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

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

By

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Bachelor of Arts
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2006

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A dissertation submitted in partial fulfillment of the requirements for the

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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
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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;
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-
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; Jezkova et 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.

<table>
<thead>
<tr>
<th>Desert</th>
<th>Average Elevation (m)</th>
<th>Climate</th>
<th>Annual Rainfall (mm)</th>
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<tr>
<td>Chihuahuan</td>
<td>1,100 – 1,500</td>
<td>Subtropical/Tropical Dry</td>
<td>150 – 400</td>
<td>Creosote, tarbush, yucca, saltbrush, mesquite</td>
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<td>Sonoran</td>
<td>Sea level – 2,000</td>
<td>Subtropical/Tropical Dry</td>
<td>&lt; 90</td>
<td>Saguaro, creosote, cholla, cacti, bursage, mesquite</td>
</tr>
<tr>
<td>Peninsular</td>
<td>200 – 1,000</td>
<td>Subtropical Dry</td>
<td>&lt; 100</td>
<td>Creosote, desert bursage, xeric scrubs</td>
</tr>
<tr>
<td>Mojave</td>
<td>610 – 1,220*</td>
<td>Warm Temperate Dry</td>
<td>65 – 190</td>
<td>Joshua trees, creosote bush, all-scale, desert holly, white burrobush</td>
</tr>
<tr>
<td>Great Basin</td>
<td>4,000 – 6,500</td>
<td>Cold Temperate Dry</td>
<td>&lt; 250</td>
<td>Sagebrush, saltbrush, winterfat</td>
</tr>
</tbody>
</table>
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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 INFERENTIAL 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 (CO₂) and methane (CH₄) – 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 paleo-climates. 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
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 foraminifera 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 foraminifera and ostracods. The calcite shells of these organisms can be extracted from dated marine sediment layers and δ18O and δ13C isotopic ratios measured. δ18O is a ratio of 18O to 16O isotopes; because 18O is a heavier isotope, more of it is present in oceans during glacial time periods when ice sheets extract the lighter 16O isotope (Zachos et al., 2001). δ13C, a carbon isotopic ratio of 13C to 12C, 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 CO2 concentrations by exchanging CO2 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 δ13C levels, and thus marine foraminifera δ13C analysis can reveal paleorecords of the
NADW and consequently of global climate (Raymo, 1994). In addition, ancient foraminifera 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 $\delta$D (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. $\delta$D is also a temperature proxy, and is similar to inferences made with $\delta^{18}$O, because the ratio of deuterium to hydrogen ($^2$H to $^1$H) is higher in sea water and lower in precipitation. Consequently, there is a linear and positive correlation between annual surface temperature and $\delta$D (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 CO₂ 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.
(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 CO₂ 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 19$^{th}$ 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
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 CO₂ 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 CO₂ 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
CO₂ 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 CO₂ 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 foraminiferan 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>
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<tr>
<th>Method</th>
<th>Inferences</th>
<th>Description</th>
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<tbody>
<tr>
<td><strong>Astronomical calculations + orbital parameters</strong></td>
<td>Insolation</td>
<td>Amount of solar radiation striking surface.</td>
<td>Laskar et al. (2004)</td>
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<tr>
<td><strong>Foraminiferans and ostracods</strong></td>
<td>Species assemblages</td>
<td>Comparison of paleo-assemblages to the habitat preferences of similar extant species; for sea surface and deep sea temperatures.</td>
<td>Raymo (1994)</td>
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<td>$\delta^{18}O$ in calcite shells</td>
<td>$^{18}O$ is heavier than $^{16}O$ and more is present in oceans during glacial cycles.</td>
<td>Zachos et al. (2001)</td>
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<td></td>
<td>$\delta^{13}C$ in calcite shells</td>
<td>The North Atlantic Deep Water is correlated with high amounts of $^{13}C$ and NADW is strongest during warm interglacial periods.</td>
<td>Zachos et al. (2001)</td>
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<td><strong>Ice cores</strong></td>
<td>Dust content in air</td>
<td>Dust reflects solar radiation and increased concentrations indicate cooler temperatures.</td>
<td>Raymo (1994)</td>
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<td></td>
<td>Greenhouse gas concentrations in air (CO$_2$ and CH$_4$)</td>
<td>Greenhouse gases hold heat and prevent reflection, and increased concentrations indicate warmer temperatures.</td>
<td>Petit et al. (1999)</td>
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<td>$\delta D$ in ice</td>
<td>Deuterium is heavier than hydrogen, and thus greater amounts of $\delta D$ during warmer periods.</td>
<td>Petit et al. (1999)</td>
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<td></td>
<td>$\delta^{18}O$ in ice</td>
<td>$^{18}O$ is heavier than $^{16}O$ and greater amounts of $\delta^{18}O$ are present during warmer periods.</td>
<td>Petit et al. (1999)</td>
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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.
(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 are 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)
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, matrix-based 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 occurring 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
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 interspecies 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 ucll.stdev values closer to 0.0 were considered clock-like and had a strict clock implemented and those lineages with ucll.stdev values greater than 1.0 were not clock-like had relaxed clocks implemented. For simulations that had ucll.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 idiosyncratic 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
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, R²=0.22, p=0.69; mPACT-DELTRAN: c=0.09, z=0.45, R²=0.37, p=0.50; mPACT-Likelihood: c=0.36, z=0.20, R²=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-DLTRAN yielded more similar results compared to mPACT-Likelihood (Fig. 3.14B; PACT-DLTRAN: $y=0.36x-1.44$, $R^2=0.49$, $p=0.40$; mPACT-DLTRAN: $y=0.43x-1.74$, $R^2=0.50$, $p=0.38$; 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-DLTRAN: $y=27x-1.09$, $R^2=0.13$, $p=0.71$; mPACT-DLTRAN: $y=0.16x-0.46$, $R^2=0.10$, $p=0.82$; 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 km²) and Continental West (386,500 km²) 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).

