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Reconstructing species responses to past climatic changes using niche modeling and genetic data

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RECONSTRUCTING SPECIES RESPONSES TO PAST CLIMATIC CHANGES USING NICHE

MODELING AND GENETIC DATA

by

Tereza Jezkova

Master of Science
Charles University, Prague, Czech Republic
2002

A dissertation submitted in partial fulfillment of
the requirements for the

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School of Life Sciences
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Tereza Jezkova

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ABSTRACT

**Reconstructing Species Responses to Past Climatic Changes Through Niche
Modeling and Genetic Data**

by

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Glacial – interglacial cycles have a pronounced impact on species distributions and

genetic structure. Many species shift their distributions to lower latitudes and altitudes

during the colder glacial periods and expand northwards and up the elevation during

warmer interglacial periods. Some species however are capable of adapting to changing

environment which allows them to persist in place despite climatic changes. I explored

how climatic changes after the last glacial maximum (LGM) effected two species

inhabiting the deserts of western North America: one mammal (Chisel-toothed

Kangaroo Rat, *Dipodomys microps*) and one reptile (Desert Horned Lizard, *Phrynosoma

platyrhinos*). I used a methodology of transferal modeling which is commonly used to

predict species responses to future climatic changes. I approximated the species current

and LGM distribution by modeling their current climatic niches, which I then projected

onto the climatic conditions of the LGM. The accuracy of the transferal models,

however, is dependent on several conceptual and algorithmic assumptions. Therefore, I

compared the models with the phylogeographic structure of each species as

phylogeographic signals imprinted in species genomes can inform us about species past

geographic and demographic processes. The transferal models predicted that the

northern parts of the species current ranges were unsuitable during the LGM and that

both species could have persisted only within the more southern deserts where climatic

conditions remained suitable. The phylogeographic analyses, however, suggested that

D. microps did not experience large scale distributional changes in response to the

warming climate after the LGM as suggested by the models and instead persisted in

place throughout most of its current range. *Phrynosoma platyrhinos* expanded its range

northwards after the LGM but was able to expand further than indicated by models, into

colder and wetter areas than those experienced during the LGM. My results indicate

that the two species responded to the warming climate after the LGM in an idiosyncratic

fashion and that the transferal models did not correctly predict the species response to

the climate change. These results motivated me to explore in the last chapter several

high-priority challenges in transferal modeling through theoretical background and sets

of experiments. I demonstrated how these challenges can affect resulting models and,

when possible, offered suggestions on how uncertainties might be diminished.

ACKNOWLEDGEMENTS

mental, and financial support throughout my graduate years. Last but not least, I would like to thank my beloved dog Akira, who loved the field work and tolerated the rest.

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CHAPTER 1

INTRODUCTION

In the face of ongoing and projected future warming trends, a lot of research has

recently focused on predicting how species respond to climatic and environmental

changes. These predictions are usually accomplished using a methodology called

transferal modeling. Transferal modeling uses information on environmental

requirements delimiting species distributions to reconstruct species suitable habitat

(referred to as ecological niche) which is then projected on different climate change

scenarios. One of the assumptions of the transferal modeling methodology is 'niche

conservatism', a property of a species to maintain the same ecological niche through

time. Under niche conservatism, the species will track its ecological niche across space

as climate changes, resulting in range shifts, expansions, and contractions. If the species

ecological niche does not remain conserved and shifts through time instead, the species

might not respond to climatic changes in a predictable fashion. Niche shift versus niche

conservatism can be either studied by direct observations of species responses to

ongoing and simulated climatic changes, or by reconstructing species responses to past

climatic changes.

In the second and third chapter, I explore, whether the niches of two species (one

mammal and one reptile) remained conserved throughout the climatic changes of the

latest glacial – interglacial cycle, in particular between the last glacial maximum (LGM)

and present time. These two time periods are ideal for studying species responses to

climate change as they represent two extremes of global climate: the LGM is one of the

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coldest periods of the late Pleistocene while the current climate represents warm climate of an interglacial period. I use transferal modeling to reconstruct the species ranges under the assumption that their niches remained conserved between the LGM and present time. I then use DNA sequence data derived from samples spanning the species range to infer the species past geographic and demographic processes. For example, populations that persisted in place for quite some time will exhibit a different genetic signal than populations that expanded into the region relatively recently, in response to a major climatic event. If the species niches indeed remained conserved, the transferal models should infer the same geographic processes (i.e. range expansion, contraction, or shift) as the genetic data. If the species experienced niche shifts, however, the results from transferal models and genetic data will be incongruent.

In the last chapter, I review several other challenges and uncertainties associated with transferal modeling that I encountered during my research and that can negatively affect resulting models. Thus, my research will help us to better understand species responses to past climatic changes and ultimately also help us to improve our predictions of species responses to future changes.

CHAPTER 2

NICHE SHIFT IN SITU IN RESPONSE TO THE WARMING CLIMATE AT THE END OF THE LAST

GLACIAL MAXIMUM: INFERENCE FROM GENETIC DATA AND NICHE ASSESSMENTS IN

THE CHISEL-TOOTHED KANGAROO RAT (*DIPODOMYS MICROPS*)

Abstract

During Pleistocene glacial-interglacial cycles, species are often assumed to have

shifted ranges via tracking the climatic niche to which they have been adapted, rather

than remaining in place and adapting to a changing environment. However, species that

exploit diverse types of habitats might instead be capable of shifting their niches as

climates change, which would allow them to persist in place through time. I evaluate

whether this kind of response occurred in the Chisel-toothed Kangaroo Rat (*Dipodomys

microps*), which currently utilizes two distinct habitats: the low-elevational saltbush

(*Atriplex*) and mid-elevational blackbrush (*Coleogyne*) communities in the deserts of

western North America. I modeled how the species range would have changed between

the last glacial maximum (LGM) and present time if the climatic niche of the species

remained identical (conserved) between the two time periods. I then used

mitochondrial DNA (mtDNA) assessments of demographic parameters to evaluate

whether *D. microps* exhibits signals of distributional stability or of recent geographic

changes. The climatic models imply that if the species inhabited the same climatic niche

during the LGM as it does today, the range of *D. microps* would have changed

significantly: it would have persisted primarily within the southern, warm Mojave Desert

and expanded northwards into the cold deserts of the Great Basin and Columbia Plateau

only after the LGM. Conversely, the mtDNA assessment revealed signals of population

persistence within the current distribution of the species throughout at least the latest

glacial-interglacial cycle. My results suggest that *D. microps* did not track its climatic

niche during late Pleistocene oscillations, but rather met the challenge of a changing

environment by shifting its niche sufficiently to retain large portions of its current

distribution. I speculate that this kind of response to fluctuating climate was possible

because of 'niche-drifting', an alteration of the species' realized niche due to plasticity in

various (physiological, morphological, behavioral) characters.

Introduction

When climate changes, populations may go extinct, move to locations that remain

suitable, or stay in place and adapt to novel environmental conditions (Barnosky *et al.*

2003; Parmesan 2006; Parmesan *et al.* 1999; Pounds *et al.* 1999; Vrba 1992). Local

extinction often is encountered when climate change generates environmental

conditions that exceed the existing tolerance limits of the organism if its ecological niche

remains conserved (identical) through time (Warren *et al.* 2008; Wiens & Graham 2005).

During the late Pleistocene, the desert regions of the western United States (Fig. 2.1)

experienced pronounced and repeated climate change (Spaulding 1990a; Thompson

1990). During the latest glacial period, lower temperatures and higher precipitation

caused downward (latitudinal or elevational) shifts in plant assemblages, resulting in a

general reduction of size and continuity of desert habitats (Thompson & Anderson 2000;

Thompson & Mead 1982). This shift was most extreme during the last glacial maximum

(LGM), about 21,000 years before present (Harrison 2000). During this time, many kinds of desert organisms that are currently widespread throughout the western deserts were extirpated from the northern regions (i.e. the Great Basin Desert and Columbia Plateau) during the LGM and persisted within southern refugia (located within the Mojave or Sonoran deserts) where environmental conditions remained suitable (e.g. Jones 1995; Mulcahy 2008). These taxa expanded into the northern regions only when desert habitats were re-established as climate warmed after the LGM (Britten & Rust 1996; Hockett 2000; Jones 1995).

Some populations, however, persisted without substantial range shifts during major environmental changes, perhaps because of an ability to adapt (i.e. shift their niches) to novel conditions. For example, several species of woodrats (*Neotoma* spp.) were documented to have responded to cooling climate during glacial periods by increasing their body mass (Bergmann's Rule) instead of shifting their distributions to lower latitudes or altitudes as would be predicted if their climatic niches remained conserved (Smith & Betancourt 2003). Consequently, one could ask, why are some taxa or populations capable of adapting to novel conditions (Smith & Betancourt 2003) while others respond to an environmental change by tracking the conditions to which they are already adapted (Parmesan *et al.* 1999; Pounds *et al.* 1999)?

