperature changes, the strength of winds, and the depth and steepness of the eastern Pacific thermocline (Cane, 2005).

Alterations of ENSO variability can also result from orbitally-independent perturbation

to these parameters, such as increases in CO_2, producing higher global temperatures

(Overpeck and Webb, 2000). In conjunction with anthropogenically-induced increased

CO_2 emissions, there have been numerous ENSO events in the past century, during

which La Niña-related droughts have persisted in the southern warm deserts from the

late 19th century to the present (Overpeck & Webb, 2000).

CURRENT AND FUTURE CLIMATE TRENDS

General circulation models of future climate are becoming increasingly used in

biogeographic research to project the future of regional biodiversity (e.g., Jezkova et al.,

2009; Waltari & Guralnick, 2009; Wiens et al., 2009). Predicting species distributions in

modern times can be difficult because of incomplete sampling and/or sampling bias

(Peterson, 2001). Future predictions may have compounding error of climate and

evolutionary model selection, parameterization, and model interpretations, and

scientists cannot test the performance of predictive climate and evolutionary models

(Araújo & Guisan, 2006). It is important for biogeographers to note that error can exist

both on the side of evolutionary model selection and inference as well as the potential

unpredictability of future climates.

Even though paleoclimatologists can infer the relationship between past CO_2

levels and climate, the interactions between the various processes altering climate is

still not fully known. For example, it would be easier to predict future patterns if all

climate altering mechanisms acted independently, but the complexity of their

32

interactions and feedbacks, such as tectonic change resulting in altered sensitivity of

Earth's climate to orbital parameters, can reduce predictability of future climate models

(Zachos et al., 2001). Moreover, sudden aberrations of climate (on the order of 100 –

10,000 years) produce more extreme amplitudes and are unpredictable because they

are the result of highly nonlinear responses in climate forcing and/or the result of

crossing a climatic threshold. These nonlinear responses or thresholds are still not fully

understood, and thus are not currently predictable (Zachos et al., 2001).

We are currently in the longest interglacial cycle during the past 420 ky, when

there was a shift from longer cycles with less extreme amplitudes to shorter cycles with

more extreme amplitudes (Petit et al., 1999). It is still not clear if greenhouse gas

emissions are extending the length of the current interglacial cycle or if they are making

the interglacial cycle warmer. Predictive future climate models exist, and we can infer

future CO_2 levels resulting from anthropogenic activities by examining the frequency

and quantity of fossil fuel emissions. Some models predict that within just 400 years

from now, humans will have released 5,000 gigatons of carbon by burning fossil fuels,

which would raise CO_2 levels to around those of the Eocene Climatic Optimum, which

was just barely cool enough to retain the Antarctic Ice Sheet (Zachos et al., 2008).

In addition to increasing global temperatures, there are debates about how the

frequency and amplitude of ENSOs will change in response to anthropogenically driven

CO_2 increases. Whereas some future models indicate that there will be more frequent

and stronger ENSOs that are more similar to those cycles observed in the warm Pliocene

(Fedorov et al., 2006), other simulations show a higher tendency toward La Niña-like

states, no change in ENSOs, or fewer and weaker ENSOs (Cane, 2005). Uncertainty in estimations can occur because the impact of greenhouse gas emissions on ENSO climatology may not be fully understood (Cane, 2005). However, despite these limitations, analysis of ENSOs in the 1980s and 1990s compared to previous centuries indicated that ENSOs were overall stronger and more frequent, and it has been inferred that this is due to rapid increases in CO_2 from anthropogenic activity (Trenberth & Hoar, 1997), and prediction of future ENSOs within a couple of years has been relatively reliable (Cane, 2005).

Alternatively, some precipitation patterns, such as the North American Monsoon, provide further difficulty for developing future models because they may not be controlled by the ENSO. The North American Monsoon produces the rainy July to September months in the southwest with the contrasting dry remainder of the year. Even though there is yearly variability in North American Monsoon strength, it does not appear to be strongly tied to ENSO fluctuations (Adams & Comrie, 1997).

As our climatic predictive abilities improve, there can be value to using future climate models in biogeographic research. However, biologists should still be aware of the limitations of future climate models for creating predictive species distribution models (SDMs), particularly because there are both biological and earth history limitations (e.g., our understanding of complex biotic response to changing environments as well as our understanding of climate feedback systems).

WHAT DOES THIS MEAN FOR BIOGEOGRAPHY?

Refined techniques for incorporating climate models into biogeography are rapidly developing and are necessary for estimating the potential impact of ongoing climate change on biodiversity. Biogeographers should therefore consider how paleoclimatic proxy inference, processes ("gradual vs. rapid," "long-term or short-term"?), and development of future models could impact interpretations of biogeographic analyses.

Climatic proxies are used under the assumption that historical patterns are comparable to current patterns. In particular, fossil species and species assemblages of formaniferan and ostracods are used to infer historical temperatures based on current environment-growth relationships of morphologically similar extant species (Yasuhara et al., 2012). However, these proxies would be rendered inappropriate if extant species are phylogenetically dissimilar or experience different ecological constraints, perhaps as a result of adaptation to changing climates. For this reason, biogeographers should critically consider which paleoclimatic models are being implemented in their analyses and if the models are corroborated by other abiotic paleoclimatic proxies.

Paleoclimatic processes are also important to understand because these processes may alter biodiversity more than merely "warm vs. cold" or "wet vs. dry" comparisons of two divergent points in time, although many models of habitat and climatic suitability disregard mechanisms driving species' responses (Lavergne et al., 2010). For example, organisms often experience different rates of adaptation, and some lineages may be able to adapt if extreme temperature change is gradual but not if they are abrupt (Alley et al., 2003; Parmesan, 2006; Visser, 2008). Some species may be able

to rapidly adapt to changing climates, whereas others risk extinction from rapid climate change trends (Davis & Shaw, 2001; McLaughlin et al., 2002; Lavergne et al., 2010; Husby et al., 2011). Differing rates of adaptation and climate change may render historical distribution estimates inaccurate because species distribution models (SDMs) extrapolate current environmental preferences to paleoclimatic models (Watari et al., 2007). Species' realized niches may have shifted (Guisan & Thuiller, 2005) and/or species' ranges may have altered more in response to short-term climate changes (e.g., decadal shifts of ENSOs) than slow, long-term changes from the last glacial maximum (LGM) to present. For example, decadal shifts of ENSOs alter vegetation and soil in the American Southwest, which in turn can affect regional species assemblages (Swetnam & Betancourt, 1998, 2010). Disregarding these temporally diverse events may in turn lead to the increased prevalence of pseudo-congruence in biogeographic datasets.

Implementation of future climate models is a novel technique that facilitates inference of potential impact of climate change trends on biodiversity (e.g., Thomas et al., 2004; Carstens & Richards, 2007; Elith & Leathwick, 2009; Jezkova et al., 2009; Graham et al., 2010; Brown & Knowles, 2012; Graham et al., 2013). However, similar to the production of paleo-SDMs, future SDMs extrapolate current environmental preferences of species to future climate models. These analyses may be inaccurate if future climate models are unreliable because of non-linear climate changes and crossing climate thresholds (Zachos et al., 2001). Future SDMs also do not include mechanisms driving species' responses, such as rates of adaptation and inter-specific interactions (Lavergne et al., 2010). As a consequence, rates of adaptation can alter potential future

distributions, just as they may have influenced historical range shifts in species (Somero, 2010; Hoffman & Sgrò, 2011).

In many cases, refining organismal datasets for use in climate analysis may be difficult or not possible for all species - particularly rare species or species with limited information. For example, incorporating demographic and climatic processes into paleo and future SDMs requires detailed knowledge of each species and long-term data series (Thuiller et al., 2008). However, in model construction, the limitation of results should be acknowledged and appropriate climatic and demographic data implemented when possible to develop a more robust depiction of the impact of climate change on species' distributions. Furthermore, using divergence dating techniques when possible can provide more robust interpretations regarding the formation of biodiversity, because these techniques can reveal pseudo-congruent patterns that may otherwise go undetected (e.g., Riddle et al., 2008; Mantooth & Riddle, 2011).

CONCLUSIONS

Many processes have contributed to the paleoclimate of the North American deserts based on both regional and global perturbations, although a lot is still unknown about both the past and the future of this region. Parsing out the exact events that resulted in the observed patterns is a difficult process that climatologists are still refining, and additional understanding of paleoclimatic processes may produce more reliable estimates of future climate models. Both paleoclimatic and biogeographic research address patterns that are produced by inference of complex mechanisms that interact in

ways scientists can only infer by proxy data. Thus, I urge that caution should be taken when inferring biotic responses to future global climate change because there is a substantial amount that is still unknown about i) the interaction between these mechanisms for estimations of future climate models, and ii) which climatic and environmental thresholds are most impacting organisms.

In western North America, a vast array of both global and regional mechanisms has altered regional climates during the late Cenozoic, potentially producing many pseudo-congruent patterns of diversification among organisms and not considering the detailed paleoclimatic information may produce misleading species distribution models. An enhanced understanding of these mechanisms can allow biogeographers the ability to refine hypotheses about biotic response to each of these different events in the North American deserts (a model system for examining biotic diversification) and may provide scientists with a greater understanding of what climatic mechanisms are most important for regional biotic composition (e.g., "long vs. short," or "gradual vs. abrupt" climate changes). As more succinct understandings of paleoclimatic processes are developed and more robust future climate models are generated, we may be able to more precisely predict how biotas will change in conjunction with anthropogenically-induced climate change.

Table 2.1. Descriptions of described paleoclimatic proxies.

Method	Inferences	Description	Citation
Astronomical calculations + orbital parameters	Insolation	Amount of solar radiation striking surface.	Laskar et al. (2004)
Foraminiferans and ostracods	Species assemblages	Comparison of paleo-assemblages to the habitat preferences of similar extant species; for sea surface and deep sea temperatures.	Raymo (1994)
	δ^{18}O in calcite shells	^{18}O is heavier than ^{16}O and more is present in oceans during glacial cycles.	Zachos et al. (2001)
	δ^{13}C in calcite shells	The North Atlantic Deep Water is correlated with high amounts of ^{13}C and NADW is strongest during warm interglacial periods.	Zachos et al. (2001)
Ice cores	Dust content in air	Dust reflects solar radiation and increased concentrations indicate cooler temperatures.	Raymo (1994)
	Greenhouse gas concentrations in air (CO_2 and CH_4)	Greenhouse gases hold heat and prevent reflection, and increased concentrations indicate warmer temperatures.	Petit et al. (1999)
	δD in ice	Deuterium is heavier than hydrogen, and thus greater amounts of δD during warmer periods.	Petit et al. (1999)
	δ^{18}O in ice	^{18}O is heavier than ^{16}O and greater amounts of δ^{18}O are present during warmer periods.	Petit et al. (1999)
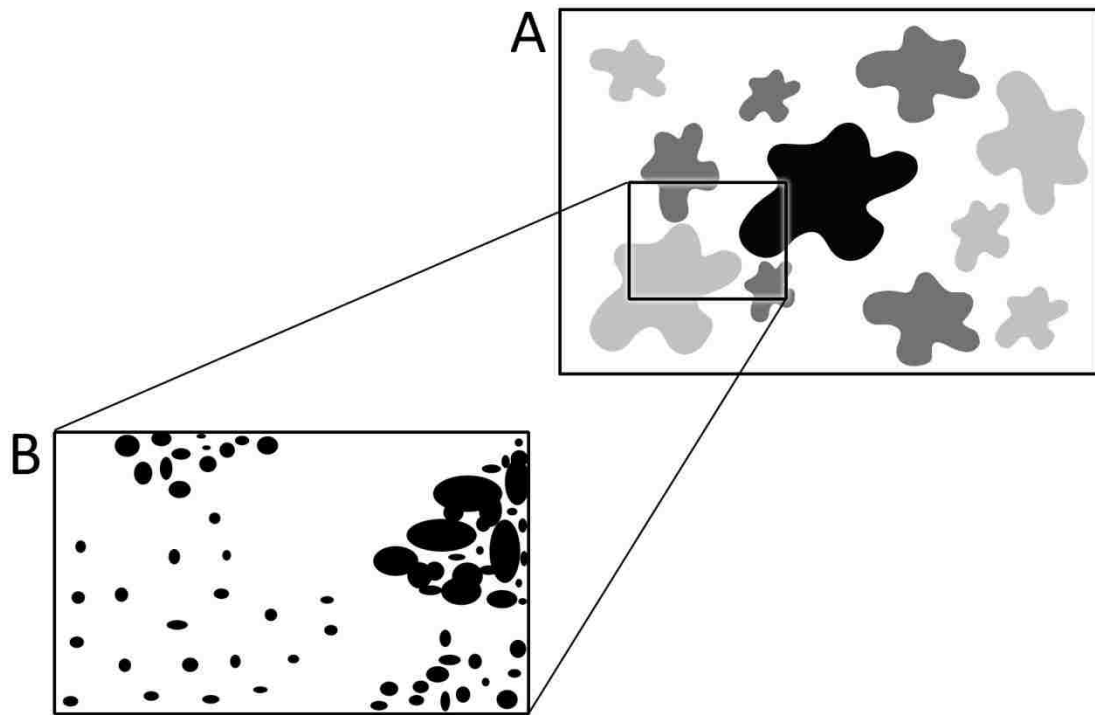
Figure 2.1. Model of (A) metapopulation densities across a species' range, where darker colors indicate populations with increased density and lighter colors indicate populations with decreased density, and (B) the connectivity of suitable climate and habitat in these areas (adapted and modified from Opdam & Wascher, 2004). The edges of species' ranges are frequently less stable during periods of environmental change because of less suitable habitat and decreased habitat connectivity.
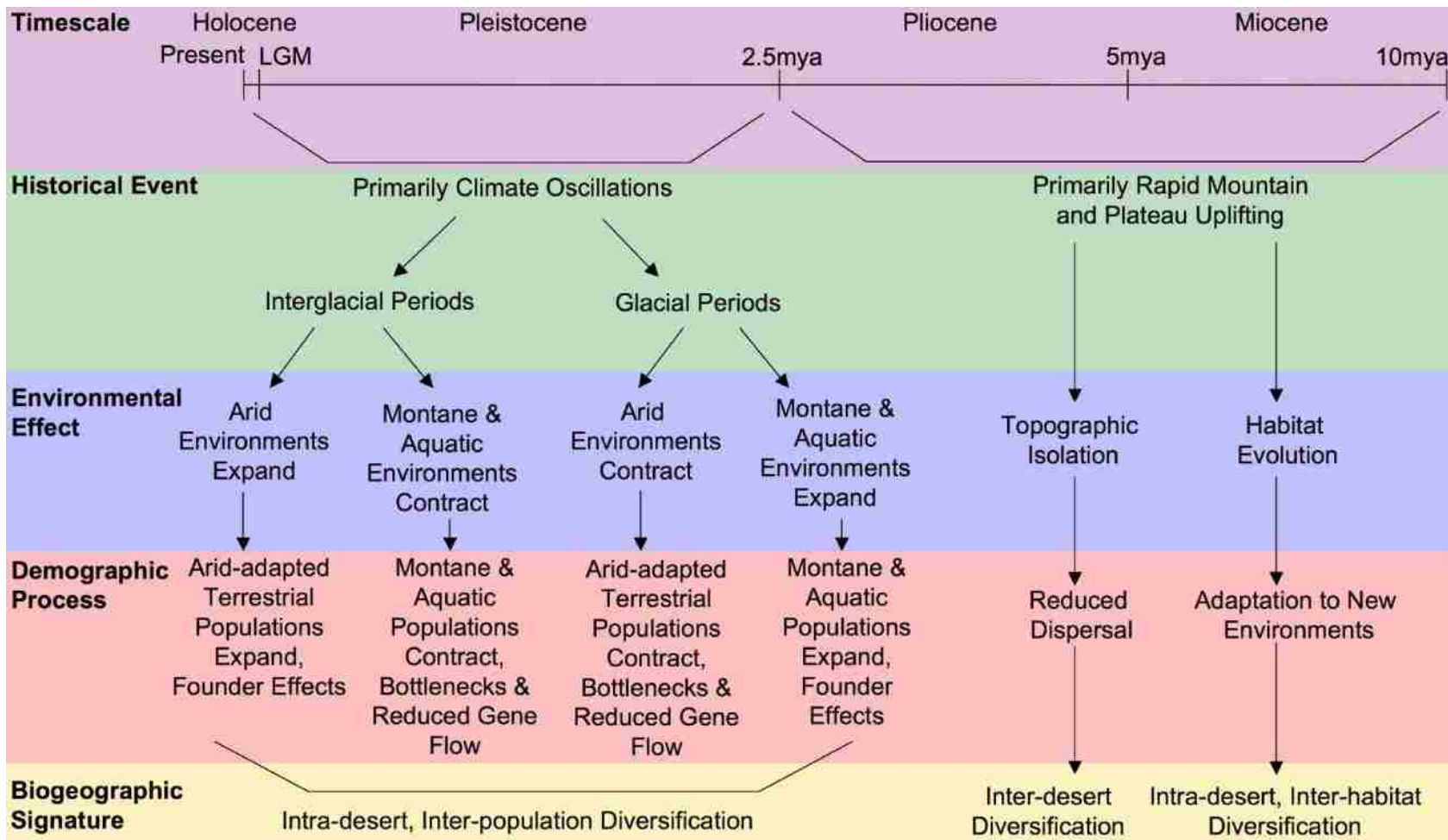
Figure 2.2. Hypothesized influence of historical events (climate oscillations and geologic events) on biogeographic patterns of the western North American biodiversity.

Figure 2.3. Pleistocene reconstruction of western North America circa 126,000 years ago, indicating glacial extents and prevalence of pluvial lakes. This image was obtained and modified from Dr. Ron Blakey, http://www2.nau.edu/rcb7/nam.html.

CHAPTER 3:

PACT PROTOCOL MODIFICATIONS TO REDUCE PSEUDO-CONGRUENCE, DISTINGUISH

UNIQUE FROM GENERAL PATTERNS, AND FACILITATE LIKELIHOOD RECONSTRUCTION:

A CASE STUDY IN THE NORTH AMERICAN WARM DESERTS

ABSTRACT

Phylogenetic Analysis for Comparing Trees (PACT) is a multi-clade analytical method

that integrates both phylogenetically-based patterns of distribution and ecologically-

based patterns of species richness. PACT is also a tool capable of revealing patterns of

the taxon pulse, Hennig's progression rule, and species-area relationships. However,

this algorithm was developed without explicit reconstruction of a temporal component,

which can be problematic because pseudo-congruence of temporally and spatially

discordant events results in superficially identical cladogram patterns. Additionally,

there is currently no way to distinguish unique from general diversification events

(events occurring in 1 taxon or 2+ taxa, respectively), and only parsimony-based

optimization can be implemented for ancestral area reconstruction. To alleviate these

issues, I developed a modified PACT protocol that incorporates a temporal component

and branch lengths. To test the performance of this modification, I conducted modified

and standard PACT (mPACT and PACT, respectively) analyses on data previously

generated for the North American warm deserts, which have relatively distinct biotic

assemblies that have diversified under an array of geologic processes that have

produced a complex topography and climatic processes that have produced diverse

environmental conditions. I then compared mPACT and PACT results to those of a prior

analysis of the warm deserts that used Secondary Brooks Parsimony Analysis

(Secondary BPA), which is a binary-coded, matrix-based pre-cursor to PACT that infers

multi-clade historical biogeographic patterns. My results show that Secondary BPA and

PACT both underestimated the role of pseudo-congruence and underestimated the

total number of unique and general diversification events. Distinct instances of pseudo-

congruent patterns as well as unique and general patterns are revealed only by the

modified PACT analysis. Additionally, I make recommendations for future development

of and integration of this approach into biogeographic research.

INTRODUCTION

Biogeographic studies have traditionally focused on describing distributional patterns

either by using phylogenetic patterns of distributions to address large spatial and

deeper temporal scales, or ecologically relevant patterns of species richness that focus

on smaller spatial and shallower temporal scales. More recently, there has been a drive

to create methods that integrate both approaches to gain a better understanding of

the dynamics of global biodiversity. This has led to the development of a variety of

techniques with the goal of revealing biological and demographic processes that have

played important roles in current biotic structure and how these patterns have been

shaped by a region's abiotic history (as reviewed in Brooks & McLennan, 2002; Wiens &

Donoghue, 2004; Morrone, 2009; Folinsbee & Evans, 2012; Wiens, 2012).

In particular, spatially and temporally congruent patterns of biotic diversification are a topic that many biogeographers have addressed, but with variable levels of success. A time-honored premise is that spatial congruence in diversification patterns is the result of vicariance, where a barrier is formed within the ranges of ancestrally widespread taxa, simultaneously splitting co-distributed taxa (Croizat et al., 1974; Nelson & Platnick, 1981). However, non-vicariant mechanisms can also result in congruence among taxa in biogeographic patterns. Alternative mechanisms include, for example, biotic expansion by concordant dispersal following the removal of a barrier (geodispersal; Lieberman & Eldredge, 1996) and linear jump dispersal of taxa associated with temporally and spatially sequential development of new areas, where the oldest lineages are found in the oldest region and the youngest lineages are found in the youngest region (Hennig's progression rule; Hennig, 1966; Cowie & Holland, 2008).

The vicariance hypothesis in particular has been criticized because lineages often differentially respond to local abiotic and biotic factors, and many strictly cladistic (often vicariance-based) methods do not reconstruct unique organismal responses as prevalent mechanisms of producing regional biodiversity (e.g., de Quieroz, 2005; Parenti, 2006). Even in scenarios where vicariance and other congruent (or general) diversification mechanisms have been argued as the prevalent mechanism (e.g., Madagascar and the North American aridlands), there are many instances of idiosyncratic (or unique) dispersal events, and it can be difficult to discern whether general or unique events contributed most substantially to a biogeographic system

45

(e.g., Zink et al., 2000a; Yoder & Nowak, 2006; Riddle et al., 2008; Hoberg & Brooks, 2010). Additionally, excluding divergence times from analyses, which is common in cladisitc analyses, may over-predict the number of vicariance events because of pseudo-congruent patterns, which are similar biogeographic patterns produced by historically dissimilar events (Donoghue & Moore, 2003; Ree & San Martín, 2008; Eckstut et al., 2011; Fig. 1.1).

In light of the complex nature of formation of regional biotas, no single analytical approach so far has allowed the teasing apart of diversification complexity of biotas. However, the development of integrative, step-wise frameworks (e.g., Riddle & Hafner, 2006; Fig. 3.1) has been proposed as a way to optimally reveal historical biogeographic complexity (Richards et al., 2007; Morrone, 2009; Riddle & Hafner, 2010). Part 3 of Riddle & Hafner (2006)'s proposed step-wise framework (Fig. 3.1) involves identifying general events using an analysis such as primary and secondary Brooks Parsimony Analysis (BPA; Brooks, 1990). Secondary BPA is the pre-cursor for a more recently development method called Phylogenetic Analysis for Comparing Trees (PACT; Wojcicki & Brooks, 2004, 2005), which is a method that incorporates all events (both general and unique). Accordingly, step-wise frameworks serve as an integrative approach, and portions of the framework (such as using PACT instead of Secondary BPA for part 3) may be valuable for inferring the relative importance of general versus unique diversification in forming regional biodiversity and reducing the prevalence of pseudo-congruence.

Phylogenetic Analysis for Comparing Trees as an Integrative Method

Phylogenetic Analysis for Comparing Trees (PACT; Wojcicki & Brooks, 2004, 2005) is a multi-clade analytical method that can integrate historical and ecological approaches and has been shown to reveal patterns of the taxon pulse (periodic episodes of expansion, colonization, and isolation), Hennig's progression rule, and species-area relationships (Halas et al., 2005; Hoberg & Brooks, 2010; Eckstut et al., 2011). PACT integrates all spatial data from each taxon-area cladogram (tracing geographic changes on a phylogenetic tree for a single taxon; Fig. 3.2) to generate general area cladograms (geographic changes traced on an area cladogram that was generated using several taxon-area cladograms; Fig. 3.3). Despite the proposed benefits of PACT, this algorithm was developed using cladograms (which do not include a temporal calibration) and without consideration for weighting or a temporal component, and as a consequence, ancestral area reconstruction is restricted to parsimony-based frameworks (Eckstut et al., 2011).

Excluding time can be problematic because temporally and spatially discordant events can result in identical cladogram patterns (pseudo-congruence; similar biogeographic patterns produced by historically dissimilar events; Fig.1.1), which can then be misidentified as vicariant events (Cunningham & Collins, 1994). Likewise, when dissimilar patterns emerge from similar historical events, pseudo-incongruence can also occur (e.g., Donoghue & Moore, 2003; Riddle & Hafner, 2006). Wojcicki & Brooks (2004, 2005) suggested that the PACT algorithm inherently reduces errors in congruence because the algorithm proceeds in a top-down fashion, and younger nodes

(at the top of a tree) are presumed to be more similar to each other than older nodes (deeper in a tree) because nodes toward the top of a tree should represent younger events and deeper nodes should represent older events.

The top-down approach is conducted under the assumption that all phylogenetic trees area occur on the same temporal scale (i.e., the youngest node on two trees would represent recent divergences at approximately the same time, and the oldest nodes on the same two trees would represent older divergences at approximately the same time). However, the top-down approach can be problematic even if analyses are restricted to the same taxonomic scale (e.g., species or genera-level inferences) in instances where named species, subspecies, and phylogroups are not on the same temporal scale. For example, Riddle (1995) reported vast differences between amount of divergence representing species and genera in pocket mice (*Chaetodipus* and *Perognathus*) and grasshopper mice (*Onychomys*). In pocket mice, genera evolution dates back between 9 and 10 million years (*Chaetodipus* and *Perognathus*, respectively), with divergences between species occurring from 4 mya (*C. penicillatus* and *C. intermedius*) and even approximately 8 mya for divergence within the species *P. parvus* (Riddle, 1995; Riddle, Jezkova, Eckstut, Oláh-Hemmings, and Carraway, *in review*). Alternatively, the grasshopper mouse genus *Onychomys* is estimated to have evolved just over 2 mya, and divergence of the three species (*O. arenicola*, *O. leucogaster*, and *O. torridus*) occurred soon after (Riddle, 1995). Thus, to correct for inconsistencies with taxonomic-temporal dynamics, molecular clocks and fossil information can each be used to reduce pseudo-congruence in general area

cladograms. Lim (2008) and Folinsbee & Evans (2012) conducted molecular dating on taxon-area cladograms that were incorporated into GACs (including PACT GACs), but there has not been formal integration of molecular dating into the PACT framework and explicit discussion of ramifications on PACT-specific analyses.

Moreover, the current PACT algorithm is only capable of producing trees with equal branch lengths (Fig. 3.4A,B). This restricts ancestral area reconstruction to parsimony-based optimization frameworks, which do not incorporate branch length into ancestral state reconstruction. Not incorporating branch lengths can produce erroneous ancestral area reconstruction results (Cunningham, 1999), especially in areas where there are high rates of dispersal (Pirie et al., 2012). For example, if unique (1 taxon) and general (2+ taxa) events are not considered when optimizing the GAC, then weighting ancestral nodes can be erroneous if the optimization protocol inadvertently favors the unique event when determining ancestral node state because of other patterns within the GAC. This issue can be alleviated by producing a GAC with branch lengths that can appropriately weight general and unique events for the reconstruction of ancestral areas, wherein the ancestral area would be more heavily weighted toward general events (Fig. 3.4C,D).

To alleviate the issues of pseudo-congruence and lack of branch weighting, I herein develop a modification to the PACT algorithm that incorporates a temporal component to analyses by conducting molecular dating techniques using the program BEAST (Drummond & Rambaut, 2007) to delineate timing of ancestral divergences (Drummond et al., 2006). Additionally, the modified PACT algorithm (mPACT)

49

incorporates branch lengths based on frequency of events, and this facilitates a

Maximum Likelihood-based approach for ancestral area reconstruction of the PACT

GAC (Fig. 3.4).