<table>
<thead>
<tr>
<th>Group</th>
<th>Clade</th>
<th>Common Name</th>
<th>Original Source</th>
<th>Genbank Accession Numbers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Plants</td>
<td>Lophocereus schotti</td>
<td>Whisker cactus</td>
<td>Nason et al. (2002)</td>
<td>AF328628-AF328664</td>
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<td>Amphibians</td>
<td>Bufo punctatus</td>
<td>Red-spotted toad</td>
<td>Riddle et al. (2000), Jaeger et al.</td>
<td>AF152531-AF152551, DQ085629-DQ085776</td>
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<td></td>
<td>Uta stansburiana</td>
<td>Common side-blotched lizard</td>
<td>Upton and Murphy (1997)</td>
<td>U46695-U46742</td>
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<td>Reptiles</td>
<td>Aspidoscelis tigris</td>
<td>Western whiptail</td>
<td>Murphy and Aguirre-Léon (2002);</td>
<td>AF006266-AF006288</td>
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<td></td>
<td>Radtkey et al. (1997); Reeder et al.</td>
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<td>Birds</td>
<td>Sauromalus species</td>
<td>Chuckwalla</td>
<td>Petren &amp; Case (1997, 2002)</td>
<td>AF20223-AF20252</td>
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<td>Mud turtle</td>
<td>Serb et al. (2001)</td>
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<td>Campylorhynchus brunneicollinus</td>
<td>Cactus wren</td>
<td>Zink et al. (2000b)</td>
<td>AF291529-AF291571</td>
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<td>Verdin</td>
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<td>Curve-billed thrasher</td>
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<td>et al. (2001), Zink et al. (1999)</td>
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<td>Polioptila melanura species group</td>
<td>Black-tailed Gnatchanger</td>
<td>Zink et al. (2000a), Zink &amp; Blackwell</td>
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<td>Canyon towhee</td>
<td>Zink et al. (2001), Zink &amp; Dittman</td>
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<td></td>
<td></td>
<td>(1991), Zink et al. (1998)</td>
<td>AF298595-298622</td>
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<tr>
<td>Mammals</td>
<td>Neotoma lepida species group</td>
<td>Desert woodrat</td>
<td>Planz (1992); Patton et al. (2008)</td>
<td>DQ781162-DQ781256*</td>
</tr>
<tr>
<td></td>
<td>Onychomys species</td>
<td>Grasshopper mouse</td>
<td>Riddle (1995), Riddle &amp; Honeycutt</td>
<td>U21614-U21616, U21633-U21635, U21648-U21650</td>
</tr>
<tr>
<td></td>
<td>Peromyscus eremicus species group</td>
<td>Cactus mouse</td>
<td>Riddle et al. (2000c)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Dipodomys merriami species group</td>
<td>Merriam’s kangaroo rat</td>
<td>Riddle et al. (2000a), Jaeger et al.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Chaetodipus nelsoni species group</td>
<td>Nelson’s pocket mouse</td>
<td>Riddle et al. (2000b), Jaeger et al.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Chaetodipus arenarius</td>
<td>Little desert pocket mouse</td>
<td>Riddle et al. (2000a)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Chaetodipus penicillatus species group</td>
<td>Desert pocket mouse</td>
<td>Lee et al. (1996), Riddle et al. (2000b), Jeskova et al. (2009)</td>
<td>U21648-U21650</td>
</tr>
<tr>
<td></td>
<td>Chaetodipus baileyi species group</td>
<td>Bailey’s pocket mouse</td>
<td>Riddle et al. (200b)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ammospermophilus species</td>
<td>Antelope squirrel</td>
<td>Riddle et al. (2000a), Jaeger et al.</td>
<td></td>
</tr>
</tbody>
</table>

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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.”