Vrba (1992) proposed that taxa capable of utilizing alternative environments are most likely to persist through environmental changes. In general terms, a species would be able to shift their niche and maintain populations under changing climates if (1) it exhibits plasticity in relevant physiological, phenological, morphological, or behavioral

traits that allows its realized niche to expand or shift – a process I call 'niche drifting'; or

(2) it's fundamental niche is modified via evolutionary change, which I call 'niche

evolution'. Understanding which taxa or populations are capable of niche shifts (both

niche drifting and niche evolution) is critical to predicting their likely responses to

ongoing and future climate change.

The Chisel-toothed Kangaroo Rat (*Dipodomys microps*) inhabits four desert regions

of western North America (Mojave Desert, Colorado Plateau, Great Basin Desert, and

Columbia Plateau; 1.1) and exhibits two distinct ecotypes that differ in certain

ecological, behavioral, and physiological traits (Csuti 1979). Throughout most of its

range, *D. microps* occupies low-elevation saltbush habitat (dominated by several species

of *Atriplex* - *A. confertifolia*, *A. canescens*, *A. polycarpa*, or *A. spinifera*; herein referred

to as *Atriplex* habitat) where it is mostly folivorous, with 80% of its diet consisting of

Atriplex (Csuti 1979; Kenagy 1973). In the southern parts of its range, within the Mojave

Desert, the species also occupies mid-elevational blackbrush habitat (*Coleogyne

ramosissima;* herein referred to as *Coleogyne* habitat), where it is generally granivorous

and its diet comprises a variety of different plants (Csuti 1979). Accordingly, I

hypothesize that species such as *D. microps* that exploit two very distinct habitats might

be capable of niche shifts that allow them to persist in large portions of their ranges

during major episodes of climate change.

I test the null hypothesis (Fig. 2.2A) that the climatic niche of *D. microps* remained

conserved through time and that this species responded to the changing climate of the

late Pleistocene by tracking the climatic niche to which it has been adapted. In

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particular, this hypothesis predicts that *D. microps* persisted in glacial refugia within the southern deserts during the LGM and expanded northward after the LGM, in concert with many other desert taxa (Britten & Rust 1996; Hockett 2000; Jones 1995; Mulcahy 2008). Alternatively, given its rather broad habitat preferences, the 'niche shift' hypothesis predicts that *D. microps* might have been able to exploit conditions that were colder and wetter than present and persist throughout its range during the LGM (Fig. 2.2B).

To test my hypotheses, I use climatic niche modeling to estimate the distributional extent of the climatic niche of *D. microps* during the LGM under the assumption that the climatic niche between the LGM and present time remained conserved. From these models, I identify general areas that the species occupies today but would have been unsuitable during the LGM. I contrast these models with assessments of genetic data represented by mitochondrial DNA sequences sampled across the current range of *D. microps*. Mitochondrial DNA exhibits a relatively high mutation rate, which in combination with its small effective population size (four times smaller than nuclear DNA), makes it an appropriate genetic marker for tracking recent population histories including demographic and geographic changes (Avise 2000; Moore 1995; Zink & Barrowclough 2008). I contrast the genetic assessments with the climatic niche models in order to evaluate whether populations inferred by models as being nonexistent during the LGM truly exhibit a genetic signal of a recent expansion and whether those modeled as being geographically persistent exhibit a genetic signal of population stability.

'Leading edge' and 'phalanx' colonization are two general models for population expansion that were developed based on a set of predictions for the sort of phylogeographic signature that should be exhibited by a species that expanded its range (Hewitt, 1996). Based on the 'leading edge' model, newly invaded areas are colonized by a subset of individuals (and therefore a subset of genotypes) from the colonization front and this front inhibits establishment by later migrants. This type of expansion results in a decrease of genetic (i.e. nucleotide and haplotype, see Methods) diversity within newly established populations and a decrease in genetic variation among populations in the direction of the expansion (Fig. 2.2A). Leading edge colonization is typical for rapid, large-scale geographic expansions exhibited by numerous taxa after the last glacial maximum (Austerlitz *et al.* 1997; Excoffier *et al.* 2009; Hewitt 2000; Hewitt 1996; Kerdelhue *et al.* 2009). Some taxa, however, exhibit genetic signals of the 'phalanx' colonization (Hewitt 1996). Under this model, new populations at the expansion front are formed from a more even mixture of ancestral populations, resulting in only marginal decrease in local genetic diversity (Fig. 2.2A). While genetic diversity within populations remains higher under this model, genetic variation among expanding populations will be low as in the 'leading edge' model, because the expanding populations will consist of similar groups of genotypes (Fig. 2.2A). The 'phalanx' model of colonization has been documented in populations with high population densities, high geneflow, wide colonization front, and during slower expansions (Hewitt 1996; Schmitt *et al.* 2005). In both types of expansion models, stable populations exhibit higher genetic diversity within populations due to the accumulation of mutations

through time and usually higher genetic variation among populations due to geographic structuring (Hewitt 2000; Hewitt 1996). Species experiencing a recent range expansion also should exhibit a genetic signal of a recent increase in overall effective population size (Drummond *et al.* 2005).

If populations of *D. microps* experienced a niche shift and retained much of their current geographic range throughout the latest glacial-interglacial cycle, the genetic signal of stable populations (high genetic diversity within and variation among) would be detected throughout the species range (Fig. 2.2B). I employ several phylogeographic and population genetic methods to test the two competing hypotheses outlined above (Fig. 2.2A, B) and infer the recent geographic and population history of *D. microps*.

Methods

Taxon sampling

I acquired tissue samples from 364 individuals of *D. microps* from 83 unique localities; localities closer than 10 km without an obvious physical barrier were pooled together for a total of 67 general localities (Fig. 2.1; Table 2.1; Appendix 1). Of these 364 individuals, 340 were sampled specifically for this study. Most of the captured animals were ear-clipped and released (*N*=315), but some (*N*=25) were euthanized following methods approved by the American Society of Mammalogists (Gannon *et al.* 2007) and the Institutional Animal Care and Use Committee Protocol R 0709-244, and were deposited in the mammal collection at the New Mexico Museum of Natural History (NMMNH). Fourteen tissue samples were requested from the Museum of Texas

Technical University and 10 samples were requested from the Museum of Vertebrate

Zoology, University of CA (Appendix 1). These 10 samples (six of which were

represented by skin clips) came from the two most southern localities at Joshua Tree

National Park (locality 9) and Yucca Valley (locality 11) where *D. microps* might be

currently extinct (Drost & Hart 2008).

　　As different analyses require different sampling strategies, I used the following

subsets and modifications of the original dataset. For climatic niche models, I used all

unique sampling localities resulting in 83 presence records for *D. microps*. For genetic

analyses, I used three different datasets. For calculating overall genetic indices and for

phylogeographic analyses that do not require large sample size per a locality, I used all

364 individuals combined (Network, Bayesian skyline plot, overall mismatch distribution,

and diversity indices) or with each assigned to one of the 67 general localities (pairwise

genetic distances). I refer to this as "full dataset". For population genetic analyses that

require multiple individuals per locality (mismatch distributions, diversity indices for

individual localities, and the R_2 test) I excluded all localities with sample size smaller

than 10 which resulted in 12 sampling localities (165 samples), referred to as "10+

dataset". Additionally, the nucleotide and haplotype diversity, and frequency of private

haplotypes used in the landscape interpolation assessment were calculated for localities

with sample size equal or larger than five, resulting in 29 locations and referred to as

"5+ dataset".

I modeled the climatic niche of *D. microps* in order to approximate the species'

current distribution and distribution during the LGM under the assumptions that (1)

climate is an important factor driving the species distribution and (2) that the climatic

niche of *D. microps* remained conserved between the LGM and present time. The

climatic niches were reconstructed using the methodology of ecological niche modeling

where environmental data are extracted from occurrence records (represented by

geographic coordinates) and habitat suitability is evaluated across the landscape using

program-specific algorithms (Elith *et al.* 2006). The current models were then projected

on the climatic reconstructions of the LGM.

For occurrence records I used unique sampling localities and the current climate was

represented by bioclimatic variables from the WorldClim dataset v. 1.4

(http://www.worldclim.org/; Hijmans *et al.* 2005). The bioclimatic variables are derived

from monthly temperature and precipitation data, and represent biologically

meaningful aspects of local climate (Jezkova *et al.* 2009; Waltari *et al.* 2007). From the

original 19 variables, I excluded those that were highly correlated and used a total of 14

variables (for detailed methodology, see Jezkova et al., in review). For environmental

layers representing the climatic conditions of the LGM, I used ocean-atmosphere

simulations (Harrison 2000) available through the Paleoclimatic Modelling

Intercomparison Project (Braconnot *et al.* 2007). These reconstructions of the LGM

climate are based on simulated changes in concentration of greenhouse gases, ice sheet

coverage, insulation, and topography (caused by lowering sea levels). Of more than 15

available climatic models, I used the following two: Community Climate System Model v. 3 (CCSM; Otto-Bliesner *et al.* 2006) with a resolution of 1°, and the Model for Interdisciplinary Research on Climate v. 3.2 (MIROC; Hasumi & Emori 2004) with an original spatial resolution of 1.4° x 0.5° (Braconnot *et al.* 2007). The original climatic variables used in these models have been downscaled to the spatial resolution of 2.5 minutes under the assumption that changes in climate are relatively stable over space (high spatial autocorrelation) and were converted to bioclimatic variables (Peterson & Nyari 2008).