North American Warm Deserts as a Model System

The North American warm deserts (the Sonoran, Chihuahuan, Mojave, and Peninsular

deserts; Fig. 3.5) are an ideal region for experimentally testing integrative historical

biogeographic methods, particularly when optimizing methods for reducing pseudo-

congruence. These deserts have been subject to an array of geologic and climatic

processes across various timescales (ca. 3.6 mya – present) that have produced a

complex topography and diverse environmental conditions. As a consequence, unique

communities of relatively distinct biotic assemblies for which a large number of

phylogenetically-based biogeographic datasets have been generated, including

numerous vertebrates, invertebrates, and plants (e.g., Wells & Haragan, 1983; Riddle,

1995; Riddle et al., 2000a,b,c; Jaeger et al., 2005; Riddle & Hafner, 2006; Jezkova et al.,

2009; Pyron & Burbrink, 2010; Graham et al., 2013). Moreover, there is potential for a

lot of pseudo-congruent diversification patterns among taxa in these regions because

of the diverse timescale of geologic and climatic events.

Riddle & Hafner (2006) conducted a study on the North American warm deserts

where they diagnosed areas of endemism (areas producing and maintaining unique

biodiversity through time) and conducted a Secondary BPA analysis (the precursor to

PACT for inferring general diversification events). This study provided testable

hypotheses of North American warm desert biodiversity evolution and a benchmark dataset for comparing the performance of newly developed methods.

To test the performance of my modified PACT protocol (mPACT), I compared mPACT results to the Secondary BPA analysis (a binary-coded, matrixbased pre-cursor to PACT) conducted by Riddle & Hafner (2006) and a standard PACT analysis conducted in this study. Riddle & Hafner's (2006) dataset and hypotheses provide testable hypotheses and a tool for comparison of PACT and mPACT analyses with Secondary BPA. Comparison of PACT and mPACT analyses to Secondary BPA analysis provides unique insight into the performance of PACT-based algorithms and the progression of these evolutionary methods at capturing biological complexity. I test the hypotheses set forth by Riddle & Hafner (2006), where there are four distinct areas of endemism (Peninsular North, Peninsular South, Continental East, and Continental West; Fig. 3.5) and two major evolutionary clades that are hypothesized to have evolved in response to various geologic events: Peninsular and Continental, and within the Peninsular clade, there is an observed diversification back into the continental mainland (Fig. 3.6).

METHODS

Evaluating PACT Protocols

I used the 22 North American warm desert taxa that were previously used by Riddle & Hafner (2006), which include nine mammals, seven birds, four non-avian reptiles, one amphibian, and one plant (Fig. 3.7; Table 3.1). The use of this benchmark dataset allows me to directly compare the new methods (PACT and mPACT) to Riddle & Hafner

(2006)'s Secondary BPA results. Moreover, including other taxa would now allow the use of areas used in Riddle & Hafner (2006)'s Secondary BPA analysis, because the areas of endemism they diagnosed were based on the 22 taxa dataset. Additionally, I herein refer to Riddle & Hafner's (2006) diagnosed areas of endemism for designating regions to remain consistent with comparison of PACT and mPACT results to their Secondary BPA results (Fig. 3.5).

Standard PACT Analysis

Step 1: Obtain Cladograms

For the standard PACT analysis, cladograms were collected from the manuscripts in which they were initially published (Table 3.1), and each was converted into a taxon-area cladogram by replacing the names of each of the terminal species with the area(s) of their respective distributions. A single lineage occuring in numerous areas would be treated as a polytomy in the taxon-area cladogram.

Step 2: Construct General Area Cladogram (GAC)

I combined the taxon-area cladograms by hand to form a General Area Cladogram (GAC) using the PACT algorithm as described by Wojcicki & Brooks (2004, 2005). The PACT algorithm includes the following steps: 1) common elements (Y) between two cladograms are combined (Y+Y=Y); 2) novel elements (N) in a cladogram are retained into the output GAC (Y+N=YN); 3) superficially similar events that occur at different nodes are not combined (Y(Y- = Y(Y-, not Y(Y- = Y); 4) common elements are retained

even in the presence of novel elements (Y+YN = YN); and 5) multiple novel elements

are retained, but until further information is provided may remain unresolved (YN' + YN

= YN'N).

Step 3: Optimization of the GAC

The GAC was then analyzed using the parsimony-based Delayed Transformation

(DELTRAN) optimization with Mesquite version 2.5 (Maddison & Maddison, 2008) to

infer ancestral areas. In cases where strict parsimony optimization cannot distinguish

between two character states at a node, DELTRAN optimization favors convergences by

retaining the pre-existing ancestral state and transformation occurs at the last possible

moment (Fig. 3.8A). The alternative approach, Accelerated Transformation (ACCTRAN),

favors reversals by transforming ancestral states at the earliest possible moment (Fig.

3.8B). ACCTRAN can therefore be problematic in biogeographic interpretations because

a species could be interpreted as having gone extinct and subsequently "re-evolved"

(Wiley, 1986, 1988a,1988b; Agnarsson & Miller, 2008; Eckstut et al., 2011).

Step 4: Interpretation of the GAC

The PACT evolutionary biogeographic data can be used to test the species-area

relationship in an evolutionary context (Halas et al., 2005; Hoberg & Brooks, 2010;

Eckstut et al., 2011). With the species-area relationship (SAR), number of species

should linearly correlate with area size if diversity is at equilibrium (Arrhenius, 1920;

MacArthur & Wilson, 1963, 1967). Therefore, PACT can be used to test if a region is at

53

evolutionary equilibrium. Eckstut et al. (2011) found that the age of islands in the

Hawaiian Islands and Greater Antilles were reflected in the SARs: there was a strong

linear correlation of number of diversification events and area size in the older Greater

Antilles and a non-significant, weak correlation in the younger Hawaiian Islands

because the big island of Hawaii is both the largest and youngest island. However, I

herein refer to SARs as diversification-area relationships (DARs) in the context of PACT

to reflect the nature of these plots, which represent diversification events (and not

species) in the GAC.

I examined the total number of OTUs (operational taxonomic units; i.e., number

of tips on the GAC), and using GAC data inferred from DELTRAN ancestral state

reconstruction, I calculated the total number of lineages per area, number of biotic

expansion (BE) events, and number of *in situ* (*IS*) events. I used OTU, BE, and *IS* data to

construct diversification-area plots (with area in km^2). I then tested diversification-area

relationships using the power-law species-area relationship (SAR; *S=cA^z*; Arrhenius,

1920; MacArthur & Wilson, 1963, 1967) for total lineages-area relationship and linear

regressions to test biotic expansion-area and *in situ*-area relationships (Halas et al.,

2005; Eckstut et al., 2011). Preliminary analysis of residuals depicted non-uniformity of

data; thus, all data were log-transformed for analysis. Statistical analyses were run

using the Microsoft Excel Data Analysis package (2007).

Modified PACT Analysis

Step 1: Obtain Sequence Data & Convert to Taxon-Area Cladograms

I obtained DNA sequences from National Center for Biotechnology Information's

GenBank database (http://www.ncbi.nlm.nih.gov/) and locality information for each

sequence from GenBank, the original source paper, museum records, or private

records of the authors (Table 3.1). To avoid over-predicting *in situ* diversification, I

selected one specimen per species or a representation from each region for inter-

species studies (if the information were available; in some cases, researchers only

sequenced one representative per species, even if the species is widespread), and I

selected one specimen per phylogroup as described by the authors of the original

source paper for phylogeographic studies. Sequences were aligned using ClustalW2

(Larkin et al., 2007).

Step 2: Molecular Dating

To estimate the most appropriate models of evolution and prior parameters for my

analyses, I used the Akaike Information Criterion (AIC; Akaike, 1973, 1974) and either

PALM (http://palm.iis.sinica.edu.tw/), a parallel computing cluster (Chen et al., 2009),

or MEGA5 (Tamura, et al., to be submitted, 2011). The rate of substitution and date of

gene divergence were estimated using BEAST v1.4.8 (Drummond & Rambaut, 2007) on

either the University of Olso Bioportal (http://www.bioportal.uio.no) or the BioHPC

v1.4.8 parallel computing cluster at the Cornell University Computational Biology

Service Unit (http://biohpc.org/default.aspx). Multiple programs and clusters were

used because of availability at the time of analysis. However, several examples were tested on both sets of programs and clusters to ensure that results were comparable between the sources.

All BEAST analyses were run using the Yule Process tree prior and run 3 times for 10^7 Markov Chain Monte Carlo (MCMC) chains that were sampled every 1000 iterations (Drummond & Rambaut, 2007). All iterations were then pooled using Logcombiner v1.4.8 and log files were analyzed in Tracer v1.4.1 (Rambaut & Drummond, 2007), and effective sample sizes (ESS) were used to evaluate the estimates of posterior distributions (Drummond & Rambaut, 2007). The first 10% of all analyses were discarded for burn-in. A summary of the output trees was generated with TreeAnnotator v1.4.8 (Drummond & Rambaut, 2007), discarding the first 1000 trees as burn-in, and then analyzed with FigTree v1.2.1 (Rambaut, 2008).

I conducted each analysis in three ways using both relaxed and strict clock models: 1) universal substitution rates; 2) substitution rates that were both half and double the universal clock rates; and 3) (when possible) fossil calibration with a lognormal prior with a standard deviation of 1 to designate the split. Fossil calibrations suffer from numerous potential issues, including incorrect placement on the tree, insufficiency of single fossil calibrations, and they can only provide minimal estimates of divergence times (e.g., Yang & Rannala, 2006; Donoghue & Benton, 2007; Marshall, 2008). For this reason, fossil calibration was used when records were available and used by other researchers on the same system.

I tested clock-like evolution of each phylogeny with relaxed clock simulations, where ucld.stdev values closer to 0.0 were considered clock-like and had a strict clock implemented and those lineages with ucld.stdev values greater than 1.0 were not clock-like had relaxed clocks implemented. For simulations that had ucld.stdev values between 0.35-0.65, I conducted analyses using both strict and relaxed clock models. I performed likelihood ratio tests (LRTs) to evaluate which models were statistically different in terms of likelihood scores, and I used the analysis with the highest significant likelihood score and posterior probability for subsequent analyses. In instances where there was not one analysis with a distinctly higher likelihood scores or posterior probabilities, I included all analyses with similar scores to determine divergence times and I incorporated all ranges of possible dates.

I acknowledge that molecular dating, especially with only one gene, can be erroneous for precise dates, and that dates may range for different taxa in response to the same biogeographic event because of varying levels of gene flow and molecular evolution rates. Because of these potential molecular dating problems, I incorporated the 95% confidence interval of BEAST divergence dates for all nodes and placed these dates into general, but biogeographically meaningful, categories: late (0.011-0.126my), mid (0.126-0.781my), or early (0.781-2.58my) Pleistocene; late (2.58-3.6my) or early (3.6-5.3my) Pliocene; and late Miocene (5.3-11.6my). When there was overlap in dates, the node ages would be widened to include all possible dates because inclusion of all ranges maximizes information in the GAC (Folinsbee & Evans, 2012).

Step 3: GAC Construction

When constructing GACs, I followed the same rules as described by Wojcicki & Brooks (2004, 2005) and detailed in the previous section ("Standard PACT Analysis"), with the exception that i) I determined congruent events by age of diversification as determined with molecular dating, and ii) I distinguished general from unique events by recording every congruent event (E) on each branch (e.g., if three clades exhibit a diversification at area A in the late Pleistocene, E = 3 for branch A) (Fig. 3.4). For unique branches, only one character was used to describe each branch. This approach facilitates the distinction of unique from general events by providing information for relative branch lengths (i.e., clade-unique dispersal would likely only happen once on the GAC, whereas a vicariant event or concordant dispersal would occur numerous times) (Fig. 3.4). In excluded situations where there were multiple equivocal input TAC placements on the GAC from analysis.

Step 4: Optimization of the GAC

Once I constructed the GAC, I conducted ancestral area reconstruction using both likelihood and the parsimony-based delayed transformation, or DELTRAN, optimizations. I used traditional parsimony in Mesquite version 2.5 (Maddison & Maddison, 2008) because the GAC contains polytomies (which prohibits optimization using DELTRAN), and in cases where there was still ambiguity with regard to node state, I implemented DELTRAN (Wiley, 1986, 1988a, 1988b).

Maximum-Likelihood ancestral area reconstructions favor shorter branches to

reconstruct ancestral nodes, because it is inferred that the descendants are more

similar to the ancestor and that the probability of change is less likely on a short branch

than on a long branch. Therefore, I calculated branch lengths as 1/E, where E is the

number of events inferred for each branch. I designated this value as 1/E because that

weights the ancestral areas toward general events that more likely result from

congruent diversification mechanisms (e.g., vicariance), whereas unique events are

more likely the result of idiosynchratic dispersal and should not represent the ancestral

state. However, there are polytomies present in the GAC, which means that traditional

ancestral area reconstruction programs and models (e.g., DIVA, Ronquist, 1997;

Mesquite, Maddison & Maddison, 2008; and Dispersal-Extinction-Cladogenesis, Ree &

Smith, 2008) cannot be used to infer Maximum Likelihood ancestral area

reconstructions. In order to conduct Maximum-Likelihood reconstruction, I first used

Mesquite version 2.5 (Maddison &Maddison, 2008) to build the GAC with branch

lengths and then all instances of polytomies were instead converted to bifurcations

with a branch length of zero. Subsequently, the saved Nexus file was imported into the

APE package (Paradis et al., 2004) in R version 2.15.2 (R Development Core Team,

2008). I then used the ACE (ancestral character estimation) analysis within APE to

reconstruct areas using three models for discrete characters: equal rates (ER),

symmetric (SYM), and all rates different (ARD). Likelihoods for each model were

compared, and significance was tested using a likelihood test using chi-squares to

determine which model was most suitable. In cases where there were ambiguities at

59

internal nodes (equal probabilities), a delayed transformation was favored to remain

consistent with favoring biotic expansion.

Step 5: Interpretation of the GAC

I interpreted the mPACT GAC similar to how I interpreted the standard PACT GAC. I

examined the total number of OTUs (operational taxonomic units) and I calculated the

total number of lineages per area, number of BE events, and number of *IS* events. I

used OTU, BE, and *IS* data to construct diversification-area plots for each of the two

mPACT datasets (mPACT with DELTRAN and mPACT with Maximum Likelihood

optimization) for each region. I then tested diversification-area relationships using the

SAR (species-area relationship; Arrhenius, 1920; MacArthur & Wilson, 1963, 1967) and

linear regressions to test biotic expansion-area and *in situ*-area relationships (Halas et

al., 2005; Eckstut et al., 2011). Preliminary analysis of residuals depicted non-uniformity

of data and all data were log-transformed for analysis. Statistical analyses were run

using the Microsoft Excel Data Analysis package (2007).

RESULTS

Likelihood Ancestral Area Reconstruction Model Selection

The three reconstruction methods (ER, SYM, and ARD) yielded the following

likelihoods, respectively: -40.20254, -38.31762, and -36.31635. The likelihood test

showed that the ARD model was more suitable than either ER ($p<0.01$) or SYM

(p=0.045) models at p<0.05 for Maximum-Likelihood ancestral area reconstruction of the mPACT dataset.

Tree Structure

The Secondary BPA tree yielded a tree with 7 operational taxonomic units (areas; OTUs) and 6 nodes (Fig. 3.7), PACT with 18 OTUs and 16 nodes (Fig. 3.10), and mPACT with 30 OTUs and 25 nodes (Fig. 3.10; Table 3.6). For the PACT analysis (using DELTRAN optimization), 31.25% of nodes were *in situ* nodes, 31.25% were *in situ*/biotic expansion nodes, 37.5% were ambiguous, and there were no nodes showing full biotic expansion (Fig. 3.11; Table 3.3). mPACT analysis using DELTRAN ancestral area reconstruction had 48% ambiguous nodes, 28% *in situ*, 20% *in situ*/biotic expansion, and 4% full biotic expansion (Fig. 3.12; Table 3.3). Finally, mPACT analysis using Maximum Likelihood ancestral area reconstruction had 8% ambiguous nodes, 40% *in situ* nodes, and 52% *in situ*/biotic expansion nodes (Fig. 3.13; Table 3.3).

Diversification-Area Relationships

Table 3.4 and Fig. 3.12 show the data that were collected for these analyses. Diversification-area relationships for total lineages were weak and statistically not significant for all three analyses (Fig. 3.14A; PACT-DELTRAN: c=0.06, z=0.48, R^2=0.22, p=0.69; mPACT-DELTRAN: c=0.09, z=0.45, R^2=0.37, p=0.50; mPACT-Likelihood: c=0.36, z=0.20, R^2=0.16, p=0.79). Additionally, all analyses for biotic expansion- and *in situ*-area relationships were also not significant. For biotic expansion-area relationships, PACT-

DELTRAN and mPACT-DELTRAN yielded more similar results compared to mPACT-Likelihood (Fig. 3.14B; PACT-DELTRAN: y=0.36x-1.44, R^2=0.49, p=0.40; mPACT-DELTRAN: y=0.43x-1.74, R^2=0.50, p=0.38; mPACT-Likelihood: y=0.11x+0.32, R^2=0.16, p=0.75). However, all results differed for *in situ*-area relationships (Fig. 3.14C; PACT-DELTRAN: y=27x-1.09, R^2=0.13, p=0.71; mPACT-DELTRAN: y=0.16x-0.46, R^2=0.10, p=0.82; mPACT-Likelihood: y=-0.02x+0.71, R^2<0.01, p=0.86).

DISCUSSION

My newly developed method, mPACT, was able to tease apart evolutionary complexity in the North American warm deserts in a way that previous methods were unable. This study revealed that methods that exclude time (Secondary BPA and PACT) underpredicted the amount of pseudo-congruent diversification patterns. Moreover, parsimony-based ancestral area reconstruction produced more ambiguities and reconstructed less intuitive ancestral areas compared to likelihood-based reconstruction that incorporated branch lengths. I was also able to reveal interesting, novel patterns of diversification-area relationships (DARs) in this region that can lead to interesting ideas regarding the evolutionary nature of areas of endemism. Herein, I discuss how pseudo-congruence and ancestral areas are elucidated by mPACT and what these data have revealed about North American warm desert DARs. Additionally, although mPACT has revealed more complexity, there are still some potential issues with this analysis, and I discuss these caveats and potential ways to improve mPACT (including the development of a user-friendly mPACT software program).

Revealing the Prevalence of Pseudo-congruence in Analyses

The incorporation of a temporal component into analysis produced a more complex GAC compared to either standard PACT analysis or secondary BPA analysis (30 compared to 18 and 7, respectively; Table 3.3). Increased GAC complexity indicates that pseudo-congruence (Fig. 1.1) played a role in underestimating the total number of diversification events prior to the incorporation of temporally-calibrated area cladograms.

The input taxon-area cladograms show several instances of pseudo-congruent patterns among taxa, and there are event pseudo-congruent patterns within types of organisms (e.g., reptiles, rodents, or plants; Fig. 3.7; Table 3.1). Continental East/Continental West divergences occurred in the *Chaetodipus nelsoni*, *Onychomys*, and *Kinosternon flavescens* groups (2 rodents and a reptile, respectively) during the Pliocene (5.3-2.58 mya), whereas this split occurred in the *Peremicus eremicus* group (rodents) during the early Pleistocene (2.58-0.781 mya) and the *Uta stansburiana* group (reptiles) during the mid-to-late Pleistocene (0.781-0.011 mya). Continental West/Peninsular divergences occurred during the early Pliocene (5.3-3.6 mya) in the reptile *Sauromalus*, the Pliocene to mid-Pleistocene (3.7-0.781 mya) in the rodent *C. baileyi* group, and the late Pleistocene (0.126-0.011 mya) in the plant *Lophocereus schotti*. Finally, there were also pseudo-congruent patterns in Peninsular North/Peninsular South divergences, although these divergences in general were younger than in the continental divergences. *Sauromalus* experienced Peninsular North/Peninsular South divergence during the late Pliocene-early Pleistocene (3.6-

0.781 mya), whereas the *C. baileyi* group diverged north from south in the mid-Pleistocene (0.781-0.126 mya), the *C. arenarius* and *P. eremicus* groups diverged in the mid-late Pleistocene (0.781-0.011 mya) and the *U. stansburiana* group diverged in the late Pleistocene (0.126-0.011 mya).

These patterns show that distinct historical events (e.g., mountain uplift or glacial-interglacial events) can frequently produce similar biogeographic patterns among taxa. In this case, pseudo-congruent patterns can be produced by vicariant events at one point in time (e.g., as the result of tectonic uplift) and dispersal events at a different point in time (e.g., resulting from climate change). In older events circa the Quaternary-Neogene transition tectonic uplift events (particularly during the late Pliocene to early Pleistocene, 3.6-0.781 mya), vicariance as a result of mountain and plateau uplift was likely a driving force of diversification patterns, whereas dispersal was more likely prevalent during the Quaternary glacial-interglacial cycles (2.58 mya-present). Consequently, these results underscore the importance of incorporating explicit tectonic versus orbital forcing climate information and models when testing biogeographic hypotheses (Chapter 2).

Likelihood-based Ancestral Area Reconstruction

With regard to ancestral area reconstruction, the parsimony-based DELTRAN optimization produced ambiguity in both standard PACT and mPACT trees (37.5% of PACT nodes and 48% of mPACT nodes; Figs. 3.11 and 3.12, respectively). These GACs are highly complex and thus difficult to resolve with parsimony. However, by

incorporating general events to create branch lengths and subsequently conducting

likelihood ancestral state optimization, I was able to reduce the number of ambiguities

in mPACT node reconstruction (8% of nodes; Fig. 3.13). With the Maximum Likelihood

optimization, ancestral nodes were weighted more heavily toward general events (i.e.,

diversification events that were represented in numerous taxa compared to unique

events that were only represented by one taxon). For this reason, there were

differences in not only the ability of the optimization to resolve nodes that DELTRAN

could not, but both resolved and ambiguous nodes differed between trees (Figs. 3.12

and 3.13). For example, at the base of the mPACT-DELTRAN tree (Fig. 3.12), the

ambiguity occurs between resolving the basal nodes as Continental East or Peninsular

South. However, although there are a lot of Peninsular South events, many of them are

unique events (Fig. 3.11). The mPACT-Likelihood tree (Fig. 3.13) takes into account the

amount of general events, and because the Continental West has more general events,

it weights these basal nodes to ambiguous between Continental East or Continental

West. Consequently, this may be a more logical approach than equivocal weighting of

branches that is done by the parsimony-based analysis when unique events are present

on a GAC, which are present when conducting PACT or mPACT.

Diversification-Area Relationships

All diversification-area relationships were weak and statistically not significant (Fig.

3.14; Table 3.4). All analyses showed similar patterns, with the Peninsular South

(48,500 km^2) and Continental West (386,500 km^2) yielding the highest amount of

diversification, and the Peninsular North (48,000 km^2) and Continental East (479,000 km^2) yielding the least amount of diversification. This is a pattern that is consistent regardless of type of PACT analysis used, suggesting that the diversification-area relationship patterns strongly reflects the history of these regions.

The equilibrium theory of island biogeography (ETIB; MacArthur & Wilson, 1963, 1967) suggests that a species-area relationship (SAR) should be linear when richness is perfectly correlated with area, based on the mathematical relationship ($S=cA^z$) described by Arrhenius (1920). Under the ETIB model, I would expect the Peninsular North and South to yield the fewest diversification events and the Continental West and East to yield the most diversification events. The lack of a linear correlation between diversification events and area size (because the Peninsular South and Continental West had the most amount of diversification) could indicate that the Peninsular North and Continental East have not yet reached stable equilibrium (perhaps as a result of biotic instability during paleoclimatic oscillations), or this could have implications for the Continental West and Peninsular South as strong sources of biodiversity in the North American warm deserts.

Substantial debate has occurred on what constitutes an "area of endemism" (e.g., Platnick, 1991; Riddle, 1998; Humphries & Parenti, 1999; Crother & Murray, 2011). Currently, operational approaches exist to diagnose areas of endemism using modern distribution data and grid-based approaches (e.g., Rosen, 1988; Linder, 2001a; Szumik et al., 2002; Szumik & Goloboff, 2004). Riddle & Hafner (2006) suggested that areas of endemism represent areas that more stably produce and maintain biodiversity

and thus an evolutionary approach should be incorporated into area of endemism

diagnosis. If areas of endemism are stable through time, then current diagnostic

techniques insufficiently describe the areas of endemism using the grid-based method

Parsimony Analysis of Endemicity (PAE; Rosen, 1988).

Riddle & Hafner (2006) found that the Continental West, Continental East,

Peninsular South, and Peninsular North were all areas of endemism, but the data here

suggest that these may not all be equal with regard to biodiversity production and

stability. For example, even though the Continental East is the largest of the regional

warm deserts, the Continental West and Peninsular South biotas had more

diversification events (Fig. 3.15). Moreover, the Peninsular North was unique among

the areas of endemism because it only appeared three times on the GAC (as opposed

to eight times for the Continental East and Peninsular South and nine times for the

Continental West), and all were instances of general events (divergence events

occurring in 2, 3, and 5 taxa; Fig. 3.10). Interestingly, all of the analyzed events in the

Peninsular North occurred during Pleistocene times and did not represent any

ancestral areas (Figs. 3.10, 3.12). Savage (1960) suggested that herpetofaunal

distributions in the Baja California peninsula of modern species were shaped by

Pleistocene events, wherein the cape region was likely a refuge during glacial maxima

and there were invasions from the northeast, continental mainland and expansion

from the cape during interglacial cycles. The general Peninsular North events and the

overwhelming number of Peninsular North/Peninsular South divergences during the

Pleistocene (see discussion section "Revealing the Prevalence of Pseudo-congruence in

Analyses" above for examples) may be consistent with Savage (1960)'s hypothesis. The

Peninsular North may have been less stable through time than the Peninsular South,

possibly rendering the Peninsular South a stronger area of endemism than the

Peninsular North. Alternatively, perhaps the Peninsular North is a region that was

inaccurately diagnosed as an area of endemism by the method PAE because of the

large number of species that are currently distributed there.

Exploring the evolutionary dynamics of areas of endemism is something that

has been largely overlooked in the past. Riddle & Hafner (2006) conducted a novel

analysis where they reconstructed the evolutionary history of the diagnosed areas of

endemism in the North American warm deserts, but their analysis lacked detail

regarding analysis of the differences among these areas of endemism. Furthermore,

even though methods exist to diagnose areas of endemism, experimental approaches

to testing the evolutionary dynamics of areas of endemism are limited, and more

sufficient analyses are needed to adequately test these hypothetical ideas (Riddle &

Hafner, 2006; Crother & Murray, 2011).

mPACT Caveats

Whereas the mPACT protocol provides a unique means to explore the evolution of

biodiversity across time and space, there are four inherent issues with the mPACT

algorithm (Table 3.5). These issues include: i) inability of likelihood ancestral area

reconstruction to resolve complex mPACT GACs, ii) assumption of appropriate

molecular dating techniques and node ages, iii) equivocal possibilities when generating

the GAC, and iv) the lack of a software program to conduct mPACT analyses.