<table>
<thead>
<tr>
<th>Step</th>
<th>Goal</th>
<th>Input Data</th>
<th>Algorithms</th>
<th>Programs</th>
<th>Process</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Construct taxon area cladograms (TACs)</td>
<td>-Phylogenetic tree -Distributions of each lineage</td>
<td>N/A</td>
<td>N/A</td>
<td>Replace taxon names on each phylogenetic tree with areas of distribution.</td>
</tr>
<tr>
<td>2</td>
<td>Molecular dating of diversification events</td>
<td>-TACs -Genetic data -Fossil data (when available)</td>
<td>-Coalescence -Molecular clocks</td>
<td>-Mesquite -BEAST -^{BEAST}</td>
<td>Infer age of divergence for nodes on each TAC using molecular dating techniques.</td>
</tr>
<tr>
<td>3</td>
<td>Construct general area cladogram (GAC)</td>
<td>-Dated taxon area cladograms</td>
<td>-mPACT</td>
<td>N/A</td>
<td>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. 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.</td>
</tr>
<tr>
<td>4</td>
<td>Ancestral area reconstruction</td>
<td>-GAC</td>
<td>-Parsimony -Maximum Likelihood</td>
<td>-MacClade -Mesquite -LaGrange</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>Analyze nodes -BE from IS events -General from unique events</td>
<td>-GAC with ancestral areas</td>
<td>N/A</td>
<td>N/A</td>
<td>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.</td>
</tr>
</tbody>
</table>
Table 3.3. General area cladogram (GAC) node analysis.

<table>
<thead>
<tr>
<th>GAC Node Parameters</th>
<th>Secondary BPA</th>
<th>PACT: DELTRAN</th>
<th>mPACT: DELTRAN</th>
<th>mPACT: LnL</th>
</tr>
</thead>
<tbody>
<tr>
<td>OTUs (tree tips)</td>
<td>7</td>
<td>18</td>
<td>30</td>
<td>30</td>
</tr>
<tr>
<td>Total nodes</td>
<td>6</td>
<td>16</td>
<td>25</td>
<td>25</td>
</tr>
<tr>
<td><em>in situ</em> nodes</td>
<td>n/a</td>
<td>5</td>
<td>7</td>
<td>10</td>
</tr>
<tr>
<td><em>in situ</em>/biotic expansion</td>
<td>n/a</td>
<td>5</td>
<td>5</td>
<td>13</td>
</tr>
<tr>
<td>nodes</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Full biotic expansion nodes</td>
<td>n/a</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Ambiguous nodes</td>
<td>n/a</td>
<td>6</td>
<td>12</td>
<td>2</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Area of Endemism</th>
<th>Area Size (km²)</th>
<th>PACT: Total Lineages</th>
<th>PACT: BE events</th>
<th>PACT: BE out Events</th>
<th>PACT: BE in Events</th>
<th>PACT: IS Events</th>
<th>mPACT: Total Lineages</th>
<th>mPACT: BE events</th>
<th>mPACT: BE out Events</th>
<th>mPACT: BE in Events</th>
<th>mPACT: IS Events</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>DT</td>
<td>DT</td>
<td>DT</td>
<td>DT</td>
<td>ML</td>
<td>DT</td>
<td>ML</td>
<td>DT</td>
<td>ML</td>
<td>DT</td>
</tr>
<tr>
<td>PS</td>
<td>48,500</td>
<td>8</td>
<td>3</td>
<td>0</td>
<td>1</td>
<td>2</td>
<td>17</td>
<td>13</td>
<td>8</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>PN</td>
<td>40,000</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>5</td>
<td>3</td>
<td>5</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>CW</td>
<td>386,500</td>
<td>14</td>
<td>5</td>
<td>5</td>
<td>0</td>
<td>8</td>
<td>21</td>
<td>15</td>
<td>11</td>
<td>7</td>
<td>9</td>
</tr>
<tr>
<td>CE</td>
<td>479,000</td>
<td>4</td>
<td>3</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>9</td>
<td>11</td>
<td>6</td>
<td>3</td>
<td>0</td>
</tr>
</tbody>
</table>
Table 3.5. Comparative inference types, benefits, and disadvantages of secondy BPA, PACT, and mPACT. All three assume accuracy of input cladograms.