Climatic niche models were built in the software package MAXENT v. 3.2.1 (Phillips *et al.* 2006), a program that calculates relative probabilities of the species' presence in the defined geographic space, with high probabilities indicating suitable environmental conditions for the species (Phillips *et al.* 2004). I used the default parameters in MAXENT (500 maximum iterations, convergence threshold of 0.00001, and regularization multiplier of 1, 10,000 background points) with the application of random seed and logistic probabilities for the output (Phillips & Dudik 2008). I masked my models to the four regions where *D. microps* occurs (Mojave Desert, Great Basin, Columbian Plateau, and Colorado Plateau; Olson *et al.* 2001) because reducing the climatic variation being modeled to that which exists within a geographically realistic area improves model accuracy and reduces problems with extrapolation (Pearson *et al.* 2002; Randin *et al.* 2006; Thuiller *et al.* 2004). I ran 50 replicates for each model and an average model was converted to presence-absence maps using a minimum training presence threshold. I

used the receiver operating characteristic for its area under the curve (AUC) value to evaluate the model performance (Fielding & Bell 1997; Raes & ter Steege 2007).

<u>Laboratory methods</u>

I isolated total genomic DNA from preserved heart, kidney, or ear tissue following the protocol for the DNeasy Extraction Kit (Qiagen Inc.). I amplified ca. 1000 base pairs (bp) of the mitochondrial control region using genus-specific primer L15926DIOR (GTATAAAAATTACTCAGGTCTTGT) and an universal primer H651 (Kocher *et al.* 1989). Amplifications were accomplished in 12.5 μL reactions using Takara Ex Taq Polymerase Premix (Takara Mirus Bio, Inc.) followed by purification using ExoSap-IT (USB Corp.). Thermal cycling was accomplished at a 56°C annealing temperature in 40 cycles. I conducted double-stranded cycle sequencing using fluorescence-based chemistry (BigDye Terminator v. 3.1 Cycle Sequencing Kit) and the genus-specific primers L15926DIOR and H651Lpen (TAACTGCAGAAGGCTAGGAC). The electrophoresis was conducted on an ABI Prism 3130 automated sequencer (Applied Biosystems, Inc.). The sequences were aligned using SEQUENCHER v. 4.6 (Gene Codes Corp.) and verified manually. The DNA from the six museum skins of *D. microps* was isolated following the protocol for the DNeasy Extraction Kit with the following modifications: 40 μl per sample of proteinase K (double the regular value), 20 μl dithiothreitol (DTT) per sample added prior to incubation, and an extended incubation period (three days). I amplified and sequenced the targeted region using the thermal profiles described above with five overlapping genus-specific primer pairs about 250 bp each (the primer sequences can be provided upon request). Amplifications were accomplished in 25 μl reactions using

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GoldTaq (Applied Biosystems, Inc.) followed by purification using ExoSap-IT (USB Corp.). The final DNA segment for all samples included 902 bp of mtDNA control region sequence.

<div align="center">Genetic analyses</div>

For the full dataset I calculated the number of variable sites, parsimony informative sites and a net uncorrected p-distance in MEGA v. 4 (Tamura *et al.* 2007), and haplotype diversity (H_d) and nucleotide diversity (π_d) in ARLEQUIN v. 3.11 (Excoffier *et al.* 2005). Preliminary phylogenetic analyses of the mitochondrial DNA (mtDNA) dataset showed that *D. microps* exhibits shallow structuring. Accordingly, I used a median-joining network (Bandelt *et al.* 1999) to reconstruct relationships among the mtDNA sequences (referred to as haplotypes) as networks represent an ideal phylogeographic method when levels of genetic divergence are low, multifurcations occur, and ancestral haplotypes are still present in the populations (Crandall & Templeton 1996). Network analysis was conducted for the full dataset in the program NETWORK v. 4.5.1.6 (Bandelt *et al.* 1999) with transversions weighted twice as high as transitions (as recommended in the NETWORK manual), and with the maximum parsimony (MP) option employed to remove excessive links from the network (Polzin & Daneshmand 2003).

I calculated four genetic indices that can elucidate species geographic and demographic processes, such as a potential recent northward expansion of *D. microps* from southern refugia. Two indices reflect genetic variation (genetic distances among populations and frequency of private haplotypes within populations) and two indices represent genetic diversity (nucleotide and haplotypes diversity; Fig. 2.2). The genetic

distances are represented by mismatch distances between sequences from neighboring

sampling sites calculated in the program ALLELES IN SPACE (Miller 2005) for the full

dataset (67 locations). These pairwise genetic distances were assigned to mid-points

between sampling sites using the Delaunay triangulation-based connectivity network

(Miller *et al.* 2006). I used residual genetic distances derived from the linear regression

of genetic versus geographical distance to account for correlation between these two

distances (Manni *et al.* 2004; Miller *et al.* 2006). The residual genetic distances were

imported into ARCGIS 9.2 (ESRI, Redlands, CA) and interpolated across uniformly-spaced

2.5 minute grids (~5 km) using the inverse distance weighted interpolation procedure

(Watson & Philip 1985) in the Spatial Analyst extension. I restricted the interpolations to

the geographic range of *D. microps*, approximated using the climatic niche model for

current climatic conditions.

I calculated nucleotide diversity in ARLEQUIN as an average number of nucleotide

differences per site among sequences in each sampling locality and haplotype diversity

as a probability that two randomly chosen haplotypes in a population are different,

regardless of genetic distance between them. These two indices of genetic diversity can

reveal slightly different signals of population history (see Discussion). The private

haplotype frequency was calculated by hand as a frequency of DNA sequences

(haplotypes) in a population that are unique (do not occur in any other population).

Recently expanded populations should exhibit low frequency of private haplotypes as

the same haplotypes expand across large geographic areas and consequently occur in

multiple populations (Fig. 2.2A). I calculated nucleotide and haplotype diversity and

frequency of private haplotypes for the 5+ dataset, and confirmed that sample size and

the diversity indices are not positively correlated by conducting a correlation analysis in

SYSTAT v. 12 (Hilbe 2008). The three diversity indices were imported into ArcGIS and

interpolated across landscape as described above for genetic distances.

I analyzed past demographic changes of *D. microps* in order to detect any significant

changes in population sizes through time. For example, if the species experienced a

range expansion after the LGM, I would detect a significant increase in the overall

effective population size dating to sometime after the LGM. I used the Bayesian skyline

plot (BSP) coalescent model (Drummond *et al.* 2005) implemented in the program

BEAST v. 1.5.3 (Drummond & Rambaut 2007) that generates plots of estimated

posterior distribution of the effective population size through time (Drummond *et al.*

2005). Following assessment in MRMODELTEST, I selected the substitution model

GTR+I+Γ, along with a strict molecular clock (after assessing clock-like behavior), five

skyline groups, and a 1-year generation time (Gummer *et al.* 1997; Thomas *et al.* 1990).

Since mutation rates for *D. microps* control region are unavailable from the literature, I

applied a broad range of rates (1.5 and 6 % /lineage/million years) that have been used

for control region sequences of other small mammals (Galbreath *et al.* 2009). I

conducted several independent Markov Chain Monte Carlo (MCMC) runs of 80 million

generations with sampling every 8000 generations and a burn-in of 10%. For final

analysis three final MCMC runs were combined using LOGCOMBINER (distributed with

BEAST). I checked convergence (effective sample sizes > 200) and visualized the median

and 95% highest posterior density intervals using TRACER v. 1.5 (Rambaut & Drummond 2007).

I further tested for demographic changes using mismatch distribution analyses under the sudden expansion model (Rogers & Harpending 1992; Schneider & Excoffier 1999) in ARLEQUIN for all sequences combined (n=364) and for the 10+ dataset. Mismatch distribution analysis calculates the number of pairwise differences among sequences and identifies populations with star-like phylogeny, a structure typical for populations that experienced a sudden expansion (Excoffier 2002; Excoffier *et al.* 2009). The star-like phylogeny will appear as unimodal distribution of pairwise differences with the peak corresponding to a lower number of pairwise differences in younger expansions and higher number in older expansions (Excoffier 2002). This analysis results in a multimodal graph if a population is in demographic equilibrium, subdivided or in decline (Rogers & Harpending 1992; Slatkin & Hudson 1991). A significant sum of squared deviation (*SSD*; *P*<0.05) and Harpending's raggedness index (*r;* P<0.05) indicate the rejection of the null hypothesis of sudden expansion. If the sudden expansion model was not rejected, I calculated population expansion parameters τ (time since expansion), θ_0 (population size prior to expansion), and θ_1 (final population size). The parameter τ was used to calculate time in years since expansion (Rogers & Harpending 1992) using the same mutation rates and generation time as above.