Preliminary analysis of more complex mPACT GACs (81 OTUs representing 17

areas; see Chapter 4) showed that applicable likelihood-based ancestral state

reconstructions are unable to resolve ancestral states for large, complex GACs because

all most ancestral states are reconstructed as equivocal. Most likelihood-based

approaches require fully bifurcating tree topologies (e.g., DIVA, Ronquist, 1997;

Dispersal-Extinction-Cladogenesis, Ree & Smith, 2008; Mesquite, Maddison &

Maddison, 2008), and full bifurcation is uncommon for mPACT GACs because of the

PACT rules Y + N + N = YNN and YN' + YN = YN'N. The inability of current models and

software to resolve more complex GACs means that the Maximum Likelihood

algorithms are not capable of dealing with the amount of complexity in large-scale

analyses (e.g., variability of branch lengths and number of regions). However,

Maximum Likelihood ancestral state reconstruction approaches are commonly used

(Royer-Carenzi et al., 2013) and are becoming increasingly popular. A Google Scholar

search for "likelihood ancestral state reconstruction" yielded 63 publications since

2000, and 40 (63.5%) of those were published between 2009-2013. With growing

interest in methods to integrate ecology and evolution, more refined mPACT-

appropriate Maximum Likelihood ancestral area reconstruction approaches will likely

become available.

As with all phylogenetic-based analyses, the product of the mPACT GAC directly

reflects the quality of the input data. Both the input tree structure and lineage ages

(from divergence dating) are derived from a variety of algorithms that have benefits as well as inherent potential flaws. The genetic data may be inappropriate for phylogenetic analysis – for example, if a gene is assumed to be selectively neutral but further research reveals selective pressures (e.g., mitochondrial DNA; Ballard & Kreitman, 1995) – or there may be error in algorithms or fossil placement on trees for divergence dating (Donoghue & Benton, 2007). Under these scenarios, the mPACT GAC would be inaccurate.

Appropriateness and accuracy of input data are not things that are a fault of the mPACT algorithm, but it is something that potential users should be aware of when interpreting GACs. For that reason, I remained conservative in my analysis. For example, any degree of overlap in timing of divergence between TACs are considered the "same" and then the GAC date range would encompass all dates (e.g., if node A on two trees yield the results 1.5-3 and 2-4, the GAC age at node A would be 1.5-4). There is frequently error in molecular dating estimates and my approach minimizes the number of unique events in the GAC but may over predict the degree of generality for nodes. However, it should also be noted that percentage of overlap itself may be an important variable to consider in future analyses, particularly when you take into account comparison of different historical events that occur on different timescales. For example, mountain uplifting and vicariance may be a more gradual process and thus a smaller percentage of overlap may indicate a congruent diversification event. However, the shift of glacial-interglacial cycles and resulting dispersal is comparatively

more abrupt, and requiring a higher percentage of overlap to identify congruence would be more appropriate for glacial-interglacial timeframes.

The use of TACs with dissimilar depths (e.g., using overall younger or older TACs) can confound also the construction of the mPACT GAC. For very young TACs, there are multiple possible placements within the tree, and each different GAC structure is then equally likely (equivocal). In this analysis, I excluded several diversification events because there are equivocal results (i.e., there are two or more possible placements for one diversification event on the GAC). Alternatively, older TACs can also be problematic because they can overestimate the total number of unique events. In my results, I found only two instances of solely Neogene-based divergences events (one general, one unique). These two events likely do not accurately reflect the number of deep Neogene divergences in the North American warm deserts. There are several lineages of North American desert organisms with deep Neogene divergences. For example, divergences in North American Heteromyid rodents (Dipodomyinae and Perognathinae) are estimated to date back to 20 mya (Hafner et al., 2007). Using several deep lineages may provide more insight into general deep Neogene biodiversity formation as opposed to partitioning into subsets of taxa. For example, those TACs used in Riddle & Hafner (2006) and in this paper mainly focus on within species or within species-groups. Thus, given both the issues of using young and old TACs, the use of TACs of approximately the same timescale would reduce uncertainties and potential inaccuracies in the mPACT GAC.

Finally, there is currently no mPACT software available for GAC construction. Lack of software makes mPACT and PACT analyses laborious, time intensive, and subject to human error. Labor, time, and potential error make mPACT analyses less desirable for many scientists and diminish the possible impact of mPACT on the scientific community.

Development of mPACT software

The development of mPACT computer software is in development (Breckling, Eckstut, and Riddle, *in development*). The availability of a user-friendly mPACT computer software will facilitate the implementation of the mPACT algorithm by the scientific community and reduce the potential for human error in generating GACs. Additionally, this software will provide more options for conduction of the mPACT algorithm based on user preference and philosophy regarding how to incorporate equivocal results, allow users to identify general events based on different node ages, and facilitate an enhanced understanding of how different input TACs affect the overall GAC.

The program will be able to tackle equivocal results by incorporating options regarding whether the user would prefer to include or exclude equivocal results, and if they choose to include them, to construct a consensus (e.g., 70% or strict) of all possible equivocal trees or simply evaluate them each independently. In cases where I have previously remained conservative in my estimations (and thus may have favored pseudo-congruence and not revealed the true amount of incongruence among similar patterns), user options will exist to manipulate parameters such as what degree of

overlap in node ages constitutes general events (e.g., 1-100% matching of node ages on input cladograms; see "mPACT Caveats" section for further discussion). Additionally, there will be options for partitioning the tree based on timeframe to account for differences in how percentage should be considered for gradual processes, such as mountain uplifting, and abrupt processes, such as glacial-interglacial cycles. Finally, bootstrap and jackknife options for input TACs will be incorporated to understand the strength of signal of patterns in the GAC and evaluate robustness of these patterns.

Conclusions

The mPACT algorithm reveals more diversity in the North American warm deserts than was observed using either Secondary BPA or PACT analysis, and relieves several of the issues and concerns associated with PACT analysis (e.g., by reducing the impact of pseudo-congruence, revealing modes of diversification – either unique or general, and facilitating likelihood-based optimization). Incorporating a temporal component both reduces pseudo-congruence and facilitates inference of general or unique diversification events, although my conservative approach to considering dates with any overlap as the "same" may still over-predict pseudo-congruent events. Use of likelihood-based ancestral area reconstruction helps resolve ambiguities that were apparent in parsimony-based DELTRAN optimizations. However, despite the benefits of the mPACT protocols, mPACT is a much more liberal approach than PACT and may overestimate regional biodiversity dynamics. However, even though mPACT still suffers from potential issues (Table 3.5), is it nonetheless an exciting new approach that can be

used as an alternative to the more conservative PACT algorithm should scientists desire

the opportunity to integrate taxon- and area-based biogeographic methods.

Table 3.1. List of North American desert taxa as used by Riddle & Hafner (2006) and Genbank numbers for sequences used for molecular dating. * - some unpublished sequences were also used for molecular dating (provided by J. Patton).

Group	Clade	Common Name	Original Source	Genbank Accession Numbers
Plants	*Lophocereus schotti*	Whisker cactus	Nason et al. (2002)	AF328628-AF328664
Amphibians	*Bufo punctatus*	Red-spotted toad	Riddle et al. (2000), Jaeger et al. (2005)	AY010121-AY010166, DQ085629-DQ085776
Reptiles	*Uta stansburiana*	Common side-blotched lizard	Upton and Murphy (1997)	U46695-U46742
	Aspidoscelis tigris	Western whiptail	Murphy and Aguirre-Léon (2002); Radtkey et al. (1997); Reeder et al. (2002)	AF006266-AF006288
	Sauromalus species	Chuckwalla	Petren & Case (1997, 2002)	AF20223-AF20252
	Kinosternon flavescens species group	Mud turtle	Serb et al. (2001)	AF316121-AF316137
Birds	*Campylorhynchus brunneicappilus*	Cactus wren	Zink et al. (2000b)	AF291529-AF291571
	Auriparus flaviceps	Verdin	Zink et al. (2000b)	AF295205-AF295249
	Toxostoma curvirostre species group	Curve-billed thrasher	Zink & Blackwell-Rago (2000), Zink et al. (2001), Zink et al. (1999)	AF287160-AF287228, AF287496-AF2878560, AF287564-AF287629
	Toxostoma lecontei species group	LeConte's thrasher	Zink et al. (1997), Zink et al. (2001)	U75569-U75573, U75575-U75579
	Polioptila melanura species group	Black-tailed Gnatcatcher	Zink et al. (2000a), Zink & Blackwell (1998a), Zink et al. (2001), Zink et al. (2000b)	AF027827-AF27836, AF027838-AF027848, AF027849-AF027859, AF518771, AF518872
	Callipepla squamata species group	Scaled quail	Zink & Blackwell (1998b), Zink et al. (2001)	AF028750, AF028751, AF028753, AF028754, AF028756, AF028757, AF028759, AF028760, AF028762, AF028763, AF028765, AF028766, AF028768, AF028769, AF028771, AF0287712, AF028752, AF028755, AF028758, AF028761, AF028764, AF028767, AF028770, AF028773
	Pipilo fuscus species group	Canyon towhee	Zink et al. (2001), Zink &Dittman (1991), Zink et al. (1998)	AF298595-298622
Mammals	*Neotoma lepida* species group	Desert woodrat	Planz (1992); Patton et al. (2008)	DQ781162-DQ781256*
	Onychomys species	Grasshopper mouse	Riddle (1995), Riddle & Honeycutt (1990)	U21614-U21616, U21633-U21635, U21648-U21650
	Peromyscus eremicus species group	Cactus mouse	Riddle et al. (2000c)	AY009173-AY009237
	Dipodomys merriami species group	Merriam's kangaroo rat	Riddle et al. (2000a), Jaeger et al. (2005), Alexander & Riddle (2005)	AY926430, AY926437, AY926438, AY926439, AY926443, AY926445, AY926450
	Chaetodipus nelsoni species group	Nelson's pocket mouse	Riddle et al. (2000b), Jaeger et al. (2005)	AY009240, AY009246, AY009249
	Chaetodipus arenarius	Little desert pocket mouse	Riddle et al. (2000a)	AY010230-AY10197
	Chaetodipus penicillatus species group	Desert pocket mouse	Lee et al. (1996), Riddle et al. (2000b), Jezkova et al. (2009)	AB456529-AB456507
	Chaetodipus baileyi species group	Bailey's pocket mouse	Riddle et al. (2000b)	AY009253-AY009316, AY009238-AY009252
	Ammospermophilus species	Antelope squirrel	Riddle et al. (2000a), Jaeger et al. (2005)	AY010167-AY010196

Table 3.2. How to conduct PACT and mPACT. Instances where the mPACT approach differs from the PACT approach are depicted in bold-italics. In cases where algorithms or programs indicate N/A, these tasks are done by hand as indicated under "process."

Step	Goal	Input Data	Algorithms	Programs	Process
1	Construct taxon area cladograms (TACs)	-Phylogenetic tree -Distributions of each lineage	N/A	N/A	Replace taxon names on each phylogenetic tree with areas of distribution.
2	***Molecular dating of diversification events***	***-TACs*** ***-Genetic data*** ***-Fossil data (when available)***	***-Coalescence*** ***-Molecular clocks***	***-Mesquite*** ***-BEAST*** ***-*BEAST***	***Infer age of divergence for nodes on each TAC using molecular dating techniques.***
3	Construct general area cladogram (GAC)	***-Dated*** taxon area cladograms	***-mPACT***	N/A	Follow PACT protocols for construction of a GAC, except: ***i) identify congruent events by both pattern as well as age, and ii) record number of congruent events for each branch. After the GAC has been constructed, convert the number of events (E) to 1/E for each branch.***
4	Ancestral area reconstruction	-GAC	-Parsimony ***-Maximum Likelihood***	***-MacClade*** -Mesquite ***-LaGrange***	Infer ancestral states using the preferred optimization method(s). Bayesian approaches, such as those used in BayesTraits and s-DIVA/RASP are currently not compatible with mPACT because they evaluate numerous topologies and at present only one GAC is produced using the mPACT protocol.
5	Analyze nodes -BE from IS events ***-General from unique events***	-GAC with ancestral areas	N/A	N/A	Count the number of nodes for each type of event: biotic expansion (BE), in situ (IS), ***general, and unique. Dispersal from vicariance may differ in that dispersal would be unique BE events whereas vicariance would be general BE events.***

Table 3.3. General area cladogram (GAC) node analysis.

GAC Node Parameters	Secondary BPA	PACT: DELTRAN	mPACT: DELTRAN	mPACT: LnL
OTUs (tree tips)	7	18	30	30
Total nodes	6	16	25	25
in situ **nodes**	n/a	5	7	10
in situ/**biotic expansion nodes**	n/a	5	5	13
Full biotic expansion nodes	n/a	0	1	0
Ambiguous nodes	n/a	6	12	2

Table 3.4. Diversification-area relationships; PACT vs. mPACT. Total counts indicate resolved nodes as well as operational taxonomic units (OTUs). DT indicates the parsimony-based Delayed Transformation (DELTRAN) optimization, whereas ML indicates maximum likelihood-based optimization. BE in and BE out indicates biotic expansion into and out of, respectively, the designated region.*IS* indicates *in situ* diversification events. Ambiguous nodes and events were discarded for this analysis.

Area of Endemism	Area Size (km^2)	PACT: Total Lineages	PACT: BE events	PACT: BE out Events	PACT: BE in Events	PACT: *IS*Events	mPACT: Total Lineages		mPACT: BE events		mPACT: BE out Events		mPACT: BE in Events		mPACT: *IS* Events	
	-	DT	DT	DT	DT	DT	ML	DT	ML	DT	ML	DT	ML	DT	ML	DT
PS	48,500	8	3	0	1	2	17	13	8	3	4	1	4	2	8	4
PN	40,000	2	1	0	1	0	5	3	5	1	2	0	3	1	2	0
CW	386,500	14	5	5	0	8	21	15	11	7	9	4	2	3	17	4
CE	479,000	4	3	0	3	0	9	11	6	3	0	2	6	1	1	2

Table 3.5. Comparative inference types, benefits, and disadvantages of seconday BPA, PACT, and mPACT. All three assume accuracy of input cladograms.

Algorithm	Inference type	Benefits	Disadvantages
Seconday BPA	-Historical	-Allows inference into general patterns of area relationships	-Drastically oversimplifies amount of regional diversification -Restricted to historical inference
PACT	-Historical -Ecological	-Reveals more realistic degree of diversification than Secondary BPA -Can distinguish biotic expansion from *in situ* diversification events	-Pseudo-congruence -Cannot distinguish types of biotic expansion (vicariance, dispersal) -Limited options for ancestral area reconstruction -Laborious and time intensive; currently no software program available
mPACT	-Historical -Ecological	-Reduces pseudo-congruence -Facilitates distinction of dispersal from vicariance	-Likelihood-analyses may not be able to be conducted on excessively large, complex GACs -Assumes node ages (and thus, molecular dating techniques) are accurate -Equivocal possibilities impact GAC structure; currently no way to incorporate -Laborious and time intensive; currently no software program available

Step-wise Framework
from Riddle & Hafner (2006)

1) Identify biota, units of analysis (e.g., species or phylogroups), and distributional areas

2) Diagnose areas of endemism using distributional data (e.g., Parsimony Analysis of Endemicity)

3) Determine general divergences using multi-clade analysis (e.g., Primary Brooks Parsimony Analysis, or BPA)
  Note: PACT replaces BPA in this step and includes unique divergences

4) Resolve departure from general divergences (reticulate area relationships) using additional multi-clade analysis (e.g., Secondary BPA)
  Note: This step does not occur in PACT analysis

5) Test hypotheses of taxon and biotic distributions

Figure 3.1. Step-wise framework as designed and implemented by Riddle & Hafner (2006). Notes are included to identify where the method discussed in this study, PACT, would be implemented in this step-wise framework and where this step-wise framework would not be applicable to a PACT Analysis.