<table>
<thead>
<tr>
<th>Algorithm</th>
<th>Inference type</th>
<th>Benefits</th>
<th>Disadvantages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Secondary BPA</td>
<td>-Historical</td>
<td>-Allows inference into general patterns of area relationships</td>
<td>-Drastically oversimplifies amount of regional diversification</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>-Restricted to historical inference</td>
</tr>
<tr>
<td>PACT</td>
<td>-Historical</td>
<td>-Reveals more realistic degree of diversification than Secondary BPA</td>
<td>-Pseudo-congruence</td>
</tr>
<tr>
<td></td>
<td>-Ecological</td>
<td></td>
<td>-Cannot distinguish types of biotic expansion (vicariance, dispersal)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-Can distinguish biotic expansion from <em>in situ</em> diversification events</td>
<td>-Limited options for ancestral area reconstruction</td>
</tr>
<tr>
<td>mPACT</td>
<td>-Historical</td>
<td>-Reduces pseudo-congruence</td>
<td>-Likelihood-analyses may not be able to be conducted on excessively large,</td>
</tr>
<tr>
<td></td>
<td>-Ecological</td>
<td></td>
<td>complex GACs</td>
</tr>
<tr>
<td></td>
<td></td>
<td>-Facilitates distinction of dispersal from vicariance</td>
<td>-Assumes node ages (and thus, molecular dating techniques) are accurate</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>-Equivocal possibilities impact GAC structure; currently no way to incorporate</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>-Laborious and time intensive; currently no software program available</td>
</tr>
</tbody>
</table>
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.
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 ephemeral 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 & Burbank, 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.
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 hierachical, 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 consistent with the idea that the Peninsular South and Continental West are more stable 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.

<table>
<thead>
<tr>
<th>Area of Endemism Aspect</th>
<th>Conflicting Definitions</th>
<th>Citations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Endemism definitions</td>
<td>1) Constantly present in a particular place</td>
<td>de Candolle (1820),</td>
</tr>
<tr>
<td></td>
<td>2) Native to an area</td>
<td>Reviewed in Anderson (1994)</td>
</tr>
<tr>
<td></td>
<td>3) Restricted to a particular area</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4) Limited to a small area</td>
<td></td>
</tr>
<tr>
<td>Existence and use in biogeography</td>
<td>1) Naturally existing</td>
<td>de Candolle (1838),</td>
</tr>
<tr>
<td></td>
<td>2) Do not exist</td>
<td>Ghiselin (1980), Hovencamp (1997),</td>
</tr>
<tr>
<td>Biogeographic use</td>
<td>1) Fundamental units of analysis, deserves substantial attention</td>
<td>Axelius (1991), Bremer (1993), Hovencamp (1997),</td>
</tr>
<tr>
<td></td>
<td>2) Should not be considered a central question</td>
<td>Hausdorf (2002)</td>
</tr>
<tr>
<td>Area definitions</td>
<td>1) Habitat</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2) Geographic</td>
<td>Reviewed in Anderson (1994)</td>
</tr>
<tr>
<td>Area size</td>
<td>1) Large (e.g., partial overlap; compare between continents)</td>
<td>Nelson &amp; Platnick (1991), Morrone (1994),</td>
</tr>
<tr>
<td></td>
<td>2) Small (e.g., full overlap; compare within a continent)</td>
<td>reviewed in Crisci et al. (2003)</td>
</tr>
<tr>
<td></td>
<td>2) Static classes</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2) Congruent distributional and phylogenetic patterns</td>
<td></td>
</tr>
<tr>
<td>Degree of taxonomic restriction</td>
<td>1) 100%</td>
<td>Reviewed in Anderson (1994), Linder (2001b)</td>
</tr>
<tr>
<td></td>
<td>2) &lt;100%, “reduced” endemism in an area</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2) 2+ congruent taxa</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3) 3+ congruent taxa</td>
<td></td>
</tr>
<tr>
<td>Formation definitions</td>
<td>1) Taxonomic composition</td>
<td>Riddle &amp; Hafner (2006), Crother &amp; Murray (2011)</td>
</tr>
<tr>
<td></td>
<td>2) Evolutionary stability and production</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2) Area quadrating</td>
<td></td>
</tr>
<tr>
<td></td>
<td>3) Biogeographic units and overlapping or partially overlapping taxa</td>
<td></td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Theoretical Definition</th>
<th>Component</th>
<th>Area of Persistence</th>
<th>Ephemeral Area</th>
<th>Area of Turnover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stable Production Source</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area of Endemism</td>
<td>+</td>
<td>-</td>
<td>~</td>
<td></td>
</tr>
<tr>
<td>Transitional Area</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Taxonomic Composition</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Area of Endemism</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
</tr>
</tbody>
</table>
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).