To further evaluate whether the species experienced an expansion I used Ramos-Onsins and Rozas' R_2 test (Ramos-Onsins & Rozas 2002) in DnaSP v. 5.1 (Librado & Rozas 2009) for the full dataset and the 10+ dataset (Table 2.2). The R_2 test is based on the

differences between the number of singleton mutations (mutations that occur in only one individual) and the average number of nucleotide differences (Ramos-Onsins & Rozas 2002) and significantly low ($P \leq 0.02$) R_2 values indicate population growth.

Results

Ecological niche models

The model of current conditions (Fig. 2.3A) captures well the known distribution of *D. microps* but with some over-predictions of occurrence within the eastern part of the Colorado Plateau and on the Snake River Plain in southern Idaho. These areas, however, might currently be unoccupied by *D. microps* due to non climate-related factors such as insufficient time for colonization and establishment of more widespread populations (these two areas exhibit signals of a recent expansion, see below), recent habitat destruction (especially in the Snake River Plain) or possibly competition with other species (e.g. congeneric Ord's kangaroo rat, *D. ordii*). The paleo-models (Fig. 2.3B, C) indicate absence of a suitable climatic niche in the Great Basin and on the Columbia Plateau during the LGM. A suitable climatic niche is predicted to have been available within the Mojave Desert, but it is modeled as being fragmented and more restricted in distribution compared to present.

The mean AUC value for the current ecological niche model was only moderately high (0.82); AUC values range from 0.5 for a random prediction to 1 for perfect prediction (Winker *et al.* 2007). As pointed out by Lobo *et al.* (2008) and Peterson *et al.* (2008), the AUC values are greatly dependent on the number and variation of the

background points that are available. Because I masked my models to four ecoregions, the number of background points was limited. I believe that the moderately high AUC values in the masked models are likely the result of the methodological limitations, as the AUC values were high (<0.98) when I ran the same models with no mask.

<u>Genetic analyses</u>

Of the 902 bp of control region, 205 characters are variable and 160 are parsimony informative. The overall haplotype diversity (0.9957±0.0008) and nucleotide diversity (0.0242±0.0118) are high, and the net pairwise uncorrected p-distance is 2.4%. The median-joining network (Fig. 2.4) collapsed the 364 sequences into 243 haplotypes. The number of mutations between haplotypes ranges from 1 to 14 and the number of sequences belonging to any given haplotype ranges from 1 to 10. Most haplotypes are restricted to a single locality and of the 13 haplotypes shared among localities (Fig. 2.4), three are shared between *Atriplex* and *Coleogyne* localities. The median-joining network shows an overall star shape, with missing (extinct or unsampled) or low frequency haplotypes within the central parts of the network and with a burst of haplotypes separated from the center by up to 40 mutational steps. Nucleotide diversity within populations ranges from 0.00056 to 0.02222 (Fig. 2.5A) and there is no significant correlation between sample size and nucleotide diversity (r = -0.223, p = 0.244; Fig. 2.6). The nucleotide diversity does not decrease in the northward direction, as would be expected under the leading edge colonization model (r = - -0.148, p = 0.443; Fig. 2.2, Fig. 2.5A, Fig. 2.6). Nucleotide diversity is relatively high throughout the entire species range except the edge populations in the Colorado Plateau (northern Arizona), southern

Mojave Desert (southern CA), and northwestern Columbia Plateau (northeastern CA, southern OR and southwestern ID) regions. Haplotype diversity (Fig. 2.5B) ranges from 0.46 to 1.00 (where 1.00 represents populations with no redundant haplotypes) and is not significantly correlated with sample size ($r = -0.260$, $p = 0.174$; Fig. 2.6) or latitude ($r = 0.229$, $p = 0.232$; Fig. 2.6). Haplotype diversity is highest within the central parts of the species range and lowest within northwestern, southeastern, and southern edge localities (Fig. 2.5B).

The residual genetic distances range from -0.0209 to +0.0127 (Fig. 2.5C). The negative values indicate that the genetic distance between populations is lower than the average, given the geographic distances between them. The genetic distances among populations are relatively high throughout the entire range of *D. microps*, indicating genetic structuring and limited gene flow, inconsistent with recent northward expansion (Fig. 2.2). Low genetic distances are found within the peripheral areas and generally correspond with areas of low nucleotide and haplotype diversity. Sampling localities within the area covered with the pluvial Lake Bonneville during the LGM show intermediate genetic distances. The private haplotype frequency ranges from 0.41 to 1.00 (frequency of 1.00 represents populations where none of the haplotypes occurs in any other population), is high throughout most of the range (Fig. 2.5D), and is not correlated with sample size ($r = -0.273$, $p = 0.455$; Fig. 2.6) or latitude ($r = 0.142$, $p = 1.000$; Fig. 2.6).

The Bayesian skyline plots (BSPs; Fig. 2.7A upper plot with a mutation rate 1.5%/lineage/million years (Mys) and lower plot with 6%/lineage/Mys) indicate an

increase in genetic diversity, then a period of relatively stable genetic diversity, followed

by a recent decline. This signal is consistent (but see Discussion for possible caveats)

with an increase in effective population sizes during the middle to late Pleistocene (ca.

750 Kya, upper plot; ca. 200 Kya, lower plot), followed by constant population sizes

during the middle and late Pleistocene (starting ca. 500 Kya, upper plot; ca. 125 Kya,

lower plot) and declines during the late Pleistocene or early Holocene (ca. 20 Kya, upper

plot; ca. 5 Kya, lower plot).

The mismatch distribution (Fig. 2.7B) for the full dataset shows a unimodal

distribution of the pairwise sequence differences consistent with a rapid population

expansion. This expansion, however, was likely not recent as the median of the

distribution corresponds to 27 pairwise differences. The small sum of squared deviation

and raggedness index are not significantly different from a model of rapid population

expansion (SSD=0.003, P>0.05; r=0.001, P>0.05; Table 2.2). This expansion was further

supported by the values of θ, as $\theta_1 > \theta_0$ (θ_1 = 105.045, 95% CI = 75.418-71515.045; θ_0 =

0.004, 95% CI = 0.00-4.642). The beginning of population expansion based on the value

of τ (τ = 25.127, 95% CI = 18.389-28.549) and the two mutation rates applied roughly

correspond to 928,570 (95% CI = 679,564- 1,055,026) and 232,140 (95% CI=169,891-

263,756) years ago (early-middle Pleistocene). Out of the 12 evaluated populations

(Table 2.2; Fig. 2.8), five (localities 8, 15, 50, 61, 63) show a unimodal mismatch

distribution. Localities 8, 15, and 61 have likely experienced a relatively recent

population expansion while localities 50 and 63 probably experienced population

growth long before the LGM. Recent population expansion is not supported by the R_2

test for the full dataset and for none of the localities with the exception of locality 63 (Table 2.2). The sensitivity of the R_2 test decreases with the time since the expansion and this decrease is even more rapid when sample size is small (Ramos-Onsins & Rozas 2002) which could explain why expansion was not detected by this test.

Discussion

Discordance between climatic niche models, genetic data, and the fossil record

In this study, I evaluated whether *D. microps* shifted its range in response to climate changes of the last glacial-interglacial transition, or alternatively, whether the species retained most of its range by adapting to the changing environment. The ecological niche models, built under the assumption that the climatic niche of *D. microps* has remained conserved between the LGM and present day, indicate that the climatic niche within the Great Basin and Columbia Plateau would have been unsuitable to the species during the LGM and that the suitable climatic niche within the Mojave Desert would have been reduced and fragmented. These results imply that if the climatic niche of the species was conserved, *D. microps* would have persisted within the Mojave Desert during the LGM and experienced a substantial expansion northwards after the LGM. My climatic models are in agreement with reconstructions of the LGM environment from packrat midden and pollen records (Spaulding 1990b; Spaulding *et al.* 1983; Thompson 1990), which indicate that during the LGM, the low elevation *Atriplex* habitats within the Great Basin and Columbia Plateau that currently represent the prime habitat for *D. microps* were covered with large pluvial lakes (Grayson 1993; Reheis 1999) or replaced

by an assemblage of plants currently found in higher elevations, such as *Artemisia*

(sage), *Chrysothamnus* (rabbitbrush), and various woodland species (e.g. Utah juniper,

Juniperus osteosperma; Single-leaf Pinyon, *Pinus monophylla*) (Grayson 1993; Spaulding

1990a; Spaulding 1990b; Spaulding *et al.* 1983; Thompson 1990). *Atriplex*-dominated

communities were not established until the late Pleistocene or even the beginning of

Holocene, when the climate warmed, plant communities shifted upwards and

northwards, and the large pluvial lakes desiccated (Spaulding 1990b; Thompson 1990).

Such vegetation shifts imply that environmental conditions during the LGM within the

northern parts of the current range of *D. microps* were quite different from those that

the species experiences today. The response of *Coleogyne* to the latest climate changes

is less well understood (Summers *et al.* 2009) but it is believed that *Coleogyne* could

have persisted mostly *in situ* (Wells 1983) and therefore could have maintained suitable

niche for *D. microps* within portions of the Mojave Desert.