A) Table of Species and Associated Locations

Species	Species 1	Species 2	Species 3
Location	A	B	C

B) Phylogenetic Tree

C) Taxon-Area Cladogram
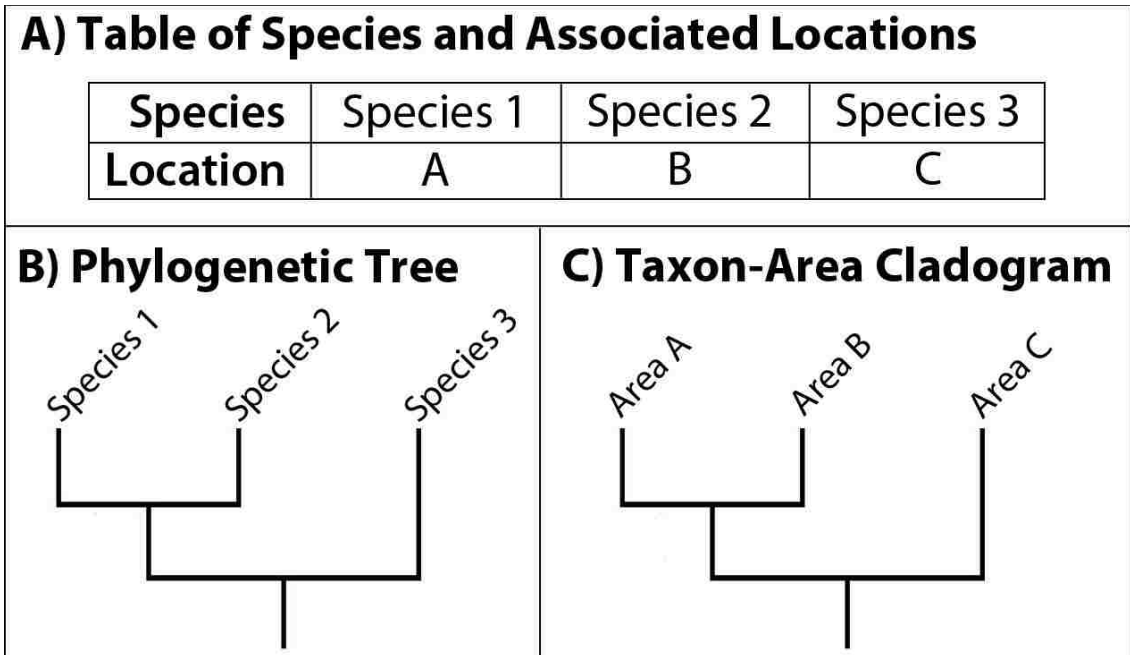
Figure 3.2. Generation of a taxon-area cladogram. A) Species distributions are collected. B) A phylogenetic tree is built. C) The areas of occurrence for each species are overlaid onto the phylogenetic tree.
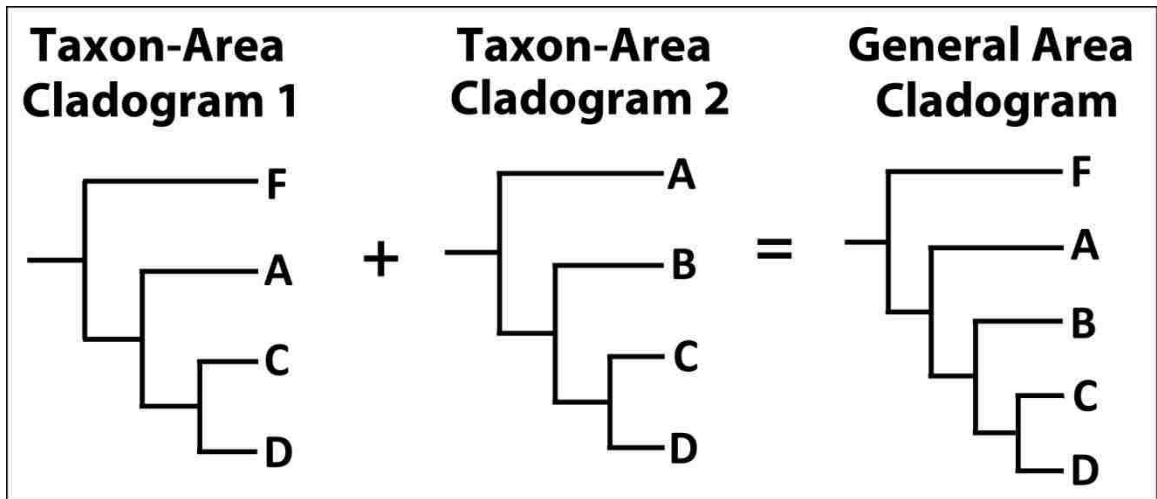
Figure 3.3. Generation of a general area cladogram using two input taxon-area cladograms (1 – F,A,C,D; 2 – A,B,C,D). All areas are included in the output general area cladogram (F,A,B,C,D).
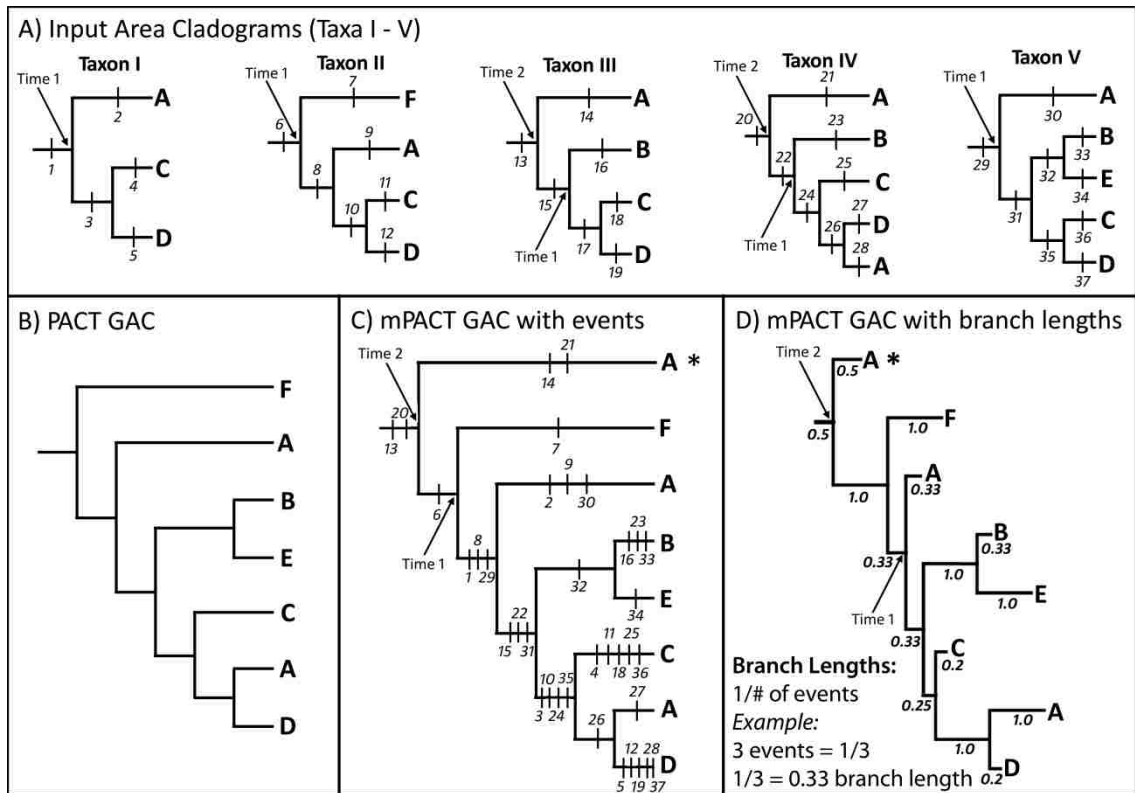
Figure 3.4. Deriving general area cladograms (GACs) from five input area cladograms using PACT and a modified version of PACT (mPACT). A) The five input taxon-area cladograms from five taxa, with areas indicated in A-F and each event numbered in italics at the hash over each branch, and timing of diversification indicated for events. B) PACT GAC. C) mPACT GAC with each event indicated by the hash with the associated italicized number from the input cladograms. D) mPACT GAC with total number of events (E) converted to branch lengths by calculating 1/E (e.g., 3 events = 1/3 = 0.33). These branch lengths facilitate likelihood-based optimization because ancestral nodes are more heavily weighted toward short branch lengths, and ancestral nodes are more likely similar to general (2+ congruent) events than unique (1) events. Structural differences between the mPACT and PACT GACs are indicated by a *.
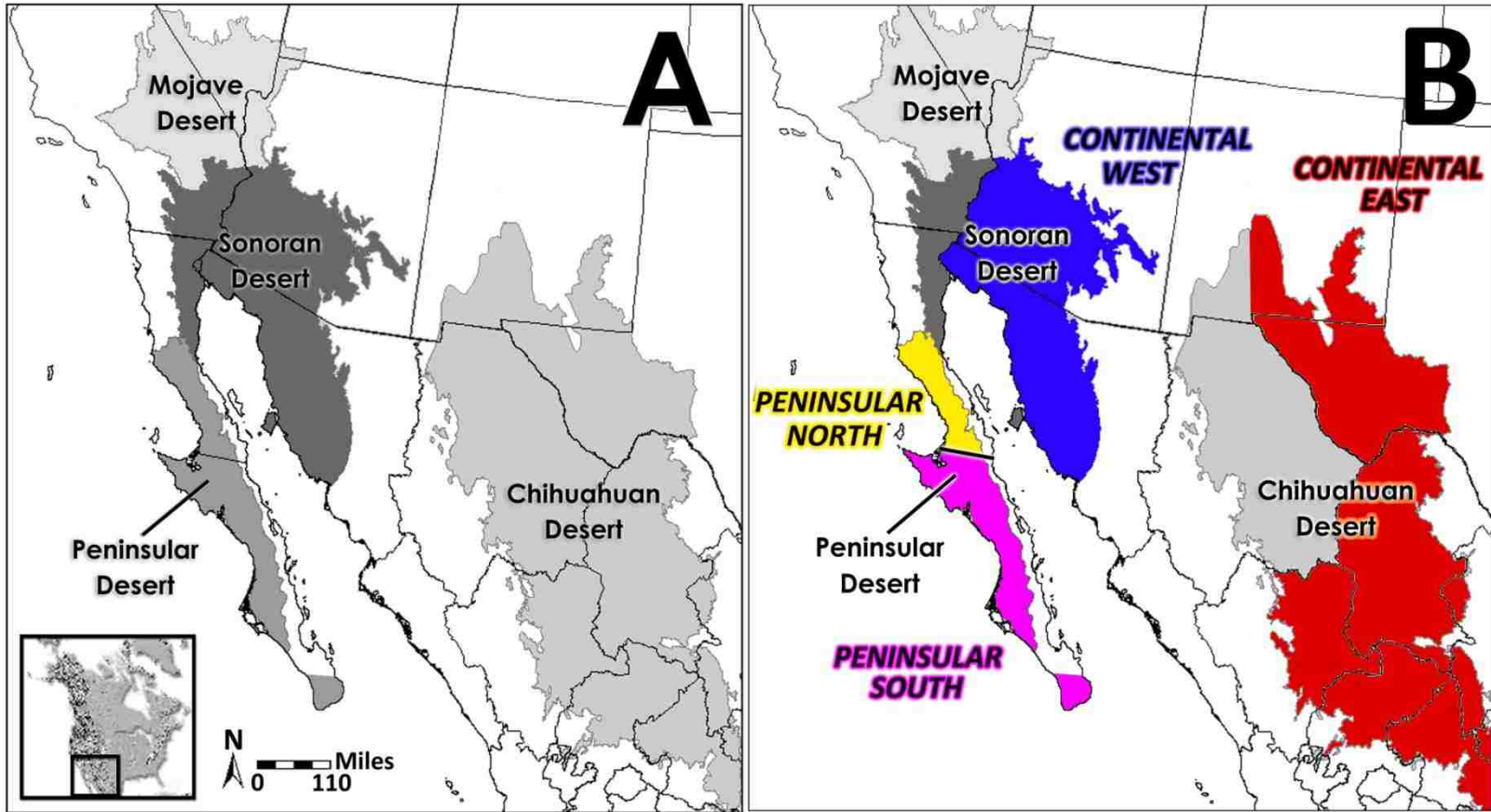
Figure 3.5. Map of the North American warm deserts (A), including the Continental East, Continental West, Peninsular North, and Peninsular South areas of endemism (B; Riddle & Hafner, 2006).
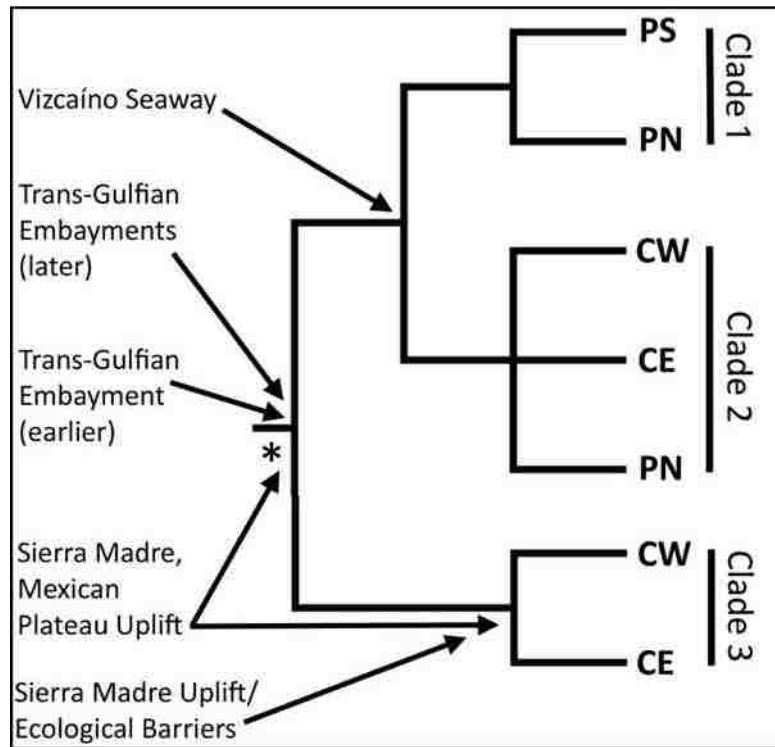
Figure 3.6. Hypotheses regarding earth history impacts on the evolution of area of endemism from Riddle & Hafner (2006).
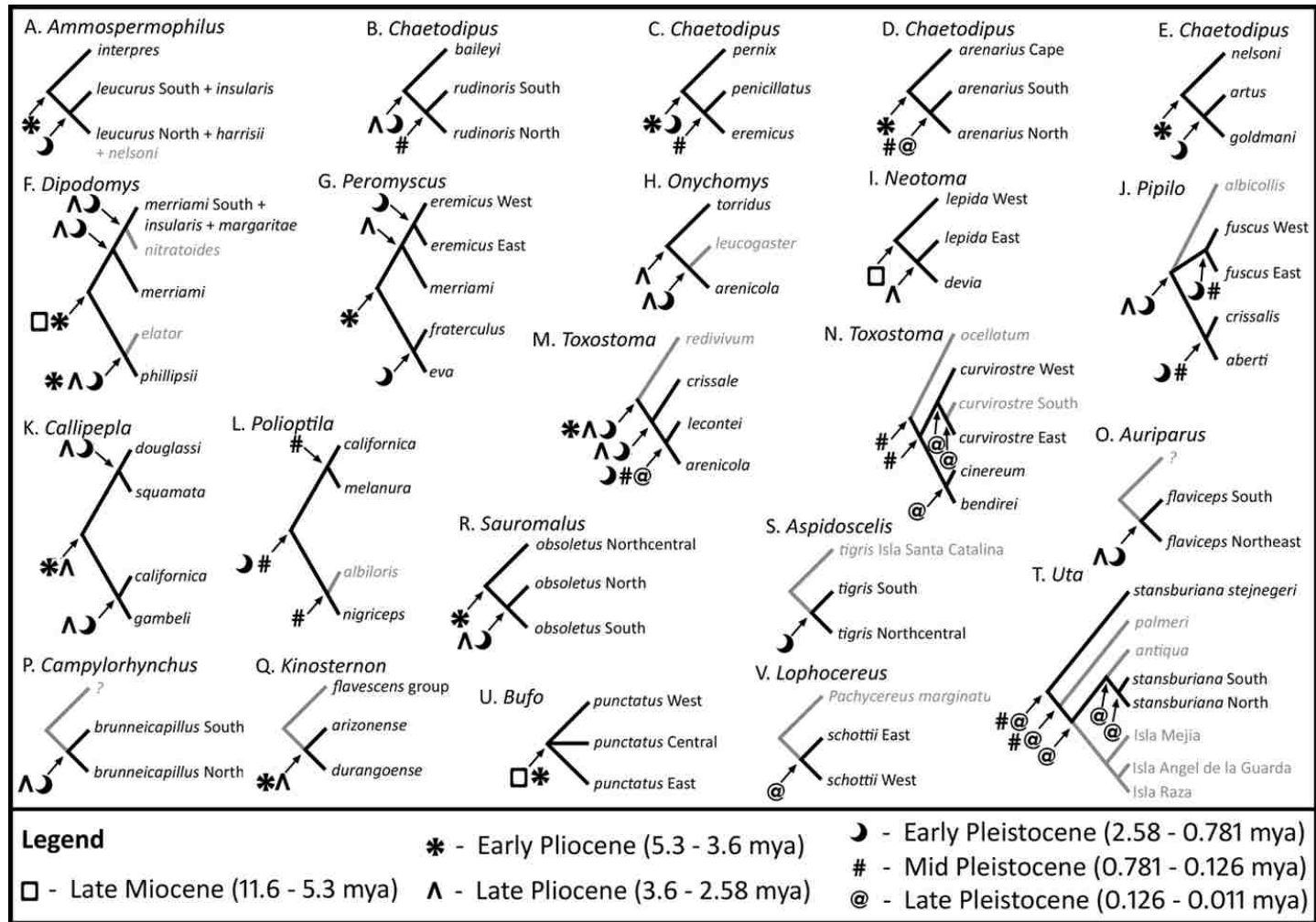
Figure 3.7. Cladograms and ages of divergence used in comparative analysis (from Riddle &Hafner, 2006). Multiple symbols indicate divergence ranges that encompass numerous time periods.
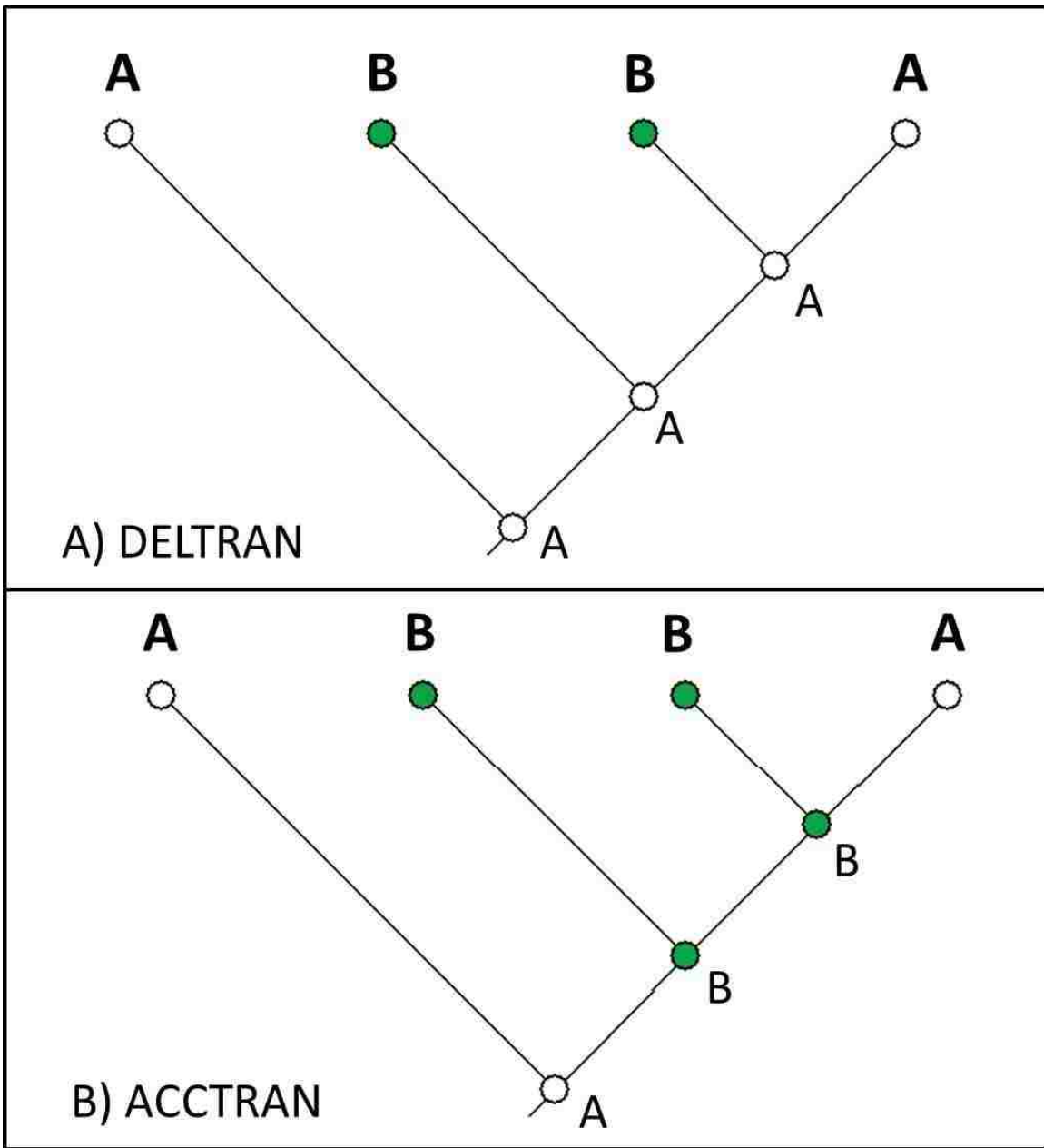
Figure 3.8. Comparison of parsimony ancestral state reconstructions in a hypothetical area cladogram. Bolded "A" and "B" at the tree tips represent areas where lineages occur. Regular "A" and "B" by nodes represent reconstructed ancestral states using A) Delayed Transformation (DELTRAN) and B) Accelerated Transformation (ACCTRAN).
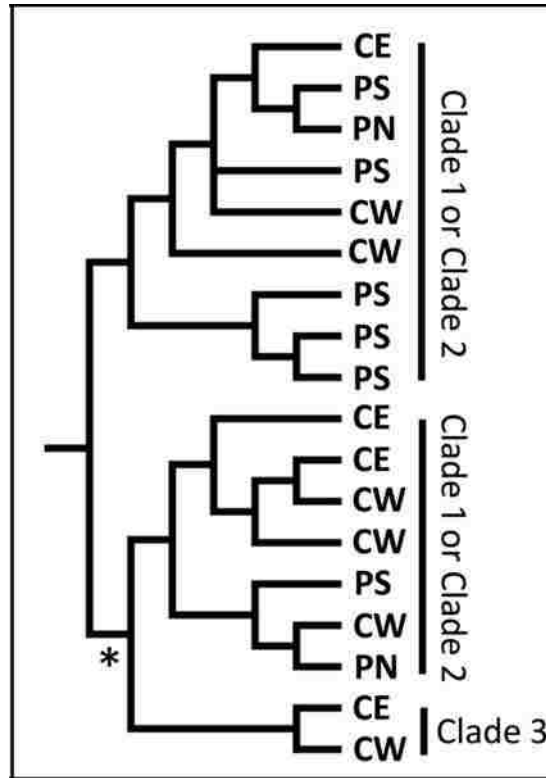
Figure 3.9. General area cladogram (GAC) derived from standard PACT analysis of the North American warm deserts. The placement of Clade 3 differs between the PACT GAC and Riddle & Hafner (2006)'s Secondary BPA GAC (as indicated with a * at the alternate nodes).
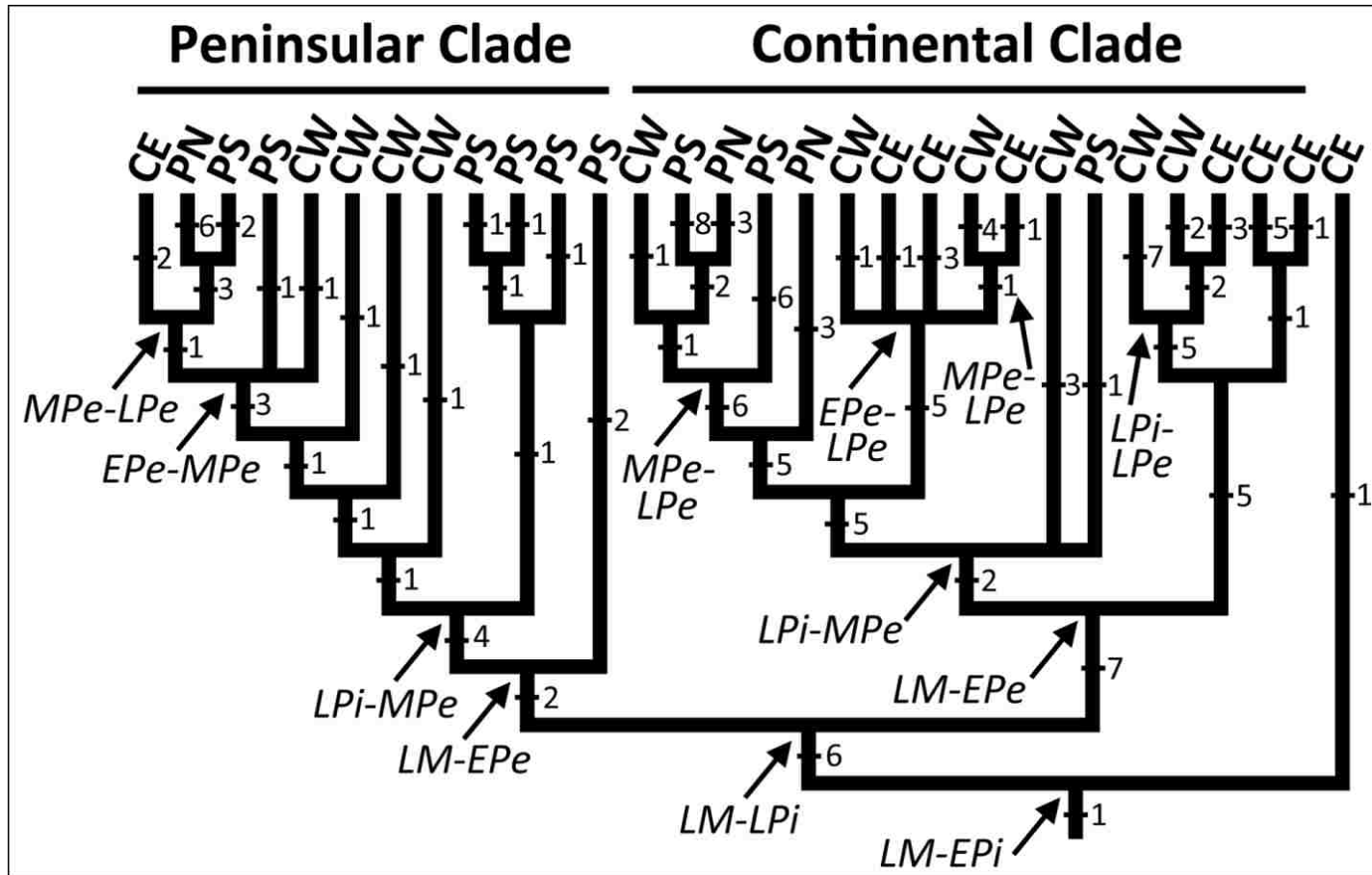
Figure 3.10. North American warm desert mPACT tree. Tick marks indicate number of lineages that experienced the event (degree of generality). Node ages are indicated as follows: LM = Late Miocene (11.6-5.3 mya), EPi = Early Pliocene (5.3-3.6 mya), LPi = Late Pliocene (3.6-2.58 mya), EPe = Early Pleistocene (2.58-0.781 mya), MPe = Mid Pleistocene (0.781-0.126 mya), and LPe = Late Pleistocene (0.126-0.011 mya).
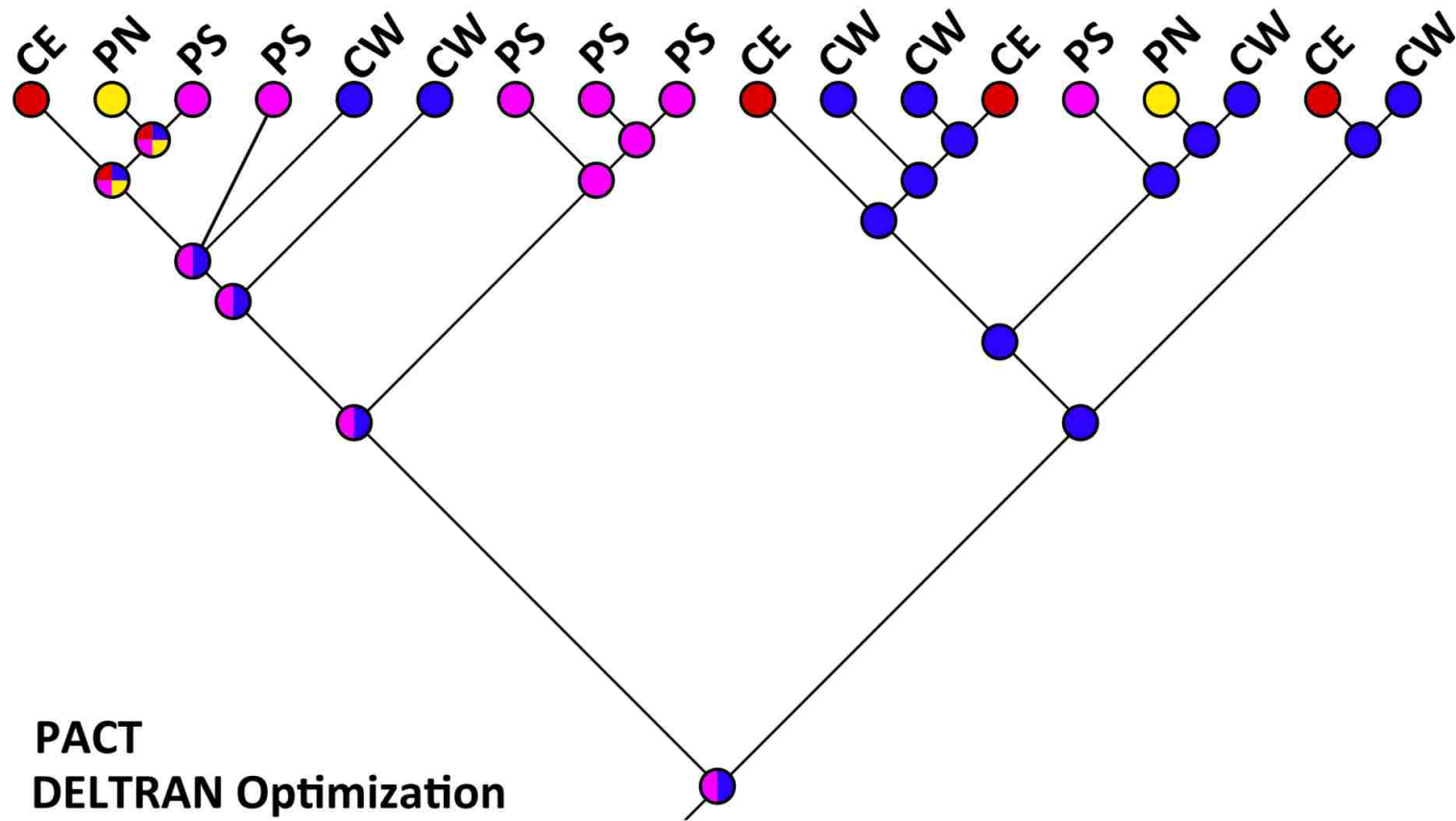
Figure 3.11. North American warm desert standard PACT tree with DELTRAN optimization.
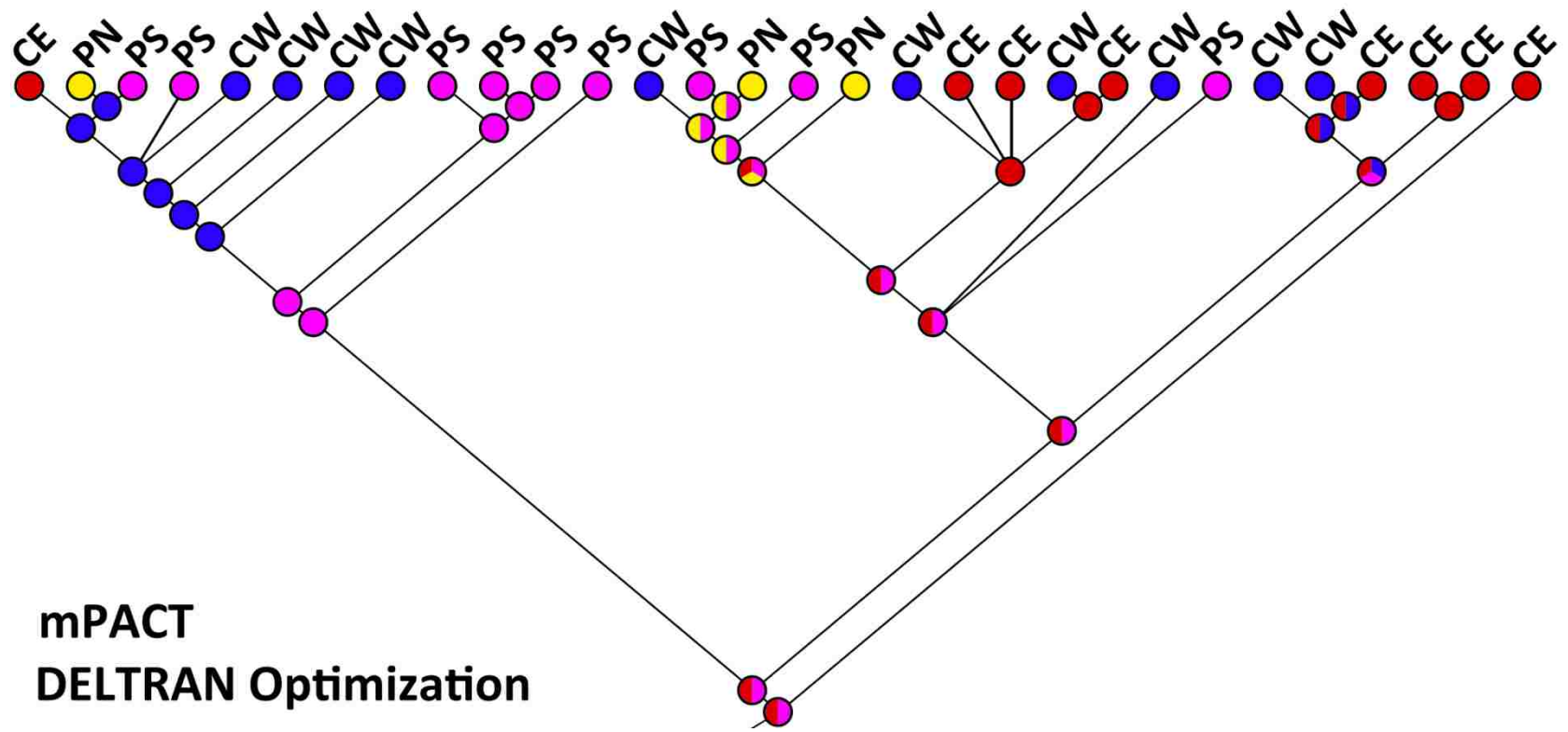
Figure 3.12. North American warm desert mPACT tree with DELTRAN optimization.
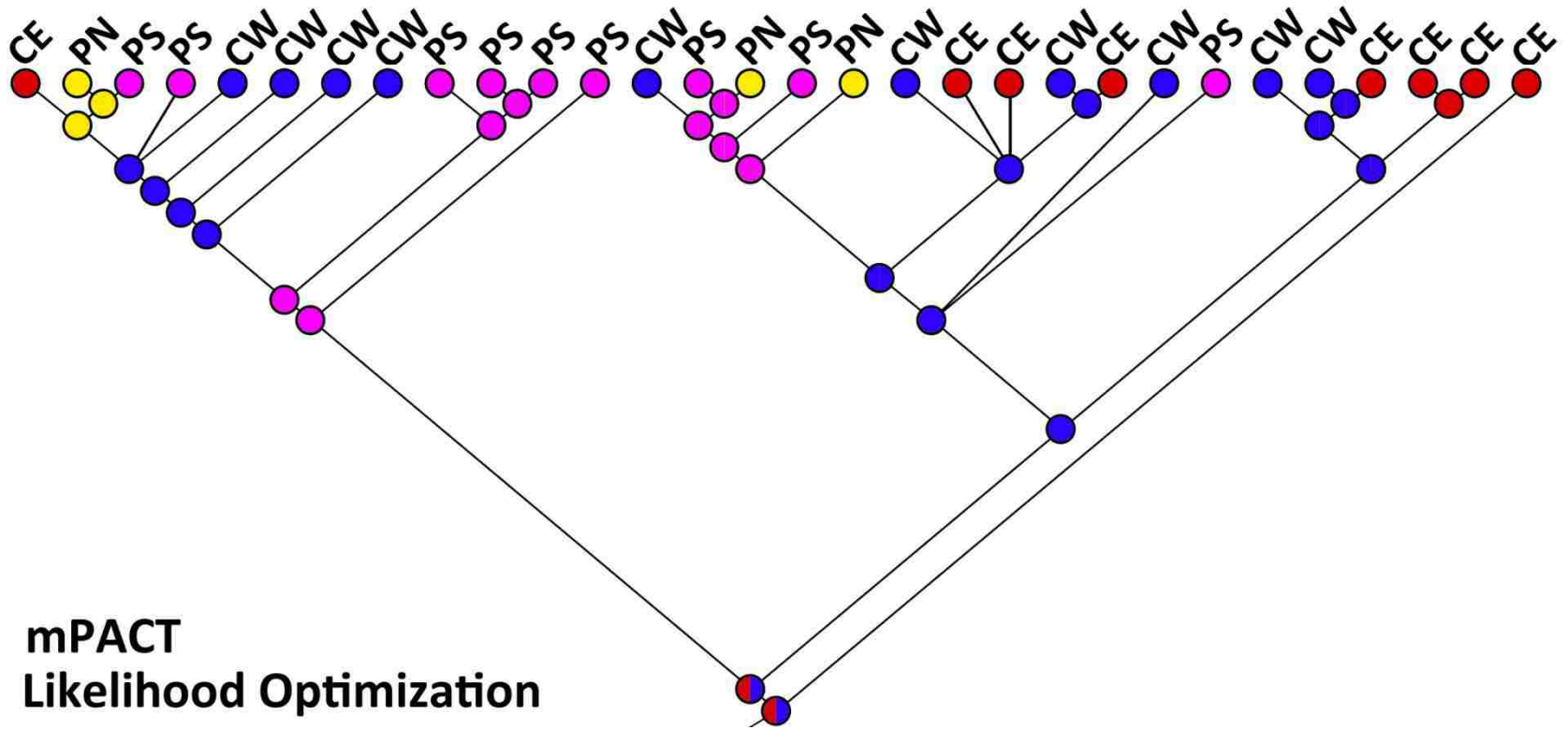
Figure 3.13. North American warm desert mPACT tree with Maximum Likelihood optimization.
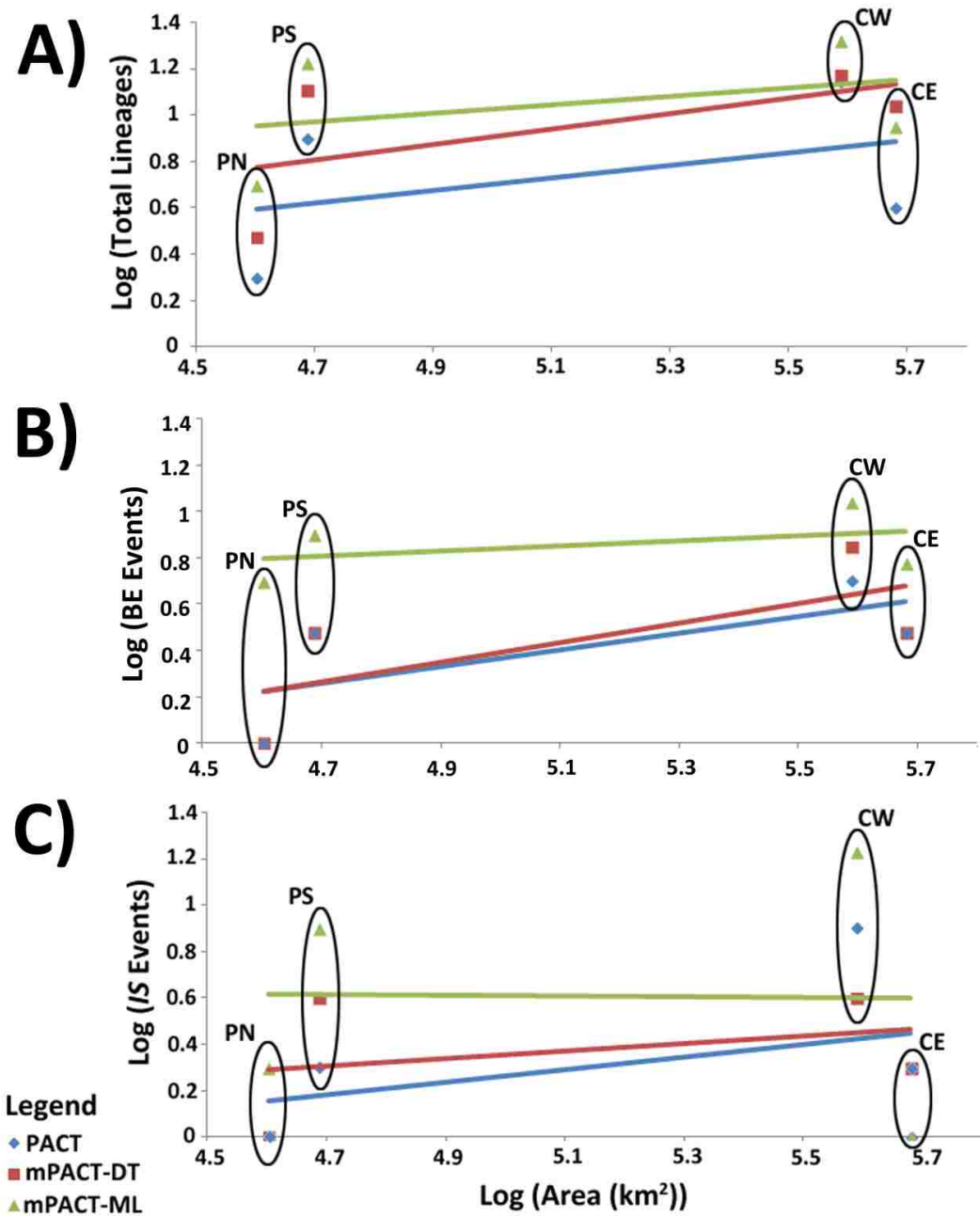
Figure 3.14. mPACT vs. PACT diversification-area relationship results.