<table>
<thead>
<tr>
<th></th>
<th>Unmodified</th>
<th>Areas of Endemism only</th>
</tr>
</thead>
<tbody>
<tr>
<td>OTUs</td>
<td>81</td>
<td>29</td>
</tr>
<tr>
<td>Unique Events (Total)</td>
<td>88</td>
<td>24</td>
</tr>
<tr>
<td>General Events (Total)</td>
<td>57</td>
<td>35</td>
</tr>
<tr>
<td>2 taxa</td>
<td>23</td>
<td>8</td>
</tr>
<tr>
<td>3 taxa</td>
<td>14</td>
<td>7</td>
</tr>
<tr>
<td>4 taxa</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>5 taxa</td>
<td>7</td>
<td>6</td>
</tr>
<tr>
<td>6 taxa</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>7 taxa</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>8 taxa</td>
<td>1</td>
<td>1</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Area</th>
<th>Degree of Generality per Event</th>
</tr>
</thead>
<tbody>
<tr>
<td>Continental East</td>
<td>1,1,1,1,3,3,3,5</td>
</tr>
<tr>
<td>Continental West</td>
<td>1,1,1,1,1,2,3,4,7</td>
</tr>
<tr>
<td>Peninsular North</td>
<td>2,3,5</td>
</tr>
<tr>
<td>Peninsular South</td>
<td>1,1,1,1,1,2,6,8</td>
</tr>
<tr>
<td>Baja California Islands</td>
<td>1,1,1, 1,1,1,1,1,1,1,1,2,3</td>
</tr>
<tr>
<td>Bonneville Basin</td>
<td>2</td>
</tr>
<tr>
<td>California Coast</td>
<td>1,1,1,3</td>
</tr>
<tr>
<td>Colorado Plateau</td>
<td>1,1,1</td>
</tr>
<tr>
<td>Deming Plains*</td>
<td>1,2,2,4,4</td>
</tr>
<tr>
<td>East Coast</td>
<td>1,1</td>
</tr>
<tr>
<td>Great Central Valley</td>
<td>1,2</td>
</tr>
<tr>
<td>Great Plains</td>
<td>2</td>
</tr>
<tr>
<td>Lahontan Basin</td>
<td>2</td>
</tr>
<tr>
<td>Mojave Desert*</td>
<td>1,3,4</td>
</tr>
<tr>
<td>Northern Intermountain Basin</td>
<td>3</td>
</tr>
<tr>
<td>San Felipe*</td>
<td>2,3,3,5</td>
</tr>
<tr>
<td>Southern Continental</td>
<td>1,2,2</td>
</tr>
<tr>
<td>Southern Intermountain Basin</td>
<td>1,2</td>
</tr>
</tbody>
</table>
Table 4.5. Temporal dynamics of the frequency of general and unique events on the mPACT GAC. In parentheses 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.

<table>
<thead>
<tr>
<th>Time</th>
<th>Congruence(Frequency)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quaternary</td>
<td>1(26), 2(9), 3(8), 4(3), 5(2), 6(1), 7(0), 8(1)</td>
</tr>
<tr>
<td>Quaternary + Neogene</td>
<td>1(55), 2(10), 3(5), 4(4), 5(4), 6(0), 7(1), 8(0)</td>
</tr>
</tbody>
</table>
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.

<table>
<thead>
<tr>
<th>Time Period</th>
<th>Unmodified</th>
<th></th>
<th>Areas of Endemism only</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Unique</td>
<td>General</td>
<td>Unique</td>
</tr>
<tr>
<td>Quaternary</td>
<td></td>
<td>36</td>
<td>32</td>
<td>9</td>
</tr>
<tr>
<td>Neogene</td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Both Quaternary &amp; Neogene</td>
<td></td>
<td>21</td>
<td>48</td>
<td>13</td>
</tr>
</tbody>
</table>
**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.
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; gc, 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.
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.


Rambaut, A. (2008). FigTree v. 1.1. 2. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, United Kingdom.


of the California gnatcatcher (*Polioptila california*). *Molecular Phylogenetics and Evolution, 9*(1), 26-32.


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