Despite these environmental changes, none of the genetic analyses supported post-

LGM range expansion from the Mojave Desert into the Great Basin and Colombia

Plateau. I did not detect the decrease in nucleotide or haplotype diversity in a

northward direction (Fig. 2.5A, B; Fig. 2.6) that would be predicted under the 'leading

edge' model of post-LGM range expansion (Fig. 2.2). High nucleotide and haplotypes

diversity is usually a result of population stability as mutations are accumulated over

time, but can also be maintained under the 'phalanx' model of population expansion

(Fig. 2.2). Relatively high nucleotide diversity can also be observed within expanding

areas when previously isolated (and therefore quite divergent) populations come to

secondary contact, such as after expansion from multiple refugia (Hewitt 1999). In such

cases, however, I would observe lower levels of haplotype diversity within the areas of

secondary contact in comparison to the stable areas, because of the reduced number of

individual haplotypes coming from each of the colonization fronts.

I detected high genetic distances among populations (Fig. 2.5C) and high frequency

of private haplotypes within populations (Fig. 2.5D), suggesting geographic structuring

typical for long term population persistence with limited gene flow (Kerdelhue *et al.*

2009). Such signal contradicts the 'leading edge' as well as the 'phalanx' models of

population expansion, where certain genotypes expand across large areas in the

direction of the expansion, promoting gene flow, and resulting in decrease of genetic

distances among populations and frequency of private haplotypes (Excoffier *et al.* 2009;

Kerdelhue *et al.* 2009). Low genetic distances were only detected within the extreme

edges in the northern, southern, and southeastern parts of the species range (localities

2, 8, 9, 15, 61), in localities that also exhibit low haplotype and nucleotide diversity.

These areas could indeed be recently colonized, or might represent pockets of isolated

populations that exhibit a signal of a population bottleneck (Avise 2000). More detailed

sampling and analyses would be necessary to reveal the history of these edge

populations.

The demographic analyses (BSP and mismatch distributions) revealed constant

genetic diversity through at least the last several thousand years (Fig. 2.7A and B), which

implies no significant post-LGM increase in effective population sizes that would be

expected if the species experienced a range expansion. The estimate of effective

population size is confounded with genetic structuring which means that highly

structured populations with low gene flow will exhibit larger genetic diversity (and

therefore seemingly higher effective population size) than panmictic populations

(Drummond *et al.* 2005). Because *D. microps* exhibits pronounced geographic

structuring (as apparent from the patterns of genetic diversity; Fig. 2.5C), the

assumption of panmixia was violated in both demographic analyses. Accordingly, I also

performed mismatch distributions for the 12 sampling locations that had adequate

sample size. Samples were collected for each of these localities from a small geographic

area (less than 10 km) with no obvious barriers and should approximate a panmictic

population. The resulting graphs (Fig. 2.8) further support my conclusions that most

populations throughout the species range did not experience a recent expansion. In

summary, all genetic analyses support the hypothesis that *D. microps* has not

experienced a post-LGM northward expansion, but rather was able to retain most of its

range despite pronounced climatic and environmental changes of the late Pleistocene.

There is no fossil record for *D. microps* dating back to the LGM that would

corroborate my interpretation of the genetic data that the species persisted throughout

the northern parts of its current range. However, an abundant late Pleistocene and

Holocene fossil record spanning the last 11,300 years is available from the Homestead

Cave in Northeastern Utah. This fossil record documented fluctuations in numbers of *D.*

microps coinciding with climate oscillations throughout the Holocene (Grayson 2000). At

this locality, the species fossil record was quite rare at the end of the Pleistocene and

beginning of the Holocene, with a subsequent increase and peak in relative abundance

during the middle Holocene, presumably reflecting the warming climate that promoted

the increase of *Atriplex* in the area. As the warm middle Holocene ended, fossils of *D.*

microps declined in relative abundance again (Grayson 2000). My BSP (Fig. 2.7) could

indeed be consistent with a decrease in effective population sizes during the late

Holocene but my general conclusions do not support the increase in abundance during

early and middle Holocene. I speculate that apparent low numbers of *D. microps*

recovered from the oldest strata might result from the geographic position of the cave.

Homestead Cave is situated in the middle of the pluvial Lake Bonneville (near my locality

66) and therefore might not have been colonized until after the water level receded.

Dipodomys microps might therefore have been only locally but not regionally rare within

the Great Basin at the beginning of the Holocene.

<u>Niche drift or niche evolution?</u>

Empirical and experimental studies show that species often respond

individualistically to environmental change (Colautti *et al.* 2010; Graham *et al.* 1996;

Parmesan 2006 and citations within; Rowe *et al.* 2010). Many taxa expand and retract

their ranges in response to an oscillating climate, as implied from the fossil record

(Grayson 2000; Hockett 2000) as well as from direct observations of range shifts caused

by recent human-induced climate changes (Moritz *et al.* 2008; Parmesan *et al.* 1999).

Some taxa have showed plastic responses in morphological, phenological, or

physiological characters that allow them to meet the challenge of changing environment

in situ and thus retain large portions of their current geographic distributions (Gibbs &

Breisch 2001; Huppop & Huppop 2003; Menzel 2000; Post *et al.* 1999; Smith &

Betancourt 2003). Such niche responses resulting from an alteration of the realized

niche (Jackson & Overpeck 2000; Rodder & Lotters 2009) do not require evolutionary

adaptation. As such, here I defined a change in realized niche space as a 'niche drifting'

in order to differentiate it from 'niche evolution', a change in the fundamental niche of a

species. Niche evolution incorporates a shifting or broadening of the niche to meet new

environmental conditions through evolutionary adaptation (Davis & Shaw 2001; Davis *et

al.* 2005; Reale *et al.* 2003; Urban *et al.* 2007). Above, I demonstrate that the climatic

niche of *D. microps* has not been conserved between the LGM and present time but I

have not yet addressed the possible mechanisms that may have allowed the species to

adapt to changing climate. Thus I ask the question, has the niche of *D. microps* drifted or

evolved?

In a previous study, Csuti (1979) demonstrated that *D. microps* currently exhibits a

generalized genotype that allows exploitation of the *Atriplex* and *Coleogyne* habitats. In

the lab, animals from one habitat were able to adjust behaviorally and physiologically to

exploit food resources from the other habitat. Despite this general plasticity, however,

the descendants of the *Atriplex* population were still more efficient in shaving the

Atriplex leaves than the descendants of the *Coleogyne* population, which suggests a

certain level of evolutionary adaptation. The idea of a generalized genotype and

therefore 'niche drift' seems to be a favored mechanism behind the adaptations to the

developing *Atriplex*-dominated community after the last glacial period. Frequent glacial-

interglacial fluctuations of the Pleistocene likely favored the retention of a generalized

genotype and prevented fixation of a specialized genotype for any particular habitat.

Without the unpredictability conferred by climatic fluctuations, it is possible that differential selective pressure in *Atriplex* and *Coleogyne* habitats would induce genetic differences among populations and promote diversification and specialization. Furthermore, adaptation to the *Atriplex* community is likely not a novel, but rather a reoccurring event within cycles of oscillating climate. Indeed, Kenagy (1973) suggested that it was adaptation to *Atriplex* that allowed *D. microps* to diverge from granivorous congeners in the Pliocene or beginning of the Pleistocene. This adaptation is apparent from the unique, chisel-shaped lower incisors of *D. microps* that are ideal for removing hypersaline surface tissues from *Atriplex* leaves (Hayssen 1991; Kenagy 1973). This morphology is conserved even in *Coleogyne* populations where *Atriplex* consumption is low or where *Atriplex* is not consumed at all. But why would a species specialize to a plant community typical of only short interglacial periods? Although *Atriplex*-dominated communities are likely prevalent only during interglacials (Spaulding *et al.* 1983), *Atriplex* itself was likely present throughout the entire Pleistocene. Indeed, *A. confertifolia*, was recorded in non-analogous plant communities within the Mojave Desert and the Great Basin during the last glacial period, mixed with plants currently found in higher altitudes (Spaulding *et al.* 1983). It is currently not clear whether *Atriplex* represented a dominant food source during glacial periods or whether *D. microps* utilized a wider variety of plant material as it currently does in the *Coleogyne* habitat. It is possible, however, that the permanent presence of *Atriplex* facilitated persistence of *D. microps* throughout much of its current range during the profound climate transition following the LGM.

Conclusions

Pleistocene glacial-interglacial cycles have been documented to commonly induce shifts in species ranges through tracking the changing climates, rather than remaining in place and adapting to the changing environment (Parmesan 2006). In my study I show that *D. microps* was able to shift its niche and retain much of its current geographic range during at least the latest Pleistocene glacial-interglacial cycle. Such a niche shift in response to fluctuating climate and changing environment might have been possible because of the preservation of a generalized genotype and could have been enhanced by permanent availability of *Atriplex*, its dominant food source. Identification of factors that determine whether and to what extent taxa are able to adapt to a changing environment is crucial in our attempt to predict biotic responses to past, current, and future environmental changes.