CHAPTER 4:

RECONSTRUCTING THE ROLE OF AREAS OF ENDEMISM IN THE FORMATION OF THE

NORTH AMERICAN WARM DESERT BIOTAS

ABSTRACT

Exacerbated rates of climate change have made it vital to understand how changing

climates alter regional floral and faunal distributions in order to prescribe effective

conservation strategies. Identification of areas of endemism (defined by some

biogeographers as areas that generate and maintain unique lineages through time) may

offer an effective approach to understanding how species and biotas will respond to

future climate change, thus providing a novel tool for protecting regional biodiversity.

Under this area of endemism definition, transitional areas occur between areas of

endemism, and may have higher species richness as the result of the intermixture of

species dispersing out of two or more areas of endemism. As a consequence, these

regions could be the focus of conservation efforts. However, conserving transitional

areas may be inadvisable because these regions are often only ephemerally rich during

periods of environmental change, such as glacial or interglacial cycles. In order to gain

an enhanced understanding of the evolutionary dynamics of areas of endemism in the

North American warm deserts, I conducted a multi-organism evolutionary

biogeographic analysis (modified Phylogenetic Analysis for Comparing Trees; mPACT) to

investigate the impacts of landscape and climate change on the evolutionary and

distributional dynamics of North American warm desert biodiversity. Results indicate

that pseudo-congruence obscured detail of North American warm desert area of endemism evolution, and there are more instances of general diversification events (events represented by 2+ taxa) in diagnosed North American warm desert areas of endemism than in transitional areas. General events likely represent vicariant or concordant dispersal events and I suggest that these areas of endemism have more stably retained biodiversity through historical climate change than transitional areas. However, 'transitional areas proximal to areas of endemism' (TAPAE) did not statistically differ from areas of endemism when testing differences in degree of generality (number of taxa representing each diversification event, in this case from 2-8 taxa), indicating that these regions may serve as either distributional extensions of the currently diagnosed areas of endemism (and are ephemeral through time) or as a part of the areas of endemism to which they are proximal (and persist through time).

INTRODUCTION

It is essential to understand how environmental factors alter regional floral and faunal distributions in order to prescribe effective conservation strategies in the face of anthropogenically-driven climate change, habitat destruction, and landscape modification (Whittaker et al., 2005; Ladle & Whittaker, 2011). Identification of areas of endemism, which have been defined by some biogeographers as areas that generate and maintain unique lineages through time, may represent an improved approach to predicting historical responses of species and biotas to climate changes (Riddle & Hafner, 2006). Hence, areas of endemism may serve as a foundation for regional

biodiversity conservation by predicting areas where biodiversity will continue to evolve

and persist (Riddle & Hafner, 2006).

Diagnosing, Describing, and Delimiting Areas of Endemism

Diagnosing. In the most general terms, areas of endemism include species restricted to

a distribution and these areas are hierarchically structured (Anderson, 1994). For

example, in an avifaunal study, Cracraft (1985) pointed out that one species may be

endemic to North America, another to Europe, but both are endemic to the Holarctic.

However, beyond these characteristics, the criteria for recognition and diagnosis of

areas of endemism are complex and have been extensively debated (e.g., de Candolle,

1820, 1838; Rosen, 1978; Ghiselin, 1980; Rosen, 1988; Anderson, 1994; Harold & Mooi,

1994; Linder, 2001a; Szumik & Goloboff, 2004; Crother & Murray, 2011; Table 4.1).

Debates regarding areas of endemism include everything from disagreements over

definitions of endemism, areas, philosophy, and formation to number of taxa required

to diagnose an area of endemism, degree of taxonomic restriction, and appropriate

diagnostic techniques (Table 4.1). At the forefront of these debates is the philosophical

nature of areas of endemism, and whether areas of endemism are dynamic individuals

(a particular thing with boundaries in time and space; Ghiselin, 1980) or if they are static

classes. Under the definition of areas of endemism as individuals, areas of endemism

are spatio-temporally and taxonomically-bounded entities that can shift, expand,

contract, and experience birth-death events through time (Crother & Murray, 2011; Fig.

4.1).

For biogeographers who consider areas of endemism as individuals instead of classes, there is even further debate about what criteria should be used for diagnosis. For example, some biogeographers consider a new area of endemism to be formed by new taxonomic compositions (e.g., Crother & Murray, 2011), whereas others consider areas of endemism to be defined by the ability of organisms to evolve and persist through time (e.g., Riddle & Hafner, 2006; Table 4.1; Fig. 4.2). However, even though argument exists about how to diagnose the area of endemism itself, all areas of endemism share several sub-components. These sub-components are described herein as areas of persistence, ephemeral areas, and areas of turnover (Table 4.2).

Describing. Areas of persistence comprise portions of areas of endemism where taxa persist despite temporal and, consequently, environmental change. For example, an area may have served as a glacial refugium, but organisms may also continue to persist in that region during an interglacial event, even if organisms have since expanded from the area (e.g., Hewitt, 1996; Petit et al., 2003; Hewitt, 2004; Stewart et al., 2010; Hampe et al., 2013; Fig. 4.2). An area would therefore be considered an area of persistence under conditions where taxa persist in an area despite environmental change.

Ephemeral areas may be considered portions of areas of endemism that are prone to expansion, contraction, and shifting. These fluctuations may be associated with environmental change events such as glacial-interglacial cycles. Ephemeral areas may include a glacial refugium that does not persist through an interglacial cycle and instead the endemism boundaries shift to form a new interglacial refugium in a different

region (Fig. 4.2). For example, arid-adapted taxa may expand into ephemeral areas during interglacial cycles and contract from these regions during glacial cycles.

Areas of turnover are synonymous with the formation of a new area of endemism under the philosophy that areas of endemism are formed by new taxonomic compositions (Crother & Murray, 2011). Areas of turnover are zones of contact between two existing parent components of areas of endemism (either two ephemeral areas or an ephemeral area and an area of persistence). According to the taxonomically-bounded area of endemism argument (Crother & Murray, 2011), this zone is a different area of endemism from either pre-existing parent area of endemism. However, these zones of contact and taxonomic turnover are often associated with ephemeral areas and consequently may be highly ephemeral in nature, and as a consequence may be more likely to experience birth-death events at a faster rate than either parent components of area of endemism.

Ephemeral areas and areas of turnover are primarily synonymous with the "transitional areas" described by Riddle & Hafner (2006). Areas of turnover often have the highest species richness as the result of the intermixture of species dispersing from two or more areas of persistence or ephemeral areas. As a result, these regions could be the focus of conservation efforts that equate biodiversity value with species richness (Riddle & Hafner, 2006). However, Hafner & Riddle (2011) suggested that conserving these areas may be inadvisable for conservation efforts because these regions are often only ephemerally rich during periods of environmental change, such as glacial-interglacial cycles. Instead, they argue that the stable areas (areas of persistence as

described in this study) may be more appropriate for conservation in order to mitigate

biodiversity loss. However, areas of turnover may be comprised of areas of endemism

under the stable source production definition if the area of turnover is comprised of an

area of persistence and an ephemeral area (Table 4.2).

It is important to note that all areas of endemism and their components are

ephemeral at some point in time and are hierarchically-structured (Crother & Murray,

2011). When discussing area of endemism components (i.e., areas of persistence,

ephemeral areas, and areas of turnover) and testing hypotheses, it is important to

consider both inference scale as well as temporal designation of the study. For

example, an area of persistence between glacial and interglacial cycles on the order of

thousands of years may be rendered an ephemeral area in the context of mountains

uplifting from tectonic change on the order of millions of years.

Delimiting. Areas of endemism have been both theoretically and operationally-derived

(see Crother & Murray, 2011 for a review). Parsimony Analysis of Endemicity (PAE;

Rosen, 1988) is a common technique to diagnose areas of endemism using modern day

distribution data. A few other diagnostic techniques have been described, such as

weighted grid-based methods, where species with wide-ranging distributions receive a

down-weighted contribution to each individual area (Linder, 2001a) or where

endemicity scores are weighted based on how well a distribution matches an area's

boundaries (Szumik & Goloboff, 2004). However, most empirical studies have

incorporated species distributions and used areas of endemism as units of analysis for

biogeographic research, but the evolutionary nature and dynamic properties of areas of

endemism have mostly been neglected and to date, methods have not been able to

address whether areas of endemism represent areas of biodiversity production and

stability.

Riddle & Hafner (2006) addressed the issue of area of endemism evolution by

diagnosing areas of endemism for the North American warm deserts and refining

hypotheses regarding the general patterns of evolution in these regions using

distribution data for 22 taxa (Table 3.1), although their methods were also unable to

address biodiversity production and stability through time (their definition of an area of

endemism). They diagnosed areas of endemism using Parsimony Analysis of Endemicity

(PAE; Rosen, 1988) and used the diagnosed areas of endemism as units of analysis for

Primary and Secondary Brooks Parsimony Analysis (BPA; Brooks, 1990), which examines

general historical diversification patterns (i.e., divergence events represented by

numerous taxa). Additionally, their analysis only included the diagnosed areas of

endemism and they pruned transitional areas from the phylogenetic trees. Phylogenetic

trees were pruned because the complex nature of transitional areas could lead to

erroneous results in BPA analyses. Lineages in transitional areas are often thought to be

more ephemeral than lineages in areas of endemism during episodes of glacial or

interglacial cycles and thus lineages may disperse into transitional areas during different

climate episodes (and thus on different time scales). Those lineages that would then

persist in transitional areas would thus be more likely to produce pseudo-congruent

patterns – that is, the patterns did not actually represent general events, but instead

several temporally unique events with superficially similar patterns when time is excluded from analysis (Fig. 1.1). However, more recent analytical developments, such as Phylogenetic Analysis for Comparing Trees (PACT; Wojcicki & Brooks, 2004, 2005) and a modification to PACT (mPACT; Chapter 3), facilitate the exploration of biotic-level ecological and evolutionary biogeographic patterns, reduce the prevalence of pseudo-congruence in biogeographic analysis, and provide a framework for testing hypotheses about the dynamic nature of biotas through time.

Reconstructing Area of Endemism Evolution in the North American Warm Deserts

The North American warm deserts are an ideal system for testing novel methodological approaches because they represent unique biotas that have been subjected to numerous geologic and climatic processes (e.g., Neogene uplift of the North American cordillera and Plio-Pleistocene climate oscillations, respectively) that have produced a complex topography and diverse environmental conditions. These deserts also have relatively distinct biotic assemblages with sister taxa often in adjacent deserts, which allows for phylogenetic control for comparison between the deserts. Additionally, a large number of phylogenetic datasets have been generated for organisms, including birds, mammals, reptiles, and plants (Wells & Harragan, 1983; Riddle & Hafner, 2006; Pyron & Burbrink, 2009; Hafner & Riddle, 2011).

I use the 22 lineages of North American warm desert taxa used in Riddle & Hafner (2006)'s benchmark dataset for testing methods (Fig. 3.7, Table 3.1) to conduct mPACT analyses and compare my results to the hypotheses set forth by Riddle & Hafner

(2006). The mPACT results are then used to characterize the evolutionary dynamics of North American warm desert areas of endemism to infer general and unique diversification events, which may represent instances of vicariance or concordant dispersal (or "geodispersal;" Lieberman & Eldredge, 1996) and idiosyncratic dispersal, respectively.

I test the hypothesis that if currently diagnosed areas of endemism represent areas of stability and production in the North American warm deserts, then there will be more general diversification events within and among areas of endemism than within and among transitional areas through time. I predict that, if areas of endemism represent areas of stability and production, i) there is detectable phylogenetic structure of areas of endemism, where areas of persistence have higher frequencies of general diversification events into and within these regions, and ii) areas of endemism have higher proportions of general events into and within these regions through time.

METHODS

I included the 22 North American warm desert taxa in my analysis that were previously used to identify western North American aridland areas of endemism by Riddle & Hafner (2006). These taxa include nine mammals, seven birds, four non-avian reptiles, one amphibian, and one plant (Table 3.1). This benchmark dataset facilitates the ability to directly compare novel results to robust, pre-existing hypotheses of areas of endemism in the North American warm deserts.

I designated regions based on region delineation in Riddle & Hafner (2006), including diagnosed areas of endemism (Continental West, Continental East, Peninsular North, Peninsular South) and transitional areas (e.g., Mojave Desert, Deming plains; Fig. 4.3). I included all areas within species' and sub-species' ranges, which included some areas extending beyond the warm aridlands and semi-aridlands. Including these other areas allowed me to develop a more complete picture of aridland evolution, particularly because many arid-adapted lineages formed from various other habitats, such as thornscrub, chaparral, and grassland environments (Axelrod, 1983). When the ranges of lineages extended beyond the warm aridlands and semi-aridlands, I identified areas based on pre-existing physiographic delineations (e.g., Bonneville and Lahontan basins, Great central valley, California coast; Fig. 4.3).

Modified Phylogenetic Analysis for Comparing Trees (mPACT) Analysis

I used two general area cladograms (GACs) that were generated using the modified Phylogenetic Analysis for Comparing Trees (mPACT) algorithm, which is a modified approach to the Phylogenetic Analysis for Comparing Trees (PACT; Wojcicki & Brooks, 2004, 2005) that incorporates a temporal component and distinctions of unique from general diversification events (events represent 1 taxon or 2+ taxa, respectively; Chapter 3). The first GAC was originally produced in Chapter 3 and included only the four *a priori* diagnosed areas of endemism; lineages existing in transitional areas were excluded from analysis. The second GAC was independently generated using the input taxon-area

cladograms and divergence dates derived in Chapter 3 as well as all areas of a lineage's

distributions (i.e., transitional areas were incorporated).

I conducted parsimony-based ancestral area reconstruction (Delayed

Transformation, or DELTRAN) protocols on the second, unmodified GAC to infer

ancestral distributions. Maximum Likelihood-based ancestral area reconstruction was

not used in this analysis because preliminary analyses were uninformative – Maximum

Likelihood analysis could not resolve the ancestral areas throughout the GAC that

included transitional areas because this GAC was too complex (81 operational

taxonomic units – or OTUs – representing 18 areas) and the majority of nodes were

equivocal between two or more possible areas.

Hypothetical Comparative General Area Cladograms (GACs)

To evaluate how the output mPACT GAC performs relative to theoretical expectations of

areas of endemism and transitional areas, I developed two extreme hypothetical trees

for comparison (Fig. 4.4). One tree represents 100% persistence and stability through

time with congruence among all taxa that reflects general earth history events (Fig.

4.4A). The second tree represents an entirely transitional tree represented by a stepping

stone tree from east to west including all considered regions where all events are

unique (Fig. 4.4B).

GAC Analysis

I analyzed GACs in concordance with previous studies (Halas et al., 2005; Eckstut et al., 2011) by analyzing the number of OTUs (operational taxonomic units; i.e., number of tips on the GAC). I also examined the degree of generality (number of congruent diversification events) in the context of temporal and spatial scales. I performed all statistical analyses using the Excel 2007 Data Analysis package (Microsoft, 2007), and tested all data for normality prior to analysis using a one-sample Kolmogorov-Smirnov test and for homogeneity of variance using a Levene's test. I set the significance level for all tests as $\alpha = 0.05$. I conducted ANOVAs to test the differences in spatial and temporal dynamics. For significant ANOVA analyses with more than two independent variables, I conducted a Tukey's HSD (honestly significant difference) test.

For spatial analysis, I tested the impact of area type (transitional or area of endemism) on degree of generality (number of taxa representing each diversification event. I recorded the number of diversification events per area and analyzed using a single-factor ANOVA, with area type as the independent variable and degree of generality as the dependent variable. Additionally, I ran ANOVAs including area types as i) the areas of endemism (PS, PN, CW, and CE) and three 'transitional areas proximal to areas of endemism' (TAPAE; Mojave Desert, San Felipe, and Deming plains), and ii) the areas of endemism, TAPAE, and all other non-TAPAE transitional areas (e.g., Great central valley, Lahontan basin, Bonneville basin, etc.).

For temporal analysis, I tested the impact of time period on proportion of event types (general versus unique). I conducted a single-factor ANOVA using time

(Quaternary or Quaternary-Neogene) as the independent variable and degree of

generality as the dependent variable. I did not include strictly Neogene events in

temporal analysis because there were only one general and one unique event that

occurred during the Neogene. As a consequence, I only compared events from the

Quaternary and events that range from the Quaternary to Neogene.

RESULTS

Overall GAC Analysis

The unmodified GAC (including both transitional areas and areas of endemism) yielded

81 OTUs representing 18 areas (Fig. 4.5). Areas of endemism represented 29 out of the

81 OTUs (35.8%; Fig. 4.5; Table 4.3). In the GAC, areas of endemism comprised 27% of

unique diversification events and 61.4% of general diversification events (co-divergence

of 2+ taxa; Fig. 4.5; Table 4.3). The total number of general diversification events

progressively decreased with increased number of taxa, regardless of whether or not

transitional areas were included in analysis (Table 4.3), although increased degree of

generality at the level of 6 or more taxa is limited to areas of endemism.

DELTRAN ancestral area reconstruction yielded results showing that many of the

ancestral states originated in either the Peninsular South or Baja California Islands (Fig.

4.6). However, parsimony-based optimization does not take into account degree of

generality, and can be misleading for ancestral area reconstruction (Cunningham, 1999;

Pirie et al., 2012; see Chapter 3 for a summary of how this occurs and an example using

North American warm desert areas of endemism). In particular, the majority of Baja

California Island events were unique, and these results are skewed by this analysis. A Maximum Likelihood ancestral area reconstruction would be more effective for inferring ancestral areas in this analysis, but to date there are no reconstruction methods able to compensate for both polytomies and the complexity and size of this GAC (81 OTUs representing 18 areas).

Spatial GAC Analysis

Both general and unique events occur in areas of endemism and transitional areas (Table 4.4). Spatial analysis revealed that areas of endemism (PS, PN, CW, and CE) are statistically different from transitional areas (F=4.22, p=0.043). Areas of endemism do not differ from 'transitional areas proximal to areas of endemism' (TAPAE) with regard to degree of generality (F=0.966, p=0.22; Fig. 4.7). Consequently, there is a significant difference when comparing transitional areas to areas of endemism with TAPAE included (F=13.6, p<0.01).

Temporal GAC Analysis

Time did not impact the degree of generality (Table 4.5; Single-factor ANOVA, F=2.78, p=0.10). Including transitional areas increases the proportion of unique events during the Quaternary (Pleistocene and Holocene, ca. 2.58 mya to present) from 33.3% (only areas of endemism; excluding transitional areas) to 52.9% (including transitional areas) of total diversification events, and reduces the proportion of general events (2+ taxa) from 66.7% to 47.1% (Table 4.6; Fig. 4.8). The opposite pattern emerges during the

Quaternary/Neogene transition (particularly during the late Pliocene, ca. 3.6-2.58 mya, and early Pleistocene, ca. 2.58-0.781 mya): the proportion of unique events decreases relative to proportion of general events when I included transitional areas in analysis (unique: 48.1% excluding transitional areas to 30.4% including transitional areas; general: 51.9% excluding transitional areas to 69.6% including transitional areas; Table 4.6; Fig. 4.8).

DISCUSSION

My study reveals evolutionary patterns of biodiversity production and stability in areas of endemism that other methods have not been able to address. The results show that previous analyses have underestimated how the hierarchical nature of areas of endemism (restricted vs. broadscale patterns) and the role of pseudo-congruence complicate diagnosis of areas of endemism and analysis of their evolution. Herein, I compare my results with the hypothetical general area cladograms (GACs; Fig. 4.4) and discuss the spatial and temporal dynamics of areas of endemism that my study revealed, as well as the overall implications these results have for areas of endemism.

Comparison of Results with Hypothetical GACs

Results show that the patterns of diversification in the North American warm deserts conform neither strictly to one tree that represents 100% general earth history patterns, persistence and stability through time with congruence among all taxa (Fig. 4.4A) nor to an entirely transitional tree where all events are unique (Fig. 4.4B). In the resultant

mPACT GAC (Fig. 4.5), there is a combination of unique (1 taxon) and general events (2 taxa up to 8 experiencing a similar diversification event), and a degree of generality (i.e., number of taxa that experienced congruent diversification events; 2 would be a low degree, 8 would be a high degree). These results are unsurprising with the amount of debate regarding whether vicariance or dispersal was the primary driver of diversification in the North American warm deserts (Riddle & Hafner, 2006; Pyron & Burbrink, 2009; Hafner & Riddle, 2011).

The degree of generality increased when number of taxa representing each event decreased (Table 4.2). In particular, although both areas of endemism and transitional areas showed lower degrees of generality (2-5 taxa), increased degree of generality (6 or more taxa) was only observed in areas of endemism (Table 4.3). This may indicate that many "weaker" general events (2-4 taxa diversifying in unison) into transitional areas are coincidental or driven by lineage-specific habitat tolerances and ecological constraints that result from concordant dispersal events (co-dispersal of several taxa when barriers fall). In the North American warm deserts, concordant dispersal could occur as the expansion and contraction of suitable habitat during glacial/interglacial cycles serve as barriers. Alternatively, "stronger" general events (6 or more taxa), which were only observed in areas of endemism, may be more often produced by vicariance (lineage fragmentation from habitat/topographic alterations that lead to diversification) from mountain uplift and full desert formation in the North American warm deserts.

Spatial Dynamics of Areas of Endemism

All of the areas of endemism identified by Riddle & Hafner (2006) were areas with more general diversification events than other regions (Table 4.4). The Continental West, Continental East, and Peninsular South were areas that also had several unique diversification events (Table 4.4). This may indicate that, although these areas are acting as stable areas of persistence for several organisms (as indicated by general diversification events), they may also be acting as ephemeral areas or areas of turnover for other organisms (as indicated by unique events). For example, if the Continental West is a stable area of persistence for certain lineages, the Continental East may serve as an ephemeral area for these lineages during episodes of biotic expansion. Moreover, areas of endemism are scale-specific and heirarchical, and although at this scale of comparison these areas are diagnosable as areas of endemism for several taxa, at a coarser scale we may observe that these areas are collectively a different area of endemism, perhaps including all considered taxa.

Furthermore, inclusion of so-called transitional areas into this analysis revealed that these areas may not entirely represent ephemeral areas, as predicted by Riddle & Hafner (2006). There was a statistical difference between degree of generality in areas of endemism and transitional areas (F=4.22, p=0.043), but there was no difference between areas of endemism and 'transitional areas proximal to areas of endemism' (TAPAE; F=0.22, p=0.966), and the difference between areas of endemism and transitional areas also occurred when including TAPAE as a part of the areas of endemism (F=13.6, p<0.01). These results, which show that TAPAE are not statistically

different from areas of endemism, support the idea that modern day distribution data

are likely not sufficient for diagnosing areas of endemism in an evolutionary context. It

is possible that TAPAE do not statistically differ from areas of endemism because they

represent distributional extensions of taxa from areas of endemism because they are

proximal to these areas. This pattern can be observed in the mPACT GAC, because there

is only one instance of a TAPAE (the Mojave Desert) that is not sister to an area of

endemism (Fig. 4.5). However, because the degree of generality does not differ between

TAPAE and areas of endemism, the TAPAE may evolutionarily be a part of the areas of

endemism to which they are proximal.

Testing the evolutionary dynamics of TAPAE would be ideal to determine if these

areas represent stable and persistent areas (and perhaps are a part of areas of

endemism) or if they are merely distributional extensions that are ephemeral through

time and the degree of generality a result of concordant dispersal. However, approaches

used in this study (comparing areas of endemism and full GACs) would be uninformative

because most TAPAE are sister to areas of endemism and statistically similar with

degree of generality. PACT analyses can be used to infer proportions of diversification

resulting from *in situ* (*IS*), *IS*/biotic expansion (BE), and full BE events, as well as total

amount of forward and backward BE (Halas et al., 2005; Eckstut et al., 2011). Inferring

IS, *IS*/BE, and BE events would be informative for exploring if TAPAE are persistent or

ephemeral through time. However, these analyses were not possible in this study

because of the lack of information available from either likelihood- or parsimony-based

ancestral area reconstruction. However, examining *IS* and BE events in the context of

areas of endemism, transitional areas, and TAPAE through time would be informative

with smaller datasets or the development of likelihood-based ancestral area

reconstruction software able to handle complex datasets like the mPACT GACs.

In the one instance where the Mojave Desert (a TAPAE) is not sister to a warm

desert area of endemism, it is instead sister to the Bonneville basin, Lahontan basin, and

Colorado plateau (Fig. 4.5). This lends credence to the notion that the Mojave Desert

serves as a transitional desert between biotas of the southern warm deserts and the

colder Great Basin aridlands (Riddle & Hafner, 2006). The Great Basin may in itself be a

unique area of endemism – it is comprised of a large number of lineages that have a

distinctly different origin than those of the more southern warm deserts (i.e., Arcto-

tertiary and Madro-tertiary compared to Neotropical-tertiary and Madro-tertiary;

Axelrod, 1958, 1972, 1985). Therefore, I suggest that analysis of the northern colder

aridland regions is necessary to test the potential role of the Great Basin as an

additional area of endemism (and thus potentially an area of persistence) in the North

American deserts and the potential role of the Mojave Desert as an area of turnover

between the northern and southern aridlands.

Temporal Dynamics of Areas of Endemism

In Chapter 3, I discussed how other methods that exclude a temporal component

(Secondary BPA and PACT) produced several patterns resulting from pseudo-

congruence. The reduction of pseudo-congruence by using mPACT showed that the

other analyses underestimated the role of unique diversification in biodiversity

formation. Furthermore, incorporating divergence times revealed that perhaps not all

diagnosed areas of endemism are equal with respect to biodiversity production and

stability. For example, the Peninsular North/Peninsular South divergences

predominantly occurred within the Pleistocene, which is consistently with the idea that

the Peninsular South and Continental West are more stables of diversity and that the

Peninsular North is ephemerally species rich from expansion that occurs during

interglacial cycles (e.g., Savage, 1960; Riddle & Hafner, 2006).

By including transitional areas into analysis, I observed that the proportion of

unique events is higher compared to general events (36 unique to 32 general events)

during the Quaternary, but there is a higher proportion of general events in areas of

endemism (9 unique to 18 general events; Table 4.6; Fig. 4.7). These data failed to reject

my prediction that areas of endemism serve as an area of production and stability

during episodes of climate change. Additionally, although the majority of diversification

in transitional areas were unique (27 events), there were 14 general events in

transitional areas, which may indicate that concordant dispersal (congruent dispersal

resulting from a fallen barrier; Lieberman & Eldredge, 1996) is a large driver of

diversification within the warm desert areas of endemism than previously recognized. In

the case of the Quaternary, this may mean the expansion of suitable habitat, and thus

concordant expansion, during interglacial cycles for desert taxa.

Alternatively, during the Quaternary/Neogene transition (particularly during the

late Pliocene, ca. 3.6-2.58 mya, and early Pleistocene, ca. 2.58-0.781 mya), I see the

opposite pattern: the proportion of unique events decreases relative to the proportion

of general events when I included transitional areas in analysis (unique: 48.1% to 30.4%; general: 51.9% to 69.6%; Table 4.6). I hypothesize that this indicates rapid uplift of the North American cordillera and associated habitat and landscape evolution congruently fragmented lineages into all regions in western North America via vicariance (Fig. 2.2). This timeframe also warrants further investigation because the onset of aridification during the Plio-Pleistocene uplift led to many arid-adapted desert lineages that are consequently more constrained to their extreme habitats (Fig. 2.2) and may have formed the currently recognized areas of endemism. Additionally, more frequent, older general events (ca. Plio-Pleistocene uplift) in areas of endemism may indicate that these areas serve as sources for biodiversity production and persistence (Tables 4.3, 4.6).

The lack of diversification events during just the Neogene does not mean that there was no diversification in western North America during that time. The clades used by Riddle & Hafner (2006) and subsequently in this analysis were, in several instances, sub-clades of more widespread North American taxa. For example, *Chaetodipus* pocket mice are estimated to have started diversifying in western North America approximately 20-22 million years ago (Hafner et al., 2007). However, several lineages within *Chaetodipus* were included in this analysis. As a consequence, the deepest *Chaetodipus* split (20-22 mya) was not included in analysis. In order to infer a better approximation of full western North American diversification, deeper endemic clades should be analyzed.

Implications for Areas of Endemism

I failed to reject my hypothesis that currently diagnosed areas of endemism represent areas of stability and persistence in the North American warm desert when I conducted an evolutionary analysis of areas of endemism. I also failed to reject my prediction that there is detectable phylogenetic structure in areas of endemism using spatial and degree of generality analyses. There were higher frequencies of generality and general events in diagnosed areas of endemism (potentially areas of persistence and turnover) and higher proportions of unique events in transitional areas (potentially ephemeral areas and areas of turnover; Tables 4.3, 4.4). Finally, I failed to reject my prediction that areas of endemism experience higher frequencies of general diversification events through time by conducting temporal analysis of the GACs. There were higher proportions of unique events when including transitional areas into analysis of the Quaternary and higher proportions of general events occur when including transitional areas into analysis of the Quaternary/Neogene transition (Tables 4.5, 4.6). However, spatial analysis did reveal that diagnosed areas of endemism were not statistically different from transitional areas proximal to areas of endemism (TAPAE) with regard to general and unique events, but both areas of endemism and TAPAE were statistically different from other transitional areas. These data indicate that TAPAE may be distributional extensions of areas of endemism (and are ephemeral through time) or may be a part of the more stable areas of endemism to which they are proximal.

My results also corroborate pre-existing hypotheses about the nature of diversification in the North American warm deserts. For example, although areas of

endemism have higher degrees of generality, there are still general events in the North American warm deserts, particularly that there is a mixture of older, vicariant-based events as well as younger, dispersal-driven events (Fig. 2.2). Substantial disagreement has occurred about which mechanism contributed more to the formation of the desert biodiversity (e.g., Riddle & Hafner, 2006; Jezkova et al., 2009; Pyron & Burbrink, 2009; Hafner & Riddle, 2011), but these results indicate that both vicariant and dispersal-based events appear to have taken place in these regions. As a result, excluding time from analysis is problematic because of the large number of pseudo-congruent events resulting from tectonic-change or orbital forcing on different time scales (Chapters 2 & 3). The diagnosed areas of endemism do have a stronger degree of generality than transitional areas (Table 4.3), and thus potentially serve as a stable source of biodiversity. However, these areas may be persistent for some organisms but not for others, and further analysis of the Peninsular North is suggested to reveal if this region is indeed stable through time or if the general events are concordant dispersal events produced from expansion during interglacial cycles.

This dataset revealed a large amount of pseudo-congruence and temporally-divergent patterns (i.e., tectonics-based climate and landscape change or orbital-forcing related climate change) among areas of endemism and transitional areas. For these reasons, it is important to note caution should be taken when using strictly modern distribution data and cladograms without divergence times to diagnose operational areas of endemism.

Conclusions

Exploring the dynamic nature of biota evolution in the North American warm deserts provides a unique opportunity to infer biodiversity dynamics in response to climate change events. The results of my study indicate that the currently diagnosed areas of endemism may represent areas of persistence for some taxa and ephemeral areas for other taxa and that not all areas of endemism may be equal in strength for biodiversity production and stability through time. A large number of pseudo-congruent patterns were revealed in these areas of endemism (Chapter 3), indicating that temporal components are important when testing hypotheses regarding the evolution of areas of endemism. Moreover, the role of transitional areas may be highly underestimated for biodiversity persistence, particularly because they may serve as areas of persistence for some taxa (e.g., in the 'transitional areas proximal to areas of endemism,' or TAPAE). Expanding this analysis to include more diversity of organisms (including invertebrates as well as more plants, mammals, reptiles, birds, and amphibians) may provide an enhanced understanding of how different types of organisms have responded to Pleistocene glaciations. Moreover, inclusion of more northern, colder aridland, such as the Great Basin Desert (a cold desert where many organisms have a different evolutionary history than in the southern warm deserts), may provide an enhanced understanding of desert response across environmental gradients and reveal more biotic persistence than currently recognized in the Mojave Desert, which only has a few endemic species (Bell et al., 2009).

Table 4.1. Debated definitions regarding various aspects of areas of endemism.

Area of Endemism Aspect	Conflicting Definitions	Citations
Endemism definitions	1) Constantly present in a particular place 2) Native to an area 3) Restricted to a particular area 4) Limited to a small area	de Candolle (1820), Reviewed in Anderson (1994)
Existence and use in biogeography	1) Naturally existing 2) Do not exist	de Candolle (1838), Ghiselin (1980), Hovencamp (1997), Crother & Murray (2011)
Biogeographic use	1) Fundamental units of analysis, deserves substantial attention 2) Should not be considered a central question	Axelius (1991), Bremer (1993), Hovencamp (1997), Hausdorf (2002)
Area definitions	1) Habitat 2) Geographic	Reviewed in Anderson (1994)
Area size	1) Large (e.g., partial overlap; compare between continents) 2) Small (e.g., full overlap; compare within a continent)	Nelson & Platnick (1991), Morrone (1994), reviewed in Crisci et al. (2003)
Philosophical definitions	1) Dynamic individuals 2) Static classes	Ghiselin (1980), Craw (1983), Crother & Murray (2011)
Diagnostic techniques	1) Congruent distributional patterns 2) Congruent distributional and phylogenetic patterns	Platnick (1991), Harold & Mooi (1994)
Degree of taxonomic restriction	1) 100% 2) <100%, "reduced" endemism in an area	Reviewed in Anderson (1994), Linder (2001b)
Number of diagnostic taxa	1) 1 taxon 2) 2+ congruent taxa 3) 3+ congruent taxa	de Candolle (1820), Platnick (1991), Harold & Mooi (1994), Morrone (1994), Humphries & Parenti (1986, 1999)
Formation definitions	1) Taxonomic composition 2) Evolutionary stability and production	Riddle & Hafner (2006), Crother & Murray (2011)
Discovery operations	1) Overlapping of distribution areas 2) Area quadrating 3) Biogeographic units and overlapping or partially overlapping taxa	Müller (1973), Harold & Mooi (1994), Morrone (1994), Crisci et al. (2003)

Table 4.2. Relationship between theoretical definitions of areas of endemism and the components of areas of endemism described in this paper. + indicates that a component is considered part of a definition, - indicates a component is not part of a definition, and ~ indicates that a component sometimes is considered part of a definition. Areas of turnover can be sometimes describe areas of endemism under the stable production source definition if the area of turnover is comprised of an area of persistence as well as an ephemeral area, but not if the area of turnover is comprised of two ephemeral areas.

Theoretical Definition	**Component**		
	Area of Persistence	Ephemeral Area	Area of Turnover
Stable Production Source			
Area of Endemism	+	-	~
Transitional Area	-	+	+
Taxonomic Composition			
Area of Endemism	+	+	+

Table 4.3. Relative influence of areas of endemism and transitional areas on mPACT and PACT GAC structures. Events are based on the total number of nodes throughout the GAC and thus are substantially greater in number than operational taxonomic units (OTUs).

	Unmodified	Areas of Endemism only
OTUs	81	29
Unique Events (Total)	88	24
General Events (Total)	57	35
2 taxa	23	8
3 taxa	14	7
4 taxa	6	2
5 taxa	7	6
6 taxa	4	4
7 taxa	2	2
8 taxa	1	1

Table 4.4. Spatial dynamics of the influence of general and unique events on the mPACT GAC. Areas in **bold** are operational areas of endemism; areas in *italics* are transitional areas. Areas followed with an * indicate areas that occur between two or more areas of endemism.

Area	Degree of Generality per Event
Continental East	1,1,1,1,3,3,3,5
Continental West	1,1,1,1,1,2,3,4,7
Peninsular North	2,3,5
Peninsular South	1,1,1,1,1,2,6,8
Baja California Islands	1,1,1, 1,1,1,1,1,1,1,1,1,2,3
Bonneville Basin	2
California Coast	1,1,1,3
Colorado Plateau	1,1,1
*Deming Plains**	1,2,2,4,4
East Coast	1,1
Great Central Valley	1,2
Great Plains	2
Lahontan Basin	2
*Mojave Desert**	1,3,4
Northern Intermountain Basin	3
*San Felipe**	2,3,3,5
Southern Continental	1,2,2
Southern Intermountain Basin	1,2

Table 4.5. Temporal dynamics of the frequency of general and unique events on the mPACT GAC. In parenthetics are the frequency of times each representation of congruence (1-8) is seen in the full mPACT GAC. For example 1(26) indicates that 1 unique event was observed 26 times in the GAC.

Time	Congruence(Frequency)
Quaternary	1(26), 2(9), 3(8), 4(3), 5(2), 6(1), 7(0), 8(1)
Quaternary + Neogene	1(55), 2(10), 3(5), 4(4), 5(4), 6(0), 7(1), 8(0)

Table 4.6. Temporal dynamics of the overall influence of general and unique events on the mPACT GAC. "Unmodified" includes both areas of endemism and transitional areas. "Areas of Endemism only" have been pruned to exclude transitional areas.

Time Period	Unmodified		Areas of Endemism only	
	Unique	General	Unique	General
Quaternary	36	32	9	18
Neogene	1	1	1	1
Both Quaternary & Neogene	21	48	13	14
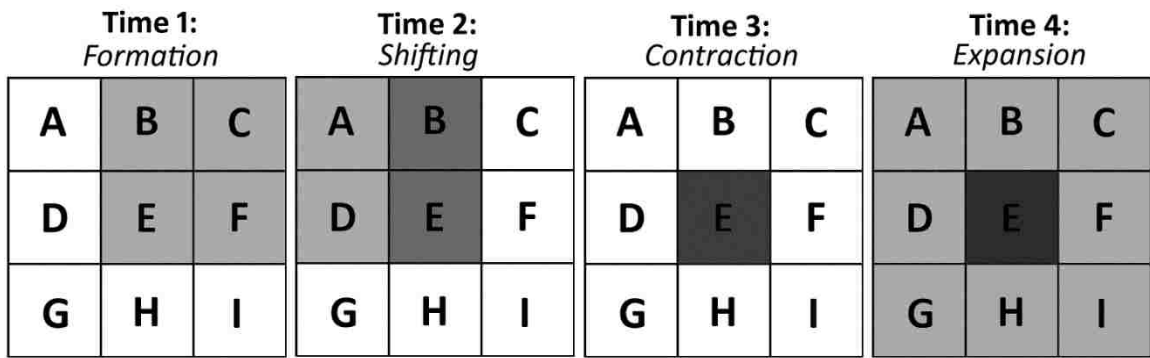
Figure 4.1. A model of the dynamic nature of areas of endemism. Lettered grids indicate distinct areas and shading indicates presence (grey) or absence (white) of the area of endemism at each point in time. Degree of biodiversity persistence is indicated by darker shades of grey.
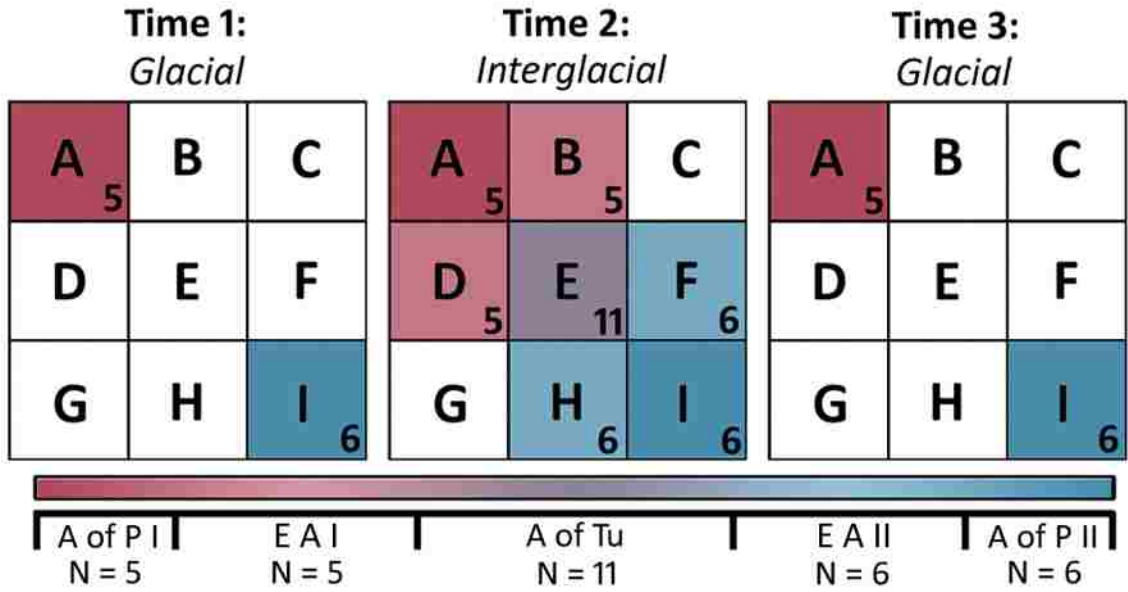
Figure 4.2. A model of the interaction of areas of endemism during periods of climate change. Blue and red are distinct areas of endemism during glacial cycles with 6 and 5 taxa, respectively. During interglacial cycles, the areas of endemism expand and overlap in area E (with 11 taxa). However, area E is transitional and less stable than areas A and I, which represent areas of persistence.

125
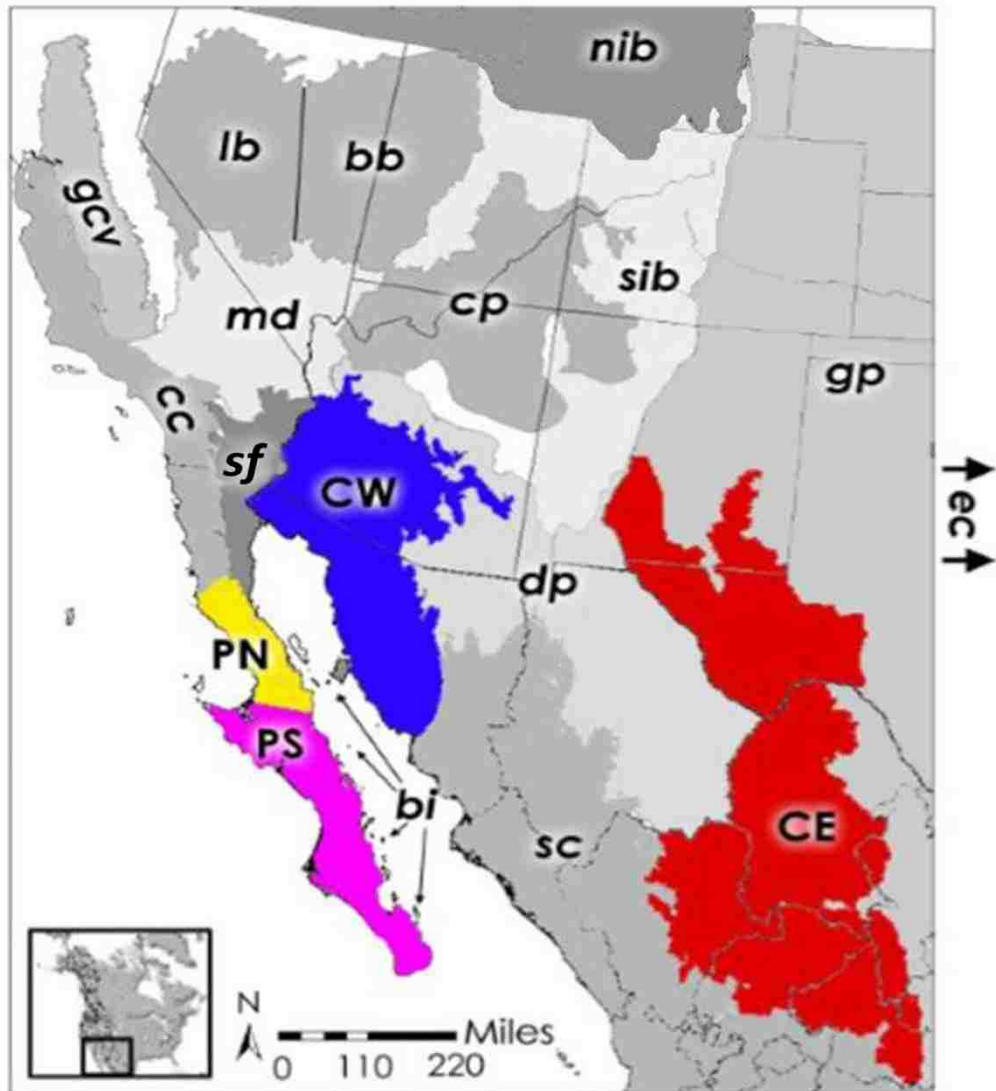
Figure 4.3. Map of western North American areas included in this analysis. Areas of endemism are indicated in capital, bold letters (**PS**, Peninsular South; **PN**, Peninsular North; **CE**, Continental East; **CW**, Continental West). Transitional areas are indicated in lower case, italicized letters (*cc*, California Coast; *gcv*, Great Central Valley; *sf,* San Felipe; *md*, Mojave Desert; *sc*, Southern Continental; *dp*, Deming Plains; *cp*, Colorado Plateau; *ec*, East Coast; *bi*, Baja California Islands; *lb*, Lahontan Basin; *bb*, Bonneville Basin; *gp*, Great Plains; *sib*, Southern Intermountain Basin; *nib*, Northern Intermountain Basin). *ec* is not on the projected area of this map.

Figure 4.4. Hypothetical tree structures under two extremes (vicariance and dispersal). A) Entirely vicariance-based diversification only occurring in the diagnosed "areas of endemism" (in bold), and there is a 100% congruence among all 22 taxa; B) Entirely dispersal-based diversification occurring in all areas, including areas tangential to the diagnosed "areas of endemism" (in lowercase italics).
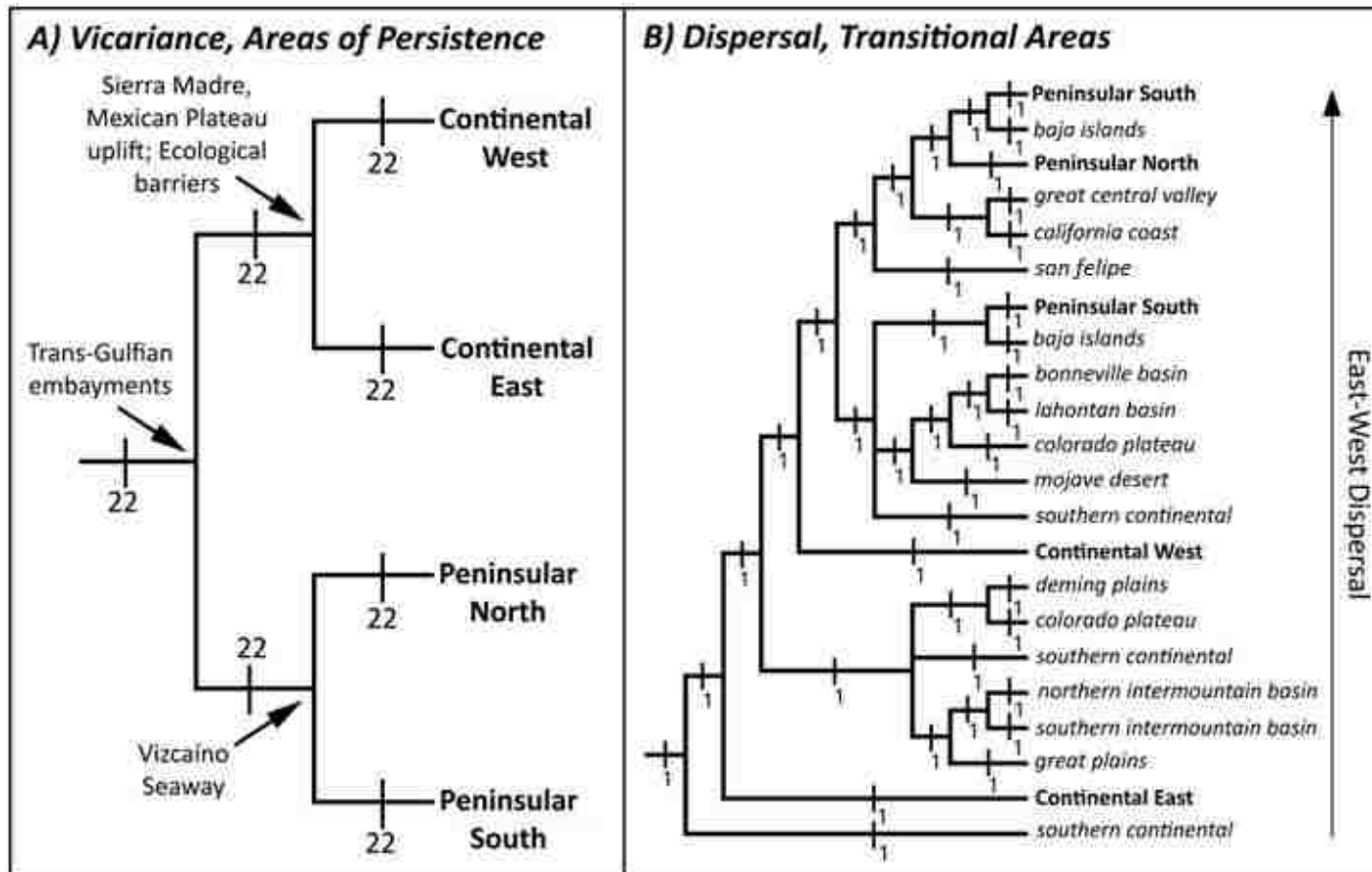
Figure 4.5. Full mPACT GAC. Areas of endemism are indicated in capital, bold letters (**PS**, Peninsular South; **PN**, Peninsular North; **CE**, Continental East; **CW**, Continental West). Transitional areas are indicated in lower case, italicized letters (*cc*, California Coast; *gcv*, Great Central Valley; *sf*, San Felipe; *md*, Mojave Desert; *sc*, Southern Continental; *dp*, Deming Plains; *cp*, Colorado Plateau; *ec*, East Coast; *bi*, Baja Islands; *lb*, Lahontan Basin; *bb*, Bonneville Basin; *gp*, Great Plains; *sib*, Southern Intermountain Basin; *nib*, Northern Intermountain Basin). Hashmarks indicate number of taxa (out of 22) that experienced each diversification event (e.g., 1 hashmark = 1 unique event; 8 hashmarks = 8 taxa congruently experience that very general event). Numbers at nodes are in millions of years and indicate divergence time estimates for each event. For nodes without ages, the ages fall between the dates of the last dated ancestral node. "Node symbols" are used to the bottom right of nodes with divergence dates where age estimates would not fit on the cladogram.