Table 2.1. General sampling localities for *Dipodomys microps* depicted in Figure 1.1. *N*

represents the sample size for each location. The geographic coordinates represent an

approximate location; the exact coordinates for each sample are listed in Appendix 1.

Locality number	State	County	Locality	Lat	Long	*N*
1	AZ	Coconino	House Rock Valley	36.49	-111.96	11
2	AZ	Mohave	Wolf's Hole	36.89	-113.56	15
3	CA	Inyo	Haiwee	36.15	-117.98	7
4	CA	Inyo	Owens Valley	36.54	-117.93	1
5	CA	Inyo	Saline Valley	36.84	-117.91	1
6	CA	Inyo	Deep Spring Valley	37.30	-118.06	4
7	CA	Kern	Koehl Lake	35.29	-117.88	12
8	CA	Modoc	Eagleville	41.16	-119.99	13
9	CA	Riverside	Joshua Tree NP	33.99	-116.23	8
10	CA	San Bernardino	Boron	35.15	-117.57	1
11	CA	San Bernardino	Yucca Valley	34.15	-116.47	2
12	CA	San Bernardino	Superior Lake	35.23	-117.03	2
13	CA	San Bernardino	Clark Mountain	35.56	-115.64	14
14	ID	Owyhee	Bruneau Canyon	42.76	-115.76	4
15	ID	Owyhee	Murphy	43.19	-116.64	10
16	NV	Churchill	Fallon	39.38	-118.88	2

17	NV	Churchill	Hot Springs Mountains	39.76	-118.87	3
18	NV	Clark	Cottonwood Valley	36.00	-115.45	2
19	NV	Clark	Kyle Canyon	36.26	-115.48	14
20	NV	Elko	Tecoma	41.32	-114.08	9
21	NV	Esmeralda	Fish Lake Valley	37.78	-118.10	1
22	NV	Esmeralda	Tonopah	37.91	-117.22	6
23	NV	Esmeralda	White River Valley	38.41	-115.12	3
24	NV	Eureka	Beowawe	40.52	-116.51	4
25	NV	Humboldt	Battle Mountain	40.48	-117.06	5
26	NV	Humboldt	Sulphur Landing	40.84	-118.76	7
27	NV	Humboldt	Golconda	40.96	-117.42	2
28	NV	Humboldt	30 mi S Denio	41.65	-118.44	2
29	NV	Lander	Monitor Valley	39.23	-116.70	6
30	NV	Lander	Big Smoky Valley	39.39	-116.93	1
31	NV	Lincoln	Coyote Spring	37.15	-114.72	3
32	NV	Lincoln	Pahranagat NWR	37.23	-115.10	8
33	NV	Lincoln	Kane Spring Valley	37. 30	-114.58	18
34	NV	Lincoln	Tickaboo Valley	37.37	-115.47	4
35	NV	Lincoln	Delmar Valley	37.52	-114.87	2
36	NV	Lincoln	Rachel	37.71	-115.81	6
37	NV	Lincoln	Dry Lake Valley	37.71	-114.80	3
38	NV	Lincoln	Tempiute	37.74	-115.58	1

39	NV	Lincoln	Dry Lake Valley	37.94	-114.83	2
40	NV	Lincoln	Cave Valley	38.37	-114.82	3
41	NV	Lincoln	Lake Valley	38.45	-114.61	3
42	NV	Mineral	Marietta, Teels Marsh	38.23	-118.31	1
43	NV	Mineral	Tonapah Junction	38.27	-118.11	3
44	NV	Mineral	Smith Valley	38.84	-119.31	1
45	NV	Nye	Ash Meadows NWR	36.47	-116.32	6
46	NV	Nye	Beatty	36.91	-116.76	9
47	NV	Nye	Nevada Test Site	37.16	-115.97	5
48	NV	Nye	Hot Creek Valley	38.21	-116.18	2
49	NV	Nye	Railroad Valley	38.51	-115.79	3
50	NV	Nye	Currant	38.79	-115.53	12
51	NV	Washoe	Mullen Pass	39.87	-119.62	13
52	NV	Washoe	Flanigan	40.19	-119.85	3
53	NV	Washoe	Gerlach	40.75	-119.29	1
54	NV	White Pine	Snake Valley	38.63	-114.27	7
55	NV	White Pine	Spring Valley	38.94	-114.42	2
56	NV	White Pine	Spring Valley	39.14	-114.50	7
57	NV	White Pine	Steptoe Valley	39.23	-114.84	1
58	NV	White Pine	Spring Valley	39.49	-114.39	1
59	OR	Harney	Fields	42.31	-118.66	4
60	OR	Harney	20 mi S Narrows	43.07	-118.87	4

61	OR	Lake	Alkali Lake	43.01	-120.01	10
62	UT	Boxelder	Kelton	41.73	-113.14	9
63	UT	Juab	Snake Valley	39.46	-113.96	13
64	UT	Millard	White Sage Valley	39.10	-112.85	9
65	UT	Tooele	Rush Valley	40.08	-112.26	1
66	UT	Tooele	Puddle Valley	40. 90	-112.95	4
67	UT	Washington	Beaver Dam Mountains	37.08	-113.92	8

Table 2.2. Genetic indices for the full dataset and localities identified by numbers and sample sizes (*N*). Shown are haplotype diversity (*H$_d$*), nucleotide diversity (*π$_d$*), *R$_2$* test (indicates significant population growth at *P*≤0.02; shown as *), and the mismatch distribution curves that are evaluated as unimodal, bimodal, or multimodal. The curves are tested for significant departure from the expansion model at *P*≤0.05 (indicated as **) using Sum of squared deviation (*SSD)* and Harpending's raggedness index (*r*).

Locality	N	H$_d$	π$_d$	R$_2$	SSD	r	Curve
1	11	0.49	0.0010	0.178	0.262**	0.151	Bimodal
2	15	0.65	0.0025	0.100	0.06	0.125	Bimodal
7	12	0.76	0.0101	0.143	0.088	0.145	Multimodal
8	13	0.53	0.0010	0.147	0.009	0.093	Unimodal
13	14	0.85	0.0220	0.189	0.070**	0.079**	Multimodal
15	10	0.87	0.0023	0.132	0.004	0.04	Unimodal
19	14	0.90	0.0215	0.136	0.049**	0.092**	Multimodal
33	18	0.87	0.0081	0.155	0.053	0.076	Multimodal
50	12	0.97	0.0183	0.139	0.014	0.031	Unimodal
51	13	0.96	0.0192	0.133	0.023	0.038	Multimodal
61	10	0.64	0.0012	0.156	0.126	0.424	Unimodal
63	13	0.96	0.0089	0.099*	0.013	0.048	Unimodal
Full dataset	364	0.99	0.0242	0.051	0.003	0.001	Unimodal

Figure 2.1. Sampling localities for *Dipodomys microps*. The circle size and shading

reflects the sample size, progressing from 1 to 18. Circles with black dots represent

populations occupying *Coleogyne* habitats; empty circles represent populations

occupying *Atriplex* habitats. The lighter shading in the inset represents the extent of the

Mojave Desert, Sonoran Desert, Great Basin, Columbia Plateau, and Colorado Plateau

ecoregions adapted from Olson *et al.* (adapted from Olson *et al.* 2001).

Figure 2.2. The genetic consequences based on the two proposed hypotheses: (A) The

null hypothesis of range shift in *D. microps* in response to the changing climate at the

end of the LGM. Stable populations that persisted throughout the LGM (top) harbor a

large number of genotypes (represented by an array of different colors) generating high

genetic diversity within population and high genetic variation among populations. Under

the leading edge model of population expansion(bottom left), random subsets of

genotypes are involved in the expansion, resulting in gradual lost of genotypes and

therefore decrease in genetic diversity within populations in the direction of the

expansion. Only the yellow genotypes are still present at the furthest front of the

expansion. The white genotype is novel and has emerged during the expansion. Under

the phalanx model (bottom right), more genotypes are involved in the expansion,

maintaining moderate to high genetic diversity within the expanding populations. Under

both models, genetic variation among expanding populations are low because

expanding populations consist of similar groups of genotypes. (B) The alternative

hypothesis of niche shift resulting in population persistence within the species range

despite climatic changes. Population persistence during the LGM generates high genetic

diversity within population and high genetic variation among populations (top) that are

preserved and detected in present populations (bottom). In this generalized illustration,

genetic diversity represents both haplotype diversity (H_d) and nucleotide diversity (π_d ;

Fig. 2.5A,B) and genetic distances represent both mismatch distances and frequency of

private haplotypes (Fig. 2.5C,D) but see Discussion for more details about each genetic

index.

Figure 2.3. Climatic niche models for *Dipodomys microps* approximating the species

range based on 14 bioclimatic variables representing current climatic conditions (A), and

projected on two reconstructions of climatic conditions at the last glacial maximum

(LGM) – CCSM (B) and MIROC (C) under the assumption of a conserved climatic niche.