128

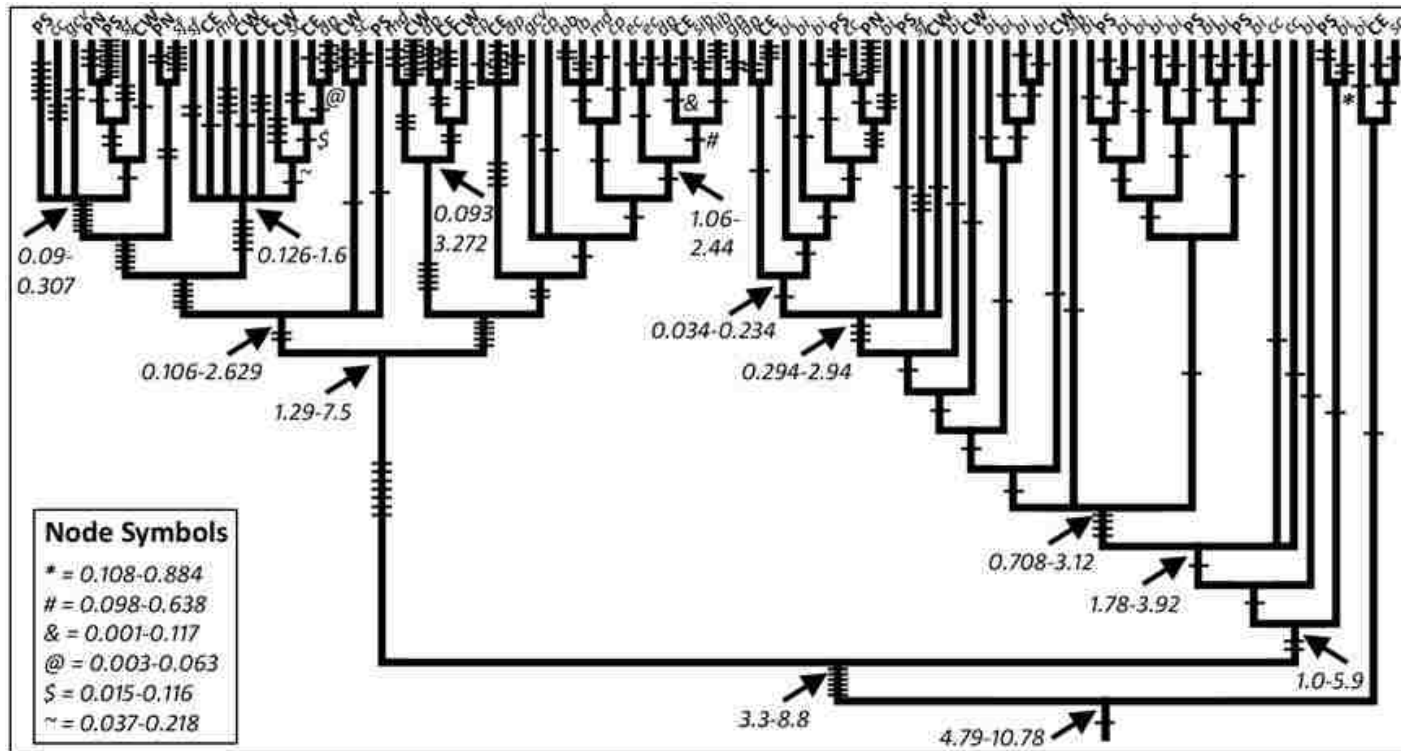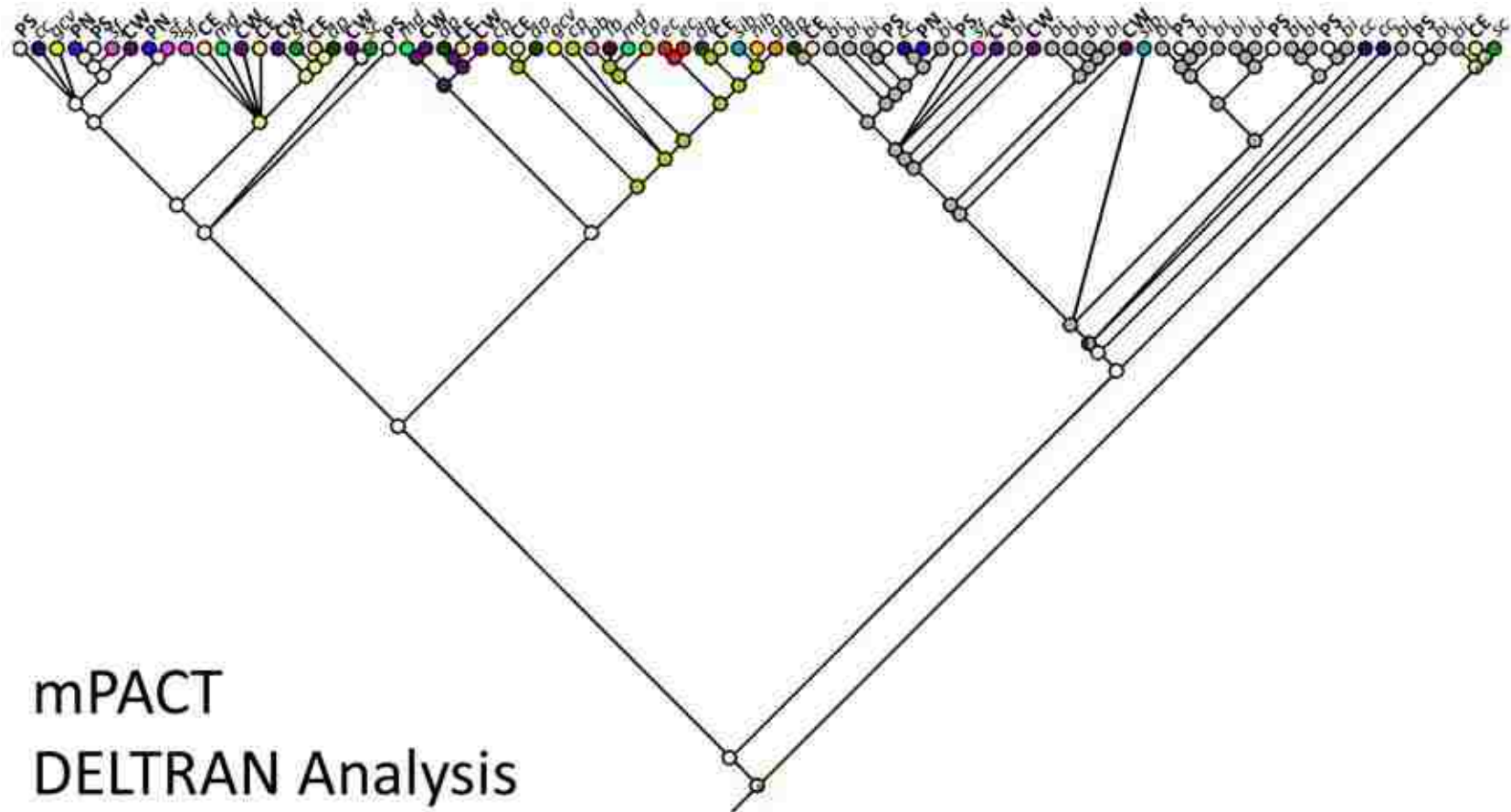**Figure 4.6.** Full mPACT GAC with reconstructed areas using DELTRAN optimization. Areas of endemism are indicated in capital, bold letters (**PS**, Peninsular South; **PN**, Peninsular North; **CE**, Continental East; **CW**, Continental West). Transitional areas are indicated in lower case, italicized letters (*cc*, California Coast; *gcv*, Great Central Valley; *sf*, San Felipe; *md*, Mojave Desert; *sc*, Southern Continental; *dp*, Deming Plains; *cp*, Colorado Plateau; *ec*, East Coast; *bi*, Baja Islands; *lb*, Lahontan Basin; *bb*, Bonneville Basin; *gp*, Great Plains; *sib*, Southern Intermountain Basin; *nib*, Northern Intermountain Basin.
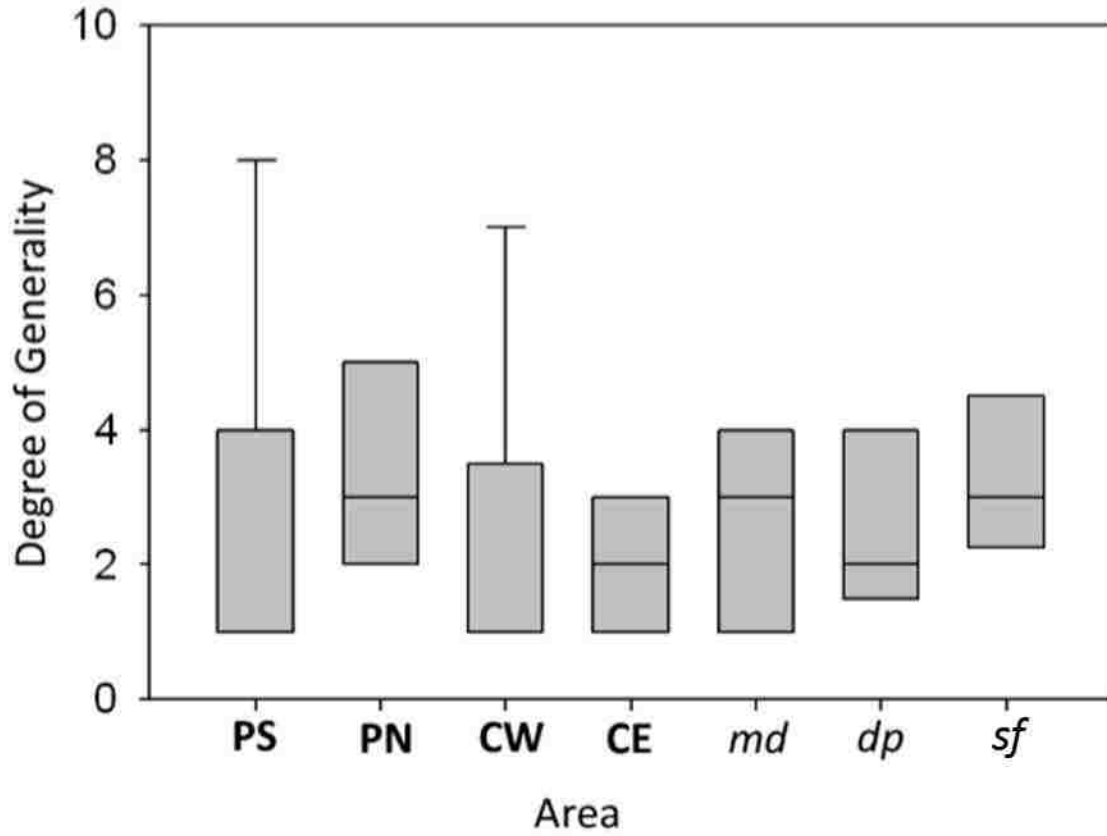
Figure 4.7. Differences between degree of generalities in areas of endemism and areas proximal to areas of endemism.**PS** = Peninsular South, **PN** = Peninsular North, **CW** = Continental West, **CE** = Continental East, *md* = Mojave Desert, *dp* = Deming Plains, and *sf* = San Felipe.
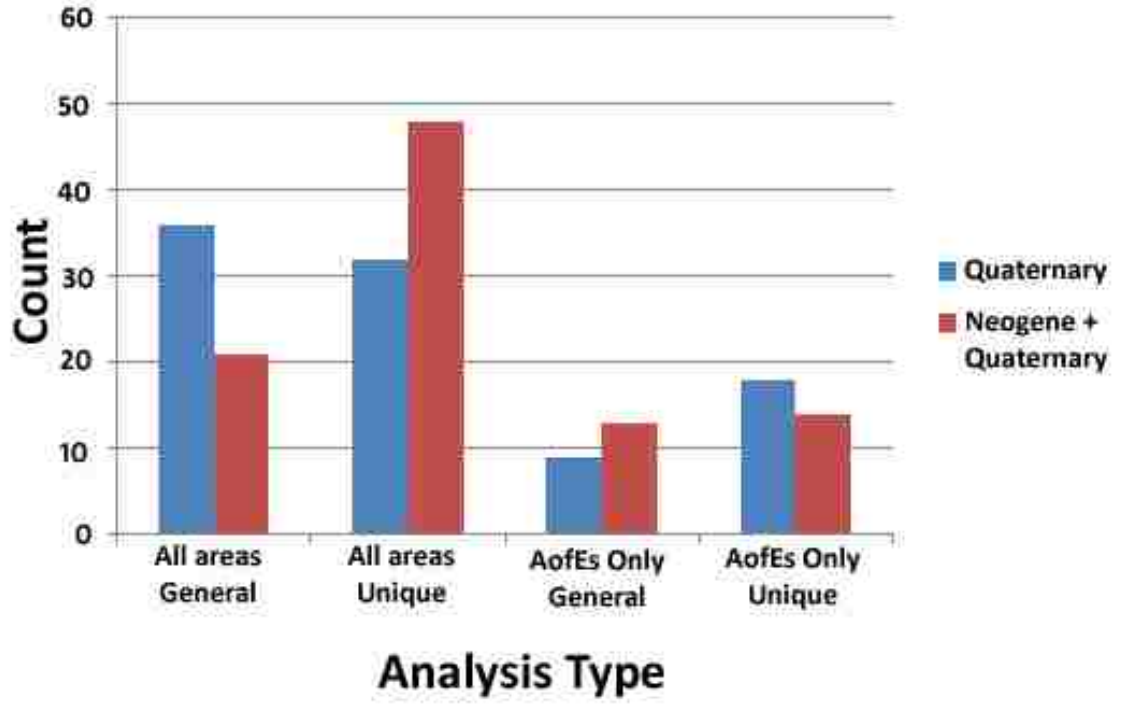
Figure 4.8. Temporal analysis of general and unique events.

BIBLIOGRAPHY

Ackerly, D. D., Loarie, S. R., Cornwell, W. K., Weiss, S. B., Hamilton, H., Branciforte, R., & Kraft, N. J. B. (2010). The geography of climate change: implications for conservation biogeography. *Diversity and Distributions*, *16*(3), 476-487.

Adams, D. K., & Comrie, A. C. (1997). The North American monsoon. *Bulletin of the American Meteorological Society*, *78*(10), 2197-2213.

Agnarsson, I., & Miller, J. A. (2008). Is ACCTRAN better than DELTRAN?.*Cladistics*, *24*(6), 1032-1038.

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In *International Symposium on Information Theory, 2nd, Tsahkadsor, Armenian SSR* (pp. 267-281).

Akaike, H. (1974). A new look at the statistical model identification. *Automatic Control, IEEE Transactions on*, *19*(6), 716-723.

Alexander, L. F., & Riddle, B. R. (2005). Phylogenetics of the New World rodent family Heteromyidae. *Journal of Mammalogy*, *86*(2), 366-379.

Alley, R. B., Marotzke, J., Nordhaus, W. D., Overpeck, J. T., Peteet, D. M., Pielke Jr, R. A., ... & Wallace, J. M. (2003). Abrupt climate change. *Science*, *299*(5615), 2005-2010.

Anderson, S. (1994). Area and endemism. *Quarterly Review of Biology*, *69*(4), 451-471.

Anderson, B. J., Akçakaya, H. R., Araújo, M. B., Fordham, D. A., Martinez-Meyer, E., Thuiller, W., & Brook, B. W. (2009). Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1661), 1415-1420.

Araújo, M. B., & Williams, P. H. (2000). Selecting areas for species persistence using occurrence data. *Biological Conservation*, *96*(3), 331-345.

Araújo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, *33*(10), 1677-1688.

Arrhenius, O. (1921). Species and area. *Journal of Ecology*, *9*(1), 95-99.

Atwater, T. (1970). Implications of plate tectonics for the Cenozoic tectonic evolution of western North America. *Geological Society of America Bulletin*,*81*(12), 3513-3536.

Augustin, L., Barbante, C., Barnes, P. R., Barnola, J. M., Bigler, M., Castellano, E., ... & van de Wal, R. S. (2004). Eight glacial cycles from an Antarctic ice core. *Nature*, *429*(6992), 623-628.

Axelius, B. (1991). Areas of distribution and areas of endemism. *Cladistics*, *7*(2), 197-199.

Axelrod, D. I. (1958). Evolution of the Madro-Tertiary geoflora. *The Botanical Review*, *24*(7), 433-509.

Axelrod, D. I. (1972). Edaphic aridity as a factor in angiosperm evolution.*American Naturalist*, 311-320.

Axelrod, D. (1983). Paleobotanical history of the western deserts. In S. G. Wells & D. R. Haragan (Eds.), *Origin and evolution of deserts* (113-129). Albuquerque: University of New Mexico Press.

Axelrod, D. I. (1985). Rise of the grassland biome, central North America. *The Botanical Review*, *51*(2), 163-201.

Barron, J. A., Lyle, M., & Koizumi, I. (2002). Late Miocene and early Pliocene biosiliceous sedimentation along the California margin. *Revista Mexicana de Ciencias Geológicas*, *19*(3), 161-169.

Bell, K. C., Hafner, D. J., Leitner, P., & Matocq, M. D. (2010). Phylogeography of the ground squirrel subgenus Xerospermophilus and assembly of the Mojave Desert biota. *Journal of biogeography*, *37*(2), 363-378.

Blake Jr, M. C., Campbell, R. H., Dibblee Jr, T. W., Howell, D. G., Nilsen, T. H., Normark, W. R., ... & Silver, E. A. (1978). Neogene basin formation in relation to plate-tectonic evolution of San Andreas fault system, California. *AAPG Bulletin*, *62*(3), 344-372.

Bremer, K. (1993). Intercontinental relationships of African and South American Asteraceae: a cladistic biogeographic analysis. In Goldbatt, P. (Ed.), *Biological relationships between Africa and South America* (105-135). New Haven: Yale University Press.

Brooks, D. R. (1990). Parsimony analysis in historical biogeography and coevolution: methodological and theoretical update. *Systematic Biology*, *39*(1), 14-30.

Brooks, D., & McLennan, D. (2002). The nature of diversity: an evolutionary voyage of discovery. Chicago, IL: University of Chicago Press.

Brown, J. L., & Knowles, L. L. (2012). Spatially explicit models of dynamic histories: examination of the genetic consequences of Pleistocene glaciation and recent climate change on the American Pika. *Molecular ecology*, *21*(15), 3757.

Candolle, A. P. de. (1820). Géographie botanique. *Dictionnaire des sciences naturelles*, *18*, 359-422.

Candolle, A. P. de. (1838). Statistique de la famille Composées. Paris: Treuttel & Wtirtz.

Cane, M. A. (2005). The evolution of El Niño, past and future. *Earth and Planetary Science Letters*, *230*(3), 227-240.

Carstens, B. C., & Richards, C. L. (2007). Integrating coalescent and ecological niche modeling in comparative phylogeography. *Evolution*, *61*(6), 1439-1454.

Chen, S. H., Su, S. Y., Lo, C. Z., Chen, K. H., Huang, T. J., Kuo, B. H., & Lin, C. Y. (2009). PALM: a paralleled and integrated framework for phylogenetic inference with automatic likelihood model selectors. *PLoS One*, *4*(12), e8116.

Coates, A. G., Jackson, J. B., Collins, L. S., Cronin, T. M., Dowsett, H. J., Bybell, L. M., Jung, P., & Obando, J. A. (1992). Closure of the Isthmus of Panama: the near-shore

marine record of Costa Rica and western Panama. *Geological Society of America Bulletin*, *104*(7), 814-828.

Coney, P. J. (1987). The regional tectonic setting and possible causes of Cenozoic extension in the North American Cordillera. *Geological Society, London, Special Publications*, *28*(1), 177-186.

Cowie, R. H., & Holland, B. S. (2008). Molecular biogeography and diversification of the endemic terrestrial fauna of the Hawaiian Islands.*Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1508), 3363-3376.

Cracraft, J. (1985). Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. *Ornithological Monographs, 1985*, 49-84.

Craw, R. C. (1983). Panbiogeography and vicariance biogeography: are they truly different? *Systematic Zoology, 32*(4), 431-437.

Crisci, J. V., Katinas, L., & Posadas, P. (2003). Historical biogeography: an introduction. Cambridge: Harvard University Press.

Crother, B. I., & Murray, C. M. (2011). Ontology of areas of endemism. *Journal of Biogeography*, *38*(6), 1009-1015.

Croizat, L., Nelson, G., & Rosen, D. E. (1974). Centers of origin and related concepts. *Systematic Biology*, *23*(2), 265-287.

Cunningham, C. W., & Collins, T. M. (1994). Developing model systems for molecular biogeography: vicariance and interchange in marine invertebrates. In B. Schierwater, B. Streit, G. P. Wagner, & R. DeSalle (Eds.), *Molecular ecology and evolution: Approaches and applications* (405–433). Basel: Birkhauser Verlad.

Cunningham, C. W. (1999). Some limitations of ancestral character-state reconstruction when testing evolutionary hypotheses. *Systematic Biology,48*(3), 665-674.

Davis, A. J., Jenkinson, L. S., Lawton, J. H., Shorrocks, B., & Wood, S. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature*, *391*(6669), 783-786.

Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, *292*(5517), 673-679.

de Queiroz, A. (2005). The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology & Evolution*, *20*(2), 68-73.

Donoghue, M. J., & Moore, B. R. (2003). Toward an integrative historical biogeography. *Integrative and Comparative Biology*, *43*(2), 261-270.

Donoghue, P. C., & Benton, M. J. (2007). Rocks and clocks: calibrating the Tree of Life using fossils and molecules. *Trends in Ecology & Evolution*, *22*(8), 424-431.

Drummond, A. J., Ho, S. Y., Phillips, M. J., & Rambaut, A. (2006). Relaxed phylogenetics and dating with confidence. *PLoS Biology*, *4*(5), e88.

Drummond, A. J., & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, *7*(1), 214.

Duque-Caro, H. (1990). Neogene stratigraphy, paleoceanography and paleobiogeography in northwest South America and the evolution of the Panama Seaway. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *77*(3), 203-234.

Eckstut, M. E., McMahan, C. D., Crother, B. I., Ancheta, J. M., McLennan, D. A., & Brooks, D. R. (2011). PACT in practice: comparative historical biogeographic patterns and species–area relationships of the Greater Antillean and Hawaiian Island terrestrial biotas. *Global Ecology and Biogeography*, *20*(4), 545-557.

Elith, J., & Leathwick, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 677-697.

Fedorov, A. V., Dekens, P. S., McCarthy, M., Ravelo, A. C., Barreiro, M., Pacanowski, R. C., & Philander, S. G. (2006). The Pliocene paradox (mechanisms for a permanent El Niño). *Science*, *312*(5779), 1485-1489.

Folinsbee, K. E., & Evans, D. C. (2011). A protocol for temporal calibration of general area cladograms. *Journal of Biogeography, 39*, 688-697.

Foster, G. L., Lunt, D. J., & Parrish, R. R. (2010). Mountain uplift and the glaciation of North America–a sensitivity study. *Climate of the Past*, *6*(5), 707-717.

Franklin, J. (2010). Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, *16*(3), 321-330.

Garrick, R. C., Rowell, D. M., & Sunnucks, P. (2012). Phylogeography of saproxylic and forest floor invertebrates from Tallaganda, south-eastern Australia. *Insects*, *3*(1), 270-294.

Ghiselin, M. T. (1980). Biogeographical units: more on radical solutions. *Systematic Zoology*, *29*(1), 80–85.

Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A., & Merilä, J. (2008). Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology, 17*(1), 167-178.

Graham, C. H., VanDerWal, J., Phillips, S. J., Moritz, C., & Williams, S. E. (2010). Dynamic refugia and species persistence: tracking spatial shifts in habitat through time. *Ecography*, *33*(6), 1062-1069.

Graham, M. R., Jaeger, J. R., Prendini, L., & Riddle, B. R. (2013). Phylogeography of the Arizona hairy scorpion (*Hadrurus arizonensis*) supports a model of biotic assembly in the Mojave Desert and adds a new Pleistocene refugium. *Journal of Biogeography*.

Grant, T. (2002). Testing methods: the evaluation of discovery operations in evolutionary biology. *Cladistics*, *18*(1), 94-111.

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology letters*, *8*(9), 993-1009.

Hafner, D., and Riddle, B. (1997). Biogeography of Baja California peninsular desert mammals. In T. L. Yates, W. L. Gannon, & D. E. Wilson (Eds.), *Life among the muses: Papers in honor of James S. Findley* (39-68). Albuquerque: The Museum of Southwestern Biology, The University of New Mexico.

Hafner, D., and Riddle, B. 2011. Boundaries and barriers of North American warm deserts: an evolutionary perspective. In P. Upchurch, A. McGowan, & C. Slater (Eds.), *Palaeogeography and palaeobiogeography: Biodiversity in space and time* (75-113). Boca Raton: CRC Press.

Hafner, J. C., Light, J. E., Hafner, D. J., Hafner, M. S., Reddington, E., Rogers, D. S., & Riddle, B. R. (2007). Basal clades and molecular systematics of heteromyid rodents. *Journal of Mammalogy*, *88*(5), 1129-1145.

Halas, D., Zamparo, D., & Brooks, D. R. (2005). A historical biogeographical protocol for studying biotic diversification by taxon pulses. *Journal of Biogeography*, *32*(2), 249-260.

Hampe, A., Rodríguez-Sánchez, F., Dobrowski, S., Hu, F. S., & Gavin, D. G. (2013). Climate refugia: from the Last Glacial Maximum to the twenty-first century. *New Phytologist*, *197*(1), 16-18.

Hansen, J., Sato, M., Kharecha, P., Beerling, D., Berner, R., Masson-Delmotte, V., Pagani, M., Raymo, M., Royer, D. L., & Zachos, J. C. (2008). Target Atmospheric CO2: Where Should Humanity Aim? *Open Atmospheric Science Journal, 2*(2008), 217-231.

Harold, A. S. & Mooi, R. D. (1994). Areas of endemism: definition and recognition criteria. *Systematic Biology, 43*(2), 261-266.

Hausdorf, B. (2002). Units in biogeography. *Systematic Biology*, *51*(4), 648-652.

Haydon, D. T., Crother, B. I., & Pianka, E. R. (1994). New directions in biogeography? *Trends in Ecology & Evolution, 9*(10), 403-406.

Henderson, G. M. (2002). New oceanic proxies for paleoclimate. *Earth and Planetary Science Letters*, *203*(1), 1-13.

Hennig, W., Davis, D. D., & Zangerl, R. (1999). *Phylogenetic systematics*. University of Illinois Press.

Hewitt, G. M. (1996). Some genetic consequences of ice ages, and their role in divergence and speciation. *Biological Journal of the Linnean Society*, *58*(3), 247-276.

Hewitt, G. M. (2004). Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *359*(1442), 183-195.

Hickerson, M. J., Stahl, E. A., & Lessios, H. A. (2006). Test for simultaneous divergence using approximate Bayesian computation. *Evolution*, *60*(12), 2435-2453.

Hill, J. K., Griffiths, H. M., & Thomas, C. D. (2011). Climate change and evolutionary adaptations at species' range margins. *Annual Review of Entomology*, *56*, 143-159.

Hoberg, E. P., & Brooks, D. R. (2010). Beyond vicariance: integrating taxon pulses, ecological fitting and oscillation in evolution and historical biogeography. In S. Morand & B. Krasnov (Eds.), *The biogeography of host-parasite interactions* (7-20). Oxford: Oxford University Press.

Hoffmann, A. A., & Sgrò, C. M. (2011). Climate change and evolutionary adaptation. *Nature, 470*(7335), 479-485.

Hovenkamp, P. (1997). Vicariance events, not areas, should be used in biogeographical analysis. *Cladistics*, *13*(1), 67-79.

Humphries, C. J. & Parenti, L. R. (1986) Cladistic biogeography. Oxford: Clarendon Press.

Humphries, C. J., & Parenti, L. R. (1999). Cladistic biogeography: Interpreting patterns of plant and animal distribution. Oxford: Oxford University Press.

Husby, A., Visser, M. E., & Kruuk, L. E. (2011). Speeding up microevolution: the effects of increasing temperature on selection and genetic variance in a wild bird population. *PLoS Biology*, *9*(2), e1000585.

Jaeger, J. R., Riddle, B. R., & Bradford, D. F. (2005). Cryptic Neogene vicariance and Quaternary dispersal of the red-spotted toad (*Bufo punctatus*): insights on the evolution of North American warm desert biotas. *Molecular Ecology*, *14*(10), 3033-3048.

Jezkova, T., Jaeger, J. R., Marshall, Z. L., & Riddle, B. R. (2009). Pleistocene impacts on the phylogeography of the desert pocket mouse (Chaetodipus penicillatus). *Journal of Mammalogy*, *90*(2), 306-320.

Jones, P. D., Osborn, T. J., & Briffa, K. R. (2001). The evolution of climate over the last millennium. *Science, 292*(5517), 662-667.

Jones, P. D., & Mann, M. E. (2004). Climate over past millennia. *Reviews of Geophysics, 42*(2), RG2002.

Kohn, M. J., & Fremd, T. J. (2008). Miocene tectonics and climate forcing of biodiversity, western United States. *Geology*, *36*(10), 783-786.