The green shading represents areas identified as suitable using the minimum presence

threshold for logistic probabilities. Dark grey shading indicates areas identified as

unsuitable. Blue areas correspond to the extent of pluvial lakes during the LGM (Raines

et al. 1996). White dots represent current occurrence records of *D. microps* used to

build the models.

Figure 2.4. Median-joining network of control region sequences for 364 samples of

Dipodomys microps. Circle size reflects the number of individuals exhibiting a haplotype

(smallest=1, largest=8). The length of connection lines between haplotypes is

proportional to the number of mutational changes, with the shortest connection line

representing one mutational change. In (A), the colored circles represent haplotypes

present in the 12 sampling localities with sample size equal or larger than 10. In (B), the

dark grey circles represent haplotypes found in individuals from *Coleogyne* populations

and white circles represent *Atriplex* populations.

Figure 2.5. Interpolated nucleotide diversity (A), haplotype diversity (B) pairwise genetic

distances (C), and frequency of private haplotypes (D) across landscape for *Dipodomys*

microps using a 2.5 minutes (ca. 5 km) grid size and restricted to the current climatic

niche model of the species. The shading gradation progresses from green (lowest),

yellow, brown to white (highest). The white circles indicate sampling localities used in

each analysis; for nucleotide and haplotype diversity and frequency of private

haplotypes, I used sampling localities with a sample size equal or larger than five while

for genetic distances, I used all sampling sites.

Figure 2.6. Scatterplot between nucleotide diversity and sample size (A), nucleotide

diversity and latitude (B), genetic distances and latitude (C), haplotype diversity and

sample size (D), haplotype diversity and latitude (E), genetic distance among populations

and latitude (E) and frequency of private haplotypes and latitude (F) based on

mitochondrial control region sequences of *Dipodomys microps.*

Figure 2.7. (A) Bayesian skyline plots derived from control region sequences for 364 samples of *Dipodomys microps* using mutation rates 1.5%/lineage/Mys (upper plot) and 6%/lineage/Mys (lower plot). The x-axis shows the time progressing from right (oldest) to left (present). The y-axis shows an index of effective population size assuming a 1-year generation time. The black line is the median for genetic diversity and the grey area shows the 95% upper and lower highest posterior density limits. The arrows point to the timing of the last glacial maximum (~21 Kya). (B) Mismatch distribution analysis under the sudden expansion model.

Figure 2.8. Mismatch distributions for 12 sampling localities with sample size greater than or equal to 10.