Ladle, R. J., & Whittaker, R. J. (Eds.). (2011). Conservation biogeography. New York: Wiley-Blackwell.

Larkin, M. A., Blackshields, G., Brown, N. P., Chenna, R., McGettigan, P. A., McWilliam, H., ... & Higgins, D. G. (2007). Clustal W and Clustal X version 2.0.*Bioinformatics*, *23*(21), 2947-2948.

Laskar, J., Robutel, P., Joutel, F., Gastineau, M., Correia, A. C. M., & Levrard, B. (2004). A long-term numerical solution for the insolation quantities of the Earth. *Astronomy and Astrophysics*, *428*(1), 261-285.

Lavergne, S., Mouquet, N., Thuiller, W., & Ronce, O. (2010). Biodiversity and climate change: integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution, and Systematics*, *41*, 321-350.

Lieberman, B. S., & Eldredge, N. (1996). Trilobite biogeography in the Middle Devonian: geological processes and analytical methods. *Paleobiology*, *22*(1), 66-79.

Lim, B. K. (2008). Historical biogeography of New World emballonurid bats (tribe Diclidurini): taxon pulse diversification. *Journal of biogeography*, *35*(8), 1385-1401.

Linder, H. P. (2001a). On areas of endemism, with an example from the African Restionaceae. *Systematic Biology*, *50*(6), 892-912.

Linder, H. P. (2001b). Plant diversity and endemism in sub-Saharan tropical Africa. *Journal of Biogeography, 28*(2), 169-182.

Lewis, P. O. (2001). A Likelihood Approach to Estimating Phylogeny from Discrete Morphological Character Data. *Systematic Biology*, *50*(6), 913-925.

Lunt, D. J., Valdes, P. J., Haywood, A., & Rutt, I. C. (2008). Closure of the Panama Seaway during the Pliocene: implications for climate and Northern Hemisphere glaciation. Climate Dynamics, 30(1), 1-18.

MacArthur, R. H., & Wilson, E. O. (1963). An Equilibrium Theory of Insular Zoogeography. *Evolution, 17*(4), 373-387.

MacArthur, R., and Wilson, E. (1967). The theory of island biography. Princeton: Princeton University Press.

Maddison, W. P., & Maddison, D. (2001). Mesquite: a modular system for evolutionary analysis. Version 2.5.

Mantooth, S. J., & Riddle, B. R. (2011). Molecular biogeography: the intersection between geographic and molecular variation. *Geography Compass*, *5*(1), 1-20.

Marko, P. B., & Moran, A. L. (2009). Out of sight, out of mind: high cryptic diversity obscures the identities and histories of geminate species in the marine bivalve subgenus *Acar*. *Journal of Biogeography*, *36*(10), 1861-1880.

Marshall, C. R. (2008). A simple method for bracketing absolute divergence times on molecular phylogenies using multiple fossil calibration points. *The American Naturalist*, *171*(6), 726-742.

McGovern, T. M., Keever, C. C., Saski, C. A., Hart, M. W., & Marko, P. B. (2010). Divergence genetics analysis reveals historical population genetic processes leading to contrasting phylogeographic patterns in co-distributed species. *Molecular Ecology*, *19*(22), 5043-5060.

McLaughlin, J. F., Hellmann, J. J., Boggs, C. L., & Ehrlich, P. R. (2002). Climate change hastens population extinctions. *Proceedings of the National Academy of Sciences*, *99*(9), 6070-6074.

Meehl, G., Covey, C., Delworth, T., Latif, M., McAvaney, B., Mitchell, J., ... & Taylor, K. (2007). The WCRP CMIP3 multi-model dataset: A new era in climate change research. *Bulletin of the American Meteorological Society*, *88*, 1383-1394.

Microsoft. (2007). Microsoft Excel. Redmond, Washington.

Morrone, J. J. (1994). On the identification of areas of endemism. *Systematic Biology*, *43*(3), 438-441.

Morrone, J. (2009). Evolutionary biogeography: An integrative approach with case studies. New York: Columbia University Press.

Müller, P. (1973). *The dispersal centres of terrestrial vertebrates in the Neotropical realm. A study in the evolution of the Neotropical biota and its native landscapes*. The Hague, Junk.

Murphy R., & Aguirre-Léon, G. (2002). The nonavian reptiles. In T. Case, M. Cody, & E. Ezcurra (Eds.), *A new island biogeography of the Sea of Cortes* (181-220). New York: Oxford University Press.

Muscheler, R., Kromer, B., Björck, S., Svensson, A., Friedrich, M., Kaiser, K. F., & Southon, J. (2008). Tree rings and ice cores reveal 14C calibration uncertainties during the Younger Dryas. *Nature Geoscience*, *1*(4), 263-267.

Nason, J. D., Hamrick, J. L., & Fleming, T. H. (2002). Historical vicariance and postglacial colonization effects on the evolution of genetic structure in *Lophocereus*, a Sonoran Desert columnar cactus. *Evolution*, *56*(11), 2214-2226.

Nelson, G., & Platnick, N. (1981). Systematics and biogeography: Cladistics and vicariance. New York: Columbia University Press.

Opdam, P., & Wascher, D. (2004). Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation, 117*(3), 285-297.

Overpeck, J., & Webb, R. (2000). Nonglacial rapid climate events: Past and future. *Proceedings of the National Academy of Sciences*, *97*(4), 1335-1338.

Patton, J. L., Huckaby, D. G., & Álvarez-Castañeda, S. T. (2008). The evolutionary history and a systematic revision of woodrats of the *Neotoma lepida* group. *University of California Publications in Zoology*, *135*, 1-472.

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*(2), 289-290.

Parenti, L. R. (2006). Common cause and historical biogeography. In M. C. Ebach & R. S. Tangney (Eds.), *Biogeography in a changing world* (61-71). London: CRC Press.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 637-669.

Pearson, R. G., & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful?.*Global Ecology & Biogeography*, *12*(5), 361-371.

Peteet, D. (2000). Sensitivity and rapidity of vegetational response to abrupt climate change. *Proceedings of the National Academy of Sciences*, *97*(4), 1359-1361.

Peterson, A. T. (2001). Predicting species' geographic distributions based on ecological niche modeling. *The Condor*, *103*(3), 599-605.

Petit, J. R., Jouzel, J., Raynaud, D., Barkov, N. I., Barnola, J. M., Basile, I., ... & Stievenard, M. (1999). Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature*, *399*(6735), 429-436.

Petit, R. J., Aguinagalde, I., de Beaulieu, J. L., Bittkau, C., Brewer, S., Cheddadi, R., ... & Vendramin, G. G. (2003). Glacial refugia: hotspots but not melting pots of genetic diversity. *Science*, *300*(5625), 1563-1565.

Petren, K., & Case, T. J. (1997). A phylogenetic analysis of body size evolution and biogeography in chuckwallas (*Sauromalus*) and other iguanines. *Evolution*,*51*(1), 206-219.

Petren, K., & Case, T. (2002). Updated mtDNA phylogeny for Sauromalus and implications for the evolution of gigantism. In T. Case, M. Cody, & E. Ezcurra (Eds.), *A new island biogeography of the Sea of Cortes* (574-579). New York: Oxford University Press.

Pirie, M. D., Humphreys, A. M., Antonelli, A., Galley, C., & Linder, H. P. (2012). Model uncertainty in ancestral area reconstruction: A parsimonious solution? *Taxon*, *61*(3), 652-664.

Planz, J. (1992). *Molecular phylogeny and evolution of the American woodrats, genus Neotoma (Muridae)*. (Unpublished doctoral dissertation). University of North Texas, Denton, TX.

Platnick, N. I. (1991). On areas of endemism. *Australian Systematic Botany, 4*, (unnumbered).

Pyron, R. A., & Burbrink, F. T. (2010). Hard and soft allopatry: physically and ecologically mediated modes of geographic speciation. *Journal of Biogeography, 37*, 2005-2015.

R Development Core Team. (2008). R: A language and environment forstatistical computing. R Foundation for Statistical Computing,Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Radtkey, R. R., Fallon, S. M., & Case, T. J. (1997). Character displacement in some *Cnemidophorus* lizards revisited: a phylogenetic analysis. *Proceedings of the National Academy of Sciences*, *94*(18), 9740-9745.

Rambaut, A. (2008). FigTree v. 1.1. 2. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, United Kingdom.

Rambaut, A., & Drummond, A. (2007). Tracer v1. 4.

Raymo, M. E. (1994). The Initiation of Northern Hemisphere Glaciation. *Annual Review of Earth and Planetary Sciences*, *22*(1), 353-383.

Raymo, M. E., & Ruddiman, W. F. (1992). Tectonic forcing of late Cenozoic climate. *Nature*, *359*(6391), 117-122.

Ree, R. H., & Sanmartín, I. (2009). Prospects and challenges for parametric models in historical biogeographical inference. *Journal of Biogeography*, *36*(7), 1211-1220.

Ree, R. H., & Smith, S. A. (2008). Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, *57*(1), 4-14.

Reeder, T. W., Cole, C. J., & Dessauer, H. C. (2002). Phylogenetic relationships of whiptail lizards of the genus *Cnemidophorus* (Squamata: Teiidae): a test of monophyly, reevaluation of karyotypic evolution, and review of hybrid origins. *American Museum Novitates*, 1-61.

Richards, C. L., Carstens, B. C., & Lacey Knowles, L. (2007). Distribution modelling and statistical phylogeography: an integrative framework for generating and testing alternative biogeographical hypotheses. *Journal of Biogeography*, *34*(11), 1833-1845.

Riddle, B. R, & Honeycutt, R. L. (1990). Historical biogeography in North American arid regions: an approach using mitochondrial-DNA phylogeny in grasshopper mice (genus *Onychomys*). *Evolution*, *44*(1), 1-15.

Riddle, B. R. (1995). Molecular biogeography in the pocket mice (*Perognathus* and *Chaetodipus*) and grasshopper mice (*Onychomys*): The late Cenozoic development of a North American aridlands rodent guild. *Journal of Mammalogy*, *76*(2), 283-301.

Riddle, B.R. (1998). The historical assembly of continental biotas: Late Quaternary range-shifting, areas of endemism, and biogeographic structure in the North American mammal fauna. *Ecography*, 21(4), 437-446.

Riddle, B. R., Hafner, D. J., Alexander, L. F., & Jaeger, J. R. (2000a). Cryptic vicariance in the historical assembly of a Baja California Peninsular Desert biota. *Proceedings of the National Academy of Sciences*, *97*(26), 14438-14443.

Riddle, B. R., Hafner, D. J., & Alexander, L. F. (2000b). Phylogeography and systematics of the *Peromyscus eremicus* species group and the historical biogeography of North American warm regional deserts. *Molecular Phylogenetics and Evolution*, *17*(2), 145-160.

Riddle, B. R., Hafner, D. J., & Alexander, L. F. (2000c). Comparative phylogeography of Baileys' pocket mouse (*Chaetodipus baileyi*) and the *Peromyscus eremicus* species group: historical vicariance of the Baja California Peninsular Desert. *Molecular Phylogenetics and Evolution*, *17*(2), 161-172.

Riddle, B. R., & Hafner, D. J. (2006). A step-wise approach to integrating phylogeographic and phylogenetic biogeographic perspectives on the history of a core North American warm deserts biota. *Journal of Arid Environments*, *66*(3), 435-461.

Riddle, B. R., Dawson, M. N., Hadly, E. A., Hafner, D. J., Hickerson, M. J., Mantooth, S. J., & Yoder, A. D. (2008). The role of molecular genetics in sculpting the future of integrative biogeography. *Progress in Physical Geography*, *32*(2), 173-202.

Riddle, B. R., & Hafner, D. J. (2010). Integrating pattern with process at biogeographic boundaries: the legacy of Wallace. *Ecography*, *33*(2), 321-325.

Riddle, B. R, Jezkova, T., Eckstut, M. E., Oláh-Hemmings, V., and Carraway, L. N. (*In review*). Cryptic divergence and revised species taxonomy within the Great Basin pocket mouse, *Perognathus parvus* (Peale, 1848), species group. Submitted to *Journal of Mammalogy*.

Ronquist, F. (1997). Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, *46*(1), 195-203.

Ropelewski, C. F., & Halpert, M. S. (1987). Global and regional scale precipitation patterns associated with the El Niño/Southern Oscillation. *Monthly Weather Review*, *115*(8), 1606-1626.

Rosen, D. E. (1978). Vicariant patterns and historical explanation in biogeography. *Systematic Biology, 27*(2), 159-188.

Rosen, B. R. (1988). From fossils to earth history: applied historical biogeography. In A. Myers & P. Giller (Eds.), *Analytical biogeography: An integrated approach to the study of animal and plant distributions* (437-481). London: Chapman and Hall.

Royer-Carenzi, M., Pontarotti, P., & Didier, G. (2012). Choosing the best ancestral character state reconstruction method. *Mathematical biosciences, 242*(1), 95-109.

Ruddiman, W. F., & Kutzbach, J. E. (1989). Forcing of late Cenozoic Northern Hemisphere climate by plateau uplift in southern Asia and the American west. *Journal of Geophysical Research*, *94*(15), 18409-18427.

Ruddiman, W. F., Raymo, M. E., Lamb, H. H., Andrews, J. T., Ruddiman, W. F., Raymo, M. E., ... & Andrews, J. T. (1988). Northern hemisphere climate regimes during the past 3 Ma: possible tectonic connections [and discussion]. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *318*(1191), 411-430.

Savage, J. M. (1960). Evolution of a peninsular herpetofauna. *Systematic Biology*, *9*(3-4), 184-212.

Serb, J. M., Phillips, C. A., & Iverson, J. B. (2001). Molecular phylogeny and biogeography of *Kinosternon flavescens* based on complete mitochondrial control region sequences. *Molecular Phylogenetics and Evolution*, *18*(1), 149-162.

Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., ... & Miller, H. L. (2007). IPCC Climate Change 2007: The physical science basis. *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental*

Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Somero, G. N. (2010). The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *Journal of Experimental Biology*, *213*(6), 912-920.

Spotila, J. R., Zimmerman, L. C., Binckley, C. A., Grumbles, J. S., Rostal, D. C., List Jr, A., ... & Kemp, S. J. (1994). Effects of incubation conditions on sex determination, hatching success, and growth of hatchling desert tortoises, Gopherus agassizii. *Herpetological Monographs*, 103-116.

Stebbins Jr, G. L. (1952). Aridity as a stimulus to plant evolution. *American Naturalist*, *86*, 33-44.

Stewart, J. R., Lister, A. M., Barnes, I., & Dalén, L. (2010). Refugia revisited: individualistic responses of species in space and time. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1682), 661-671.

Swetnam, T. W., & Betancourt, J. L. (1998). Mesoscale Disturbance and Ecological Response to Decadal Climatic Variability in the American Southwest. *Journal of Climate*, *11*(12), 3128-3147.

Szumik, C. A., & Goloboff, P. A. (2004). Areas of endemism: an improved optimality criterion. *Systematic Biology*, *53*(6), 968-977.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., & Kumar, S. (To be submitted, 2011). MEGA5: Molecular evolutionary genetics analysis using likelihood, distance, and parsimony methods. *Molecular Biology and Evolution.*

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., ... & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*(6970), 145-148.

Thompson, R. (1990). Late Quaternary vegetation and climate in the Great Basin. In J. Betancourt, T. Van Devender, & P. Martin (Eds)., Packrat middens: the last 40,000 years of biotic change (200-239). Tuscon: University of Arizona Press.

Thompson, R. S. (1991). Pliocene environments and climates in the western United
     States. *Quaternary Science Reviews*, *10*(2), 115-132.

Thuiller, W., Albert, C., Araújo, M. B., Berry, P. M., Cabeza, M., Guisan, A., ... &
     Zimmermann, N. E. (2008). Predicting global change impacts on plant species'
     distributions: future challenges. *Perspectives in Plant Ecology, Evolution and
     Systematics*, *9*(3), 137-152.

Trenberth, K. E., & Hoar, T. J. (1997). El Niño and climate change. *Geophysical Research
     Letters*, *24*(23), 3057-3060.

Upchurch, P. (2008). Gondwanan break-up: legacies of a lost world? *Trends in Ecology &
     Evolution, 23*(4), 229-236.

Unruh, J. R. (1991). The uplift of the Sierra Nevada and implications for late Cenozoic
     epeirogeny in the western Cordillera. *Geological Society of America
     Bulletin*, *103*(11), 1395-1404.

Upton, D. E., & Murphy, R. W. (1997). Phylogeny of the side-blotched lizards
     (Phrynosomatidae: *Uta*) based on mtDNA sequences: support for a
     midpeninsular seaway in Baja California. *Molecular Phylogenetics and
     Evolution*, *8*(1), 104-113.

Visser, M. E. (2008). Keeping up with a warming world; assessing the rate of adaptation
     to climate change. *Proceedings of the Royal Society B: Biological
     Sciences*, *275*(1635), 649-659.

Waltari, E., Hijmans, R. J., Peterson, A. T., Nyári, Á. S., Perkins, S. L., & Guralnick, R. P.
     (2007). Locating Pleistocene refugia: comparing phylogeographic and ecological
     niche model predictions. *PLoS one*, *2*(7), e563.

Waltari, E., & Guralnick, R. P. (2008). Ecological niche modelling of montane mammals in
     the Great Basin, North America: examining past and present connectivity of
     species across basins and ranges. *Journal of Biogeography*,*36*(1), 148-161.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J., ... & Bairlein,
     F. (2002). Ecological responses to recent climate change.*Nature*, *416*(6879), 389-
     395.

Wara, M. W., Ravelo, A. C., & Delaney, M. L. (2005). Permanent El Niño-like conditions during the Pliocene warm period. *Science*, *309*(5735), 758-761.

Whittaker, R. J., Araújo, M. B., Paul, J., Ladle, R. J., Watson, J. E., & Willis, K. J. (2005). Conservation biogeography: assessment and prospect. *Diversity and Distributions*, *11*(1), 3-23.

Wells, S., & Haragan, D. (1983). Origin and evolution of deserts. Albuquerque: University of New Mexico Press.

Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, *19*(12), 639-644.

Wiens, J. J., Sukumaran, J., Pyron, R. A., & Brown, R. M. (2009). Evolutionary and biogeographic origins of high tropical diversity in Old World frogs (Ranidae). *Evolution*, *63*(5), 1217-1231.

Wiens, J. J. (2012). Perspective: why biogeography matters: historical biogeography vs. phylogeography and community phylogenetics for inferring ecological and evolutionary processes. *Frontiers of Biogeography*, *4*(3), 129-135.

Wiley, E. (1986). Phylogenetic systematics. pp 343-346 In McGraw-Hill yearbook of science and technology (343-346). New York: McGraw-Hill.

Wiley, E. O. (1988). Parsimony analysis and vicariance biogeography.*Systematic Zoology*, *37*(3), 271-290.

Wiley, E. O. (1988). Vicariance biogeography. *Annual Review of Ecology and Systematics*, 513-542.

World Wildlife Fund. (8 April 2013). *Deserts and xeric shrublands*. Retrieved from http://worldwildlife.org/biomes/deserts-and-xeric-shrublands

Araújo, M. B., & Williams, P. H. (2000). Selecting areas for species persistence using occurrence data. *Biological Conservation*, *96*(3), 331-345.

Wojcicki, M., & Brooks, D. R. (2004). Escaping the matrix: a new algorithm for phylogenetic comparative studies of co-evolution. *Cladistics*, *20*(4), 341-361.

Wojcicki, M., & Brooks, D. R. (2005). PACT: an efficient and powerful algorithm for generating area cladograms. *Journal of Biogeography*, *32*(5), 755-774.

Yang, Z., & Rannala, B. (2006). Bayesian estimation of species divergence times under a molecular clock using multiple fossil calibrations with soft bounds. *Molecular Biology and Evolution*, *23*(1), 212-226.

Yasuhara, M., Hunt, G., Cronin, T. M., Hokanishi, N., Kawahata, H., Tsujimoto, A., & Ishitake, M. (2012). Climatic forcing of Quaternary deep-sea benthic communities in the North Pacific Ocean. *Paleobiology*, *38*(1), 162-179.

Yoder, A. D., & Nowak, M. D. (2006). Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. *Annual Review of Ecology, Evolution, and Systematics*, 405-431.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*,*292*(5517), 686-693.

Zachos, J., Dickens, G., and Zeebe, R. 2008. An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. Nature, 451:279-283.

Zhisheng, A., Kutzbach, J. E., Prell, W. L., & Porter, S. C. (2001). Evolution of Asian monsoons and phased uplift of the Himalaya–Tibetan plateau since Late Miocene times. *Nature*, *411*(6833), 62-66.

Zink, R. M., & Dittmann, D. L. (1991). Evolution of brown towhees: mitochondrial DNA evidence. *Condor*, *93*(1), 98-105.

Zink, R. M., Blackwell, R. C., & Rojas-Soto, O. (1997). Species limits in the Le Conte's thrasher. *Condor*, *99*(1), 132-138.

Zink, R. M., & Blackwell, R. C. (1998a). Molecular systematics and biogeography of aridland gnatcatchers (genus *Polioptila*) and evidence supporting species status

of the California gnatcatcher (*Polioptila california*).*Molecular Phylogenetics and Evolution*, *9*(1), 26-32.

Zink, R. M., & Blackwell, R. C. (1998b). Molecular systematics of the scaled quail complex (Genus *Callipepla*). *The Auk*, *115*(2), 394-403.

Zink, R. M., Weller, S. J., & Blackwell, R. C. (1998c). Molecular phylogenetics of the avian genus *Pipilo* and a biogeographic argument for taxonomic uncertainty. *Molecular Phylogenetics and Evolution*, *10*(2), 191-201.

Zink, R. M., Blackwell-Rago, R. C., & Ronquist, F. (2000a). The shifting roles of dispersal and vicariance in biogeography. *Proceedings of the Royal Society B: Biological Sciences*, *267*(1442), 497-503.

Zink, R. M., Barrowclough, G. F., Atwood, J. L., & Blackwell-Rago, R. C. (2000b). Genetics, taxonomy, and conservation of the threatened California gnatcatcher. *Conservation Biology*, *14*(5), 1394-1405.

Zink, R. M., Kessen, A. E., Line, T. V., & Blackwell-Rago, R. C. (2001). Comparative phylogeography of some aridland bird species. *The Condor*, *103*(1), 1-10.

CURRICULUM VITAE

Graduate College
University of Nevada, Las Vegas

Mallory Elizabeth Eckstut

Degrees:
  Bachelor of Arts, Biology, 2006
  Simon's Rock College of Bard

  Master of Science, Biological Sciences, 2008
  Southeastern Louisiana University

Special Honors and Awards:
  2013-2010. National Science Foundation Experimental Program to Stimulate
     Competitive Research (NSF EPSCoR) Climate Change Graduate Fellowship,
     Nevada NSF EPSCoR ($75,000)
  2013-2008. Research and Conference Travel Grants, Graduate and Professional
     Student Association (GPSA), University of Nevada, Las Vegas (6 awards, total:
     $4,300)
  2013. Bradley-Dill Award in Environmental Biology, School of Life Sciences,
     University of Nevada, Las Vegas ($2,000)
  2011. Grant-in-Aid of Research, American Society of Mammalogists ($1,235)
  2011. Frederick H. Stoye Award, American Society of Ichthyologists and
     Herpetologists (best student oral presentation, General Herpetology), Joint
     Meeting of Ichthyologists and Herpetologists, Minneapolis, Minnesota ($300)
  2011. Merit Award, GPSA, University of Nevada, Las Vegas ($300)
  2009. Second Place Presentation, Science and Engineering Platform Session, UNLV
     GPSA and Graduate College Research Forum, Las Vegas, Nevada ($125)
  2007. Marie Stopes Travel Award, Willi Hennig Society Meeting XXVI, New Orleans,
     Louisiana ($500)
  2005. Bard Center Junior Fellowship, Bard College at Simon's Rock, Great Barrington,
     Massachusetts ($1,500)

Peer-Reviewed Publications:
  Riddle, B.R., T. Jezkova, M.E. Eckstut, V. Olah-Hemmings, and L.N. Carraway. Cryptic
     divergence and revised species taxonomy within the Great Basin pocket mouse
     (*Perognathus parvus*, Peale, 1848) species group. Under revision to *Journal of
     Mammalogy*
  Eckstut, M.E., A.M. Hamilton, and C.C. Austin. *In press*. Variable unisexuals and
     uniform bisexuals: morphology, genetics, and biogeography of the *Nactus
     pelagicus* complex (Reptilia: Gekkonidae) on Tanna Island, Vanuatu.
     Herpetologica

Eckstut, M.E., C.D. McMahan, B.I. Crother, J.M. Ancheta, D.A. McLennan, and D.R. Brooks. 2011. PACT in practice: comparative historical biogeographic patterns and species-area relationships of the Greater Antillean and Hawaiian Island terrestrial biotas. *Global Ecology and Biogeography*, 20, 545-557

Crother, B.I., M.E. White, J.M. Savage, M. Eckstut, M. Graham, and D. Gardner. 2011. A reevaluation of the status of the Foxsnakes *Pantherophis gloydi* Conant and *P. vulpinus* Baird and Girard (Lepidosauria). *ISRN Zoology,* 2011, Article ID 436049, 15 pages

Eckstut, M.E., D.M. Sever, M.E. White, and B.I. Crother. 2009. Phylogenetic analysis of sperm storage in female squamates. In L.T. Dahnof (Ed.), <u>Animal Reproduction: New Research Developments</u> (pp. 185-218). NOVA Science Publishers, Inc., Happauge, New York

Eckstut, M.E., A.M. Hamilton, C.C. Austin, and D.M. Sever. 2009. Asynchronous oviductal seasonal variation in the unisexual-bisexual *Nactus pelagicus* complex from the Vanuatu Archipelago. In L.T. Dahnof (Ed.), <u>Animal Reproduction: New Research Developments</u> (pp. 295-307). NOVA Science Publishers, Inc., Happauge, New York

Eckstut, M.E., E.R. Lemons, and D.M. Sever. 2009. Annual dynamics of sperm production and storage in the Mediterranean Gecko, *Hemidactylus turcicus*, in the southeastern United States. *Amphibia-Reptilia*, 30, 45-56

Rheubert, J.L., E.H. Poldemann, M.E. Eckstut, M.H. Collier, D.M. Sever, and K.M. Gribbins. 2009. Temporal germ cell development strategy during mixed spermatogenesis within the male Mediterranean Gecko, *Hemidactylus turcicus* (Reptilia: Gekkonidae). *Copeia*, 2009, 793-800

Hamilton, A.M., M.E. Eckstut, E.R. Klein, and C.C. Austin. 2008. Clutch size in the tropical scincid lizard, *Emoia sanfordi*, a species endemic to the Vanuatu Archipelago. *Zoological Science*, 25, 843–848

Sever, D.M., D.S. Siegel, A. Bagwill, M.E. Eckstut, L. Alexander, A. Camus, and C. Morgan. 2008. Renal sexual segment of the Cottonmouth snake, *Agkistrodon piscivorus* (Reptilia, Squamata, Viperidae). *Journal of Morphology*, 269, 640–653

Hamilton, A.M., E.R. Klein, M.E. Eckstut, and E.E. Hartfield. 2007. A simple, inexpensive method to capture arboreal lizards. *Herpetological Conservation and Biology*, 2,164–167

Dissertation Title: Integrating, Developing, and Testing Methods to Generate More Cohesive Approaches to Biogeographic Inference

Dissertation Examination Committee:
    Chairperson, Brett Riddle, Ph.D.
    Committee Member, Brian Crother, Ph.D.
    Committee Member, Javier Rodríguez, Ph.D.
    Committee Member, Daniel Thompson, Ph.D.
    Graduate Faculty Representative, Matthew Lachniet, Ph.D.