Figure 2.1
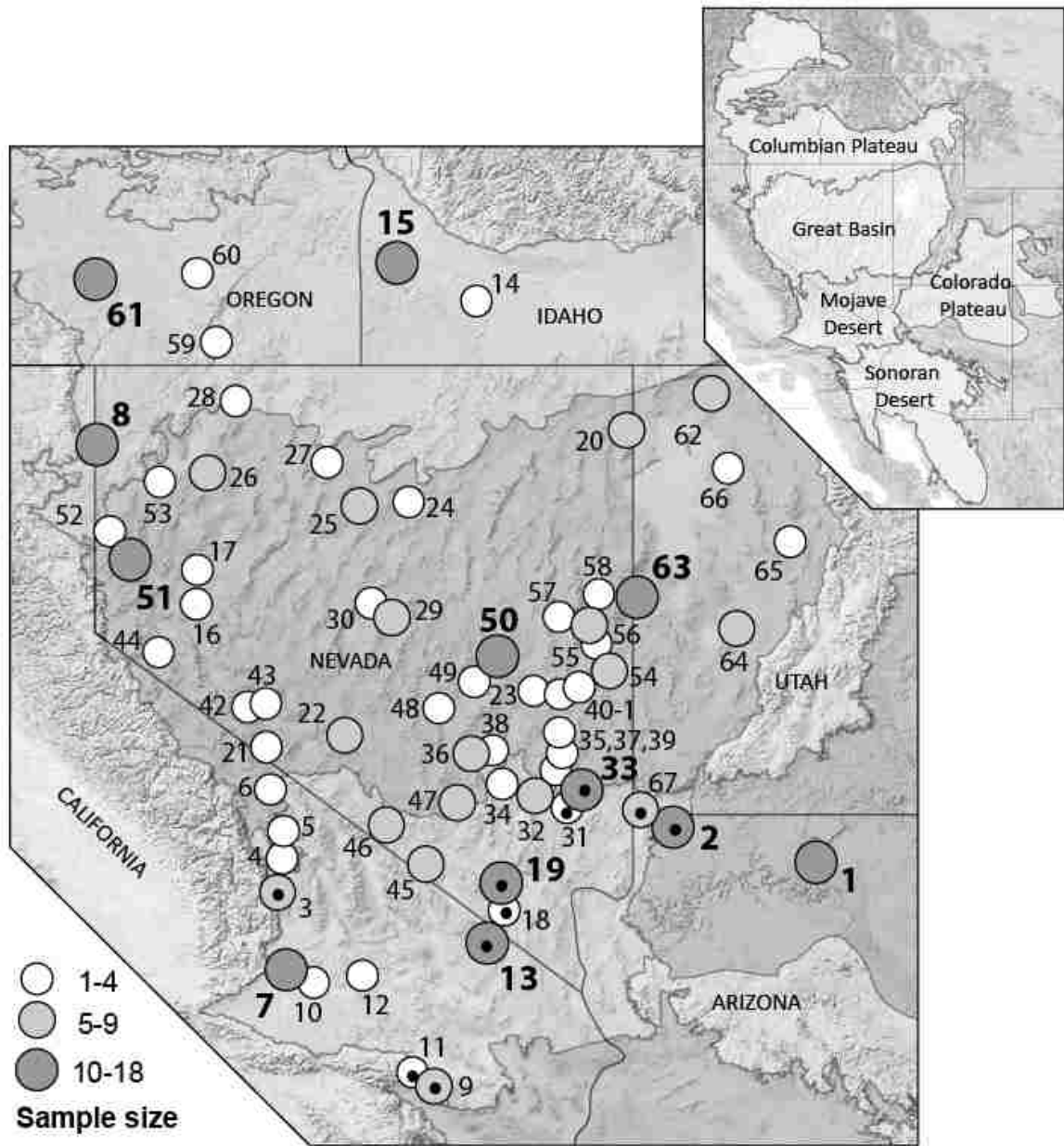
Figure 2.2
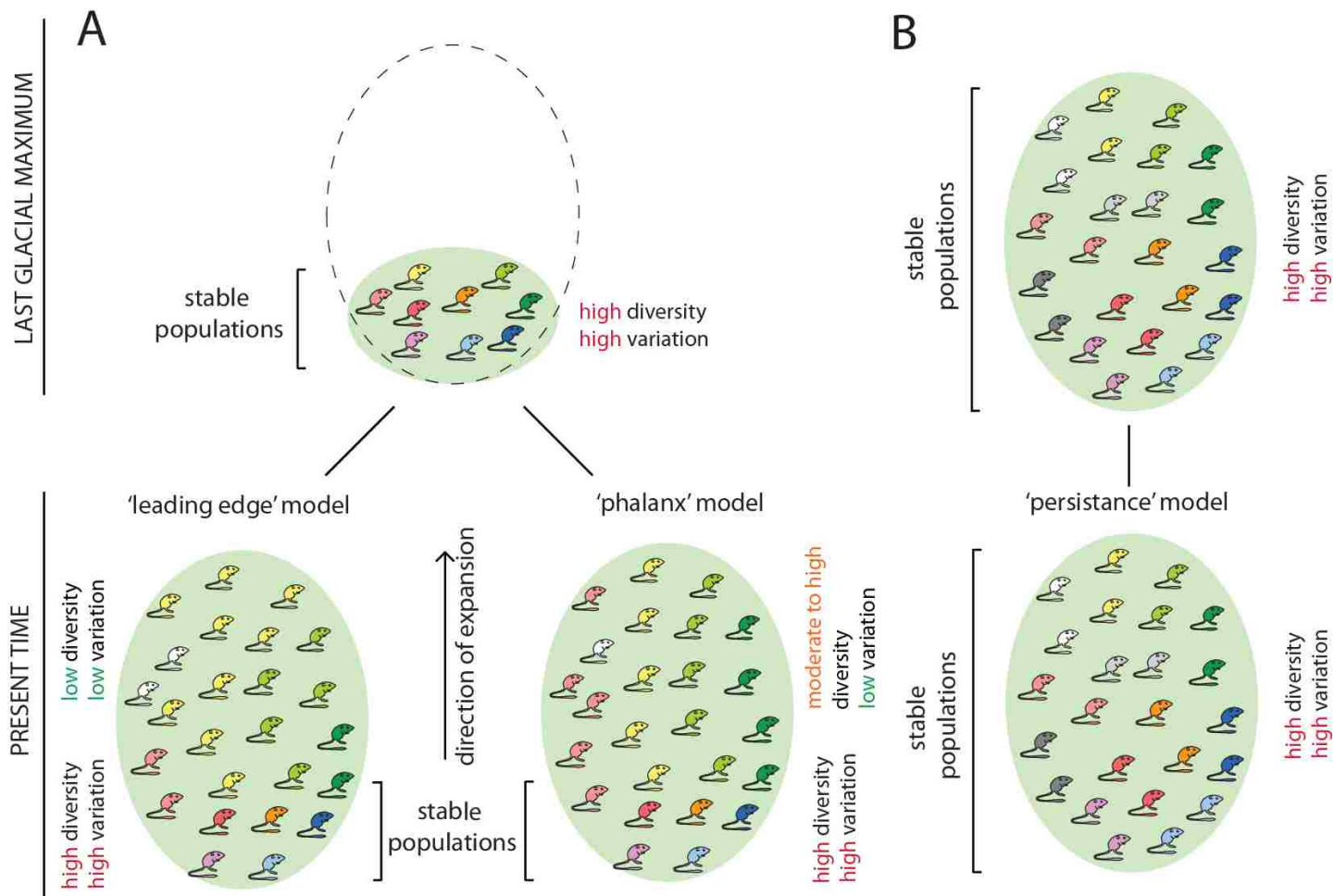
Figure 2.3
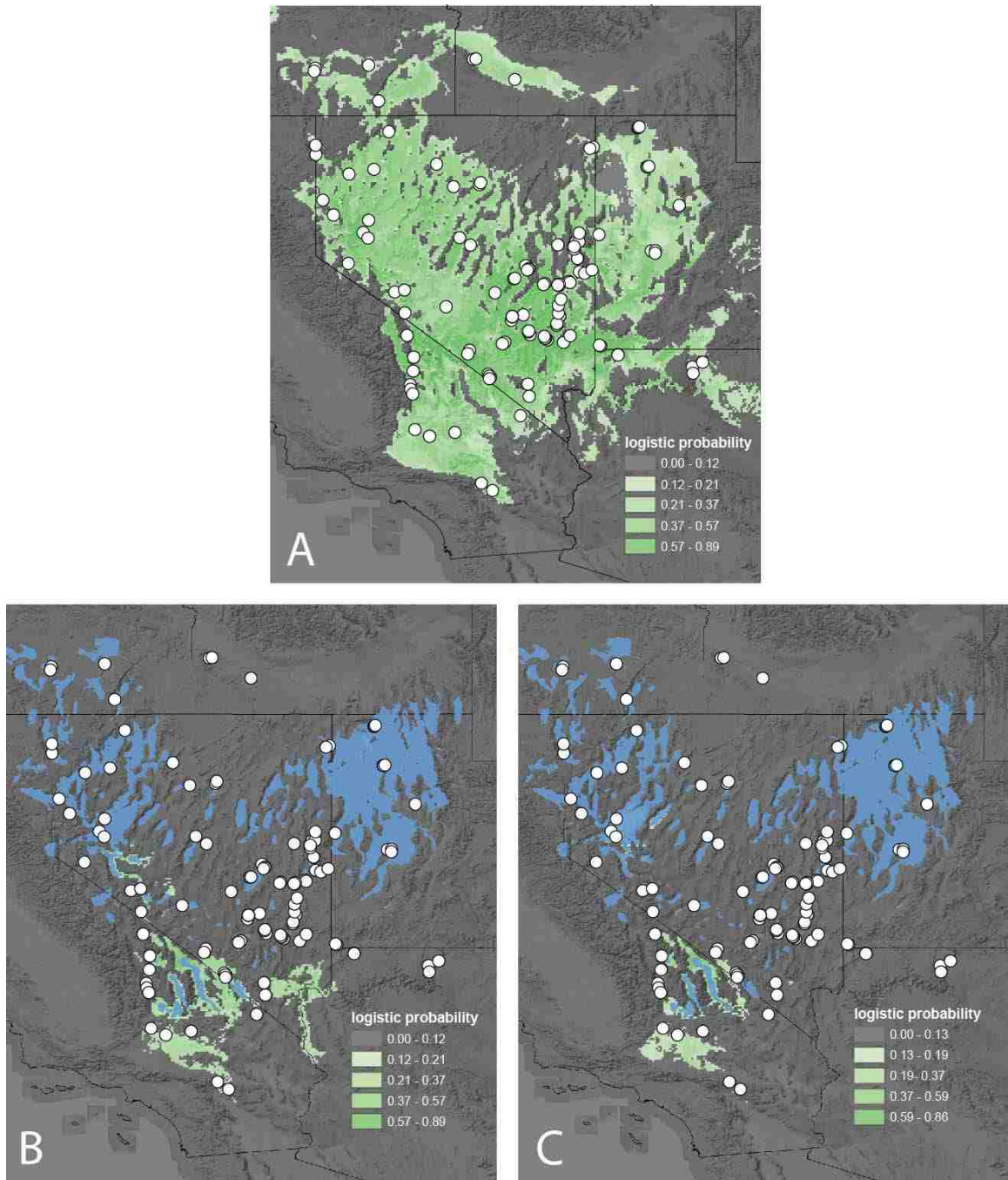
Figure 2.4
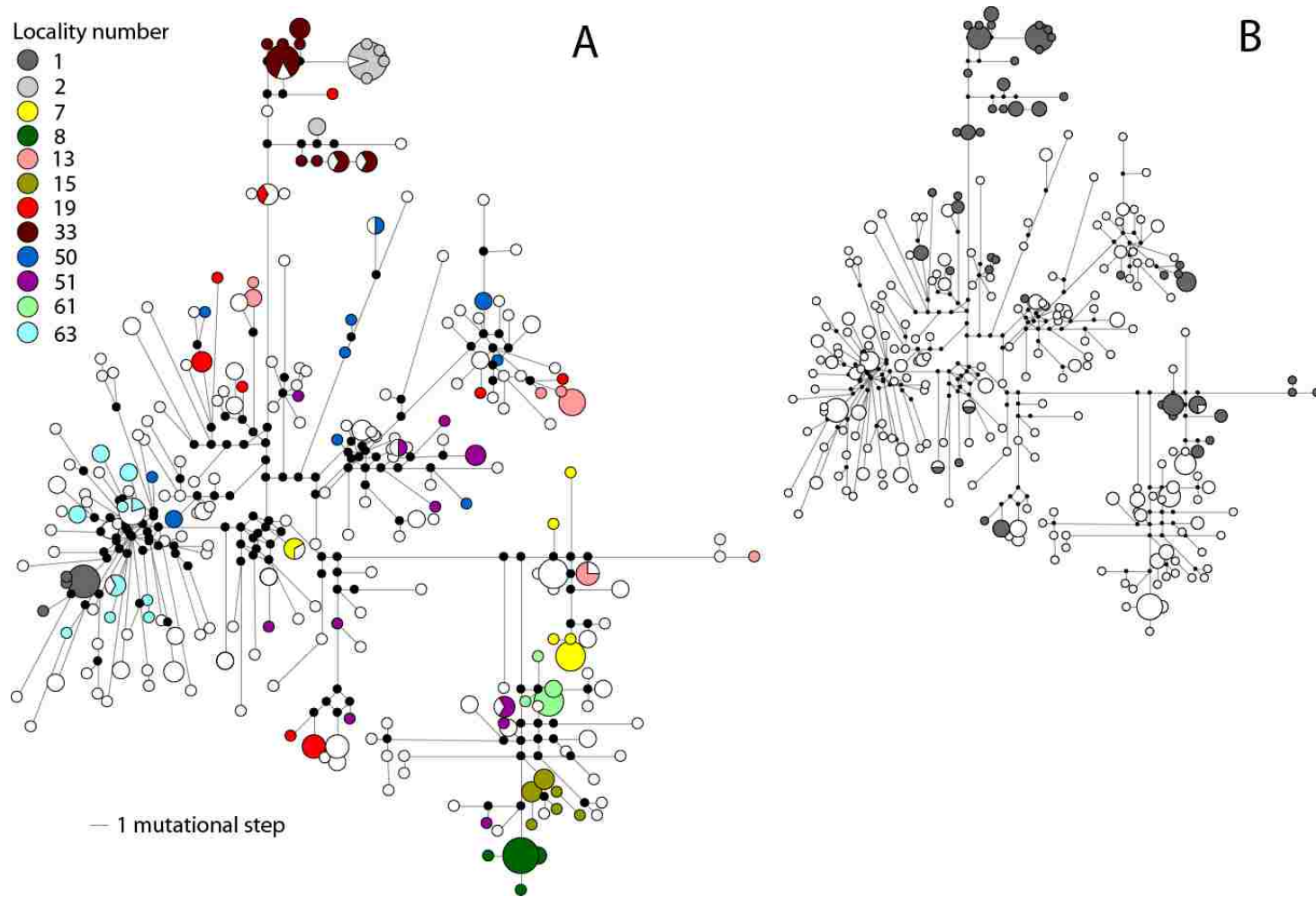
Figure 2.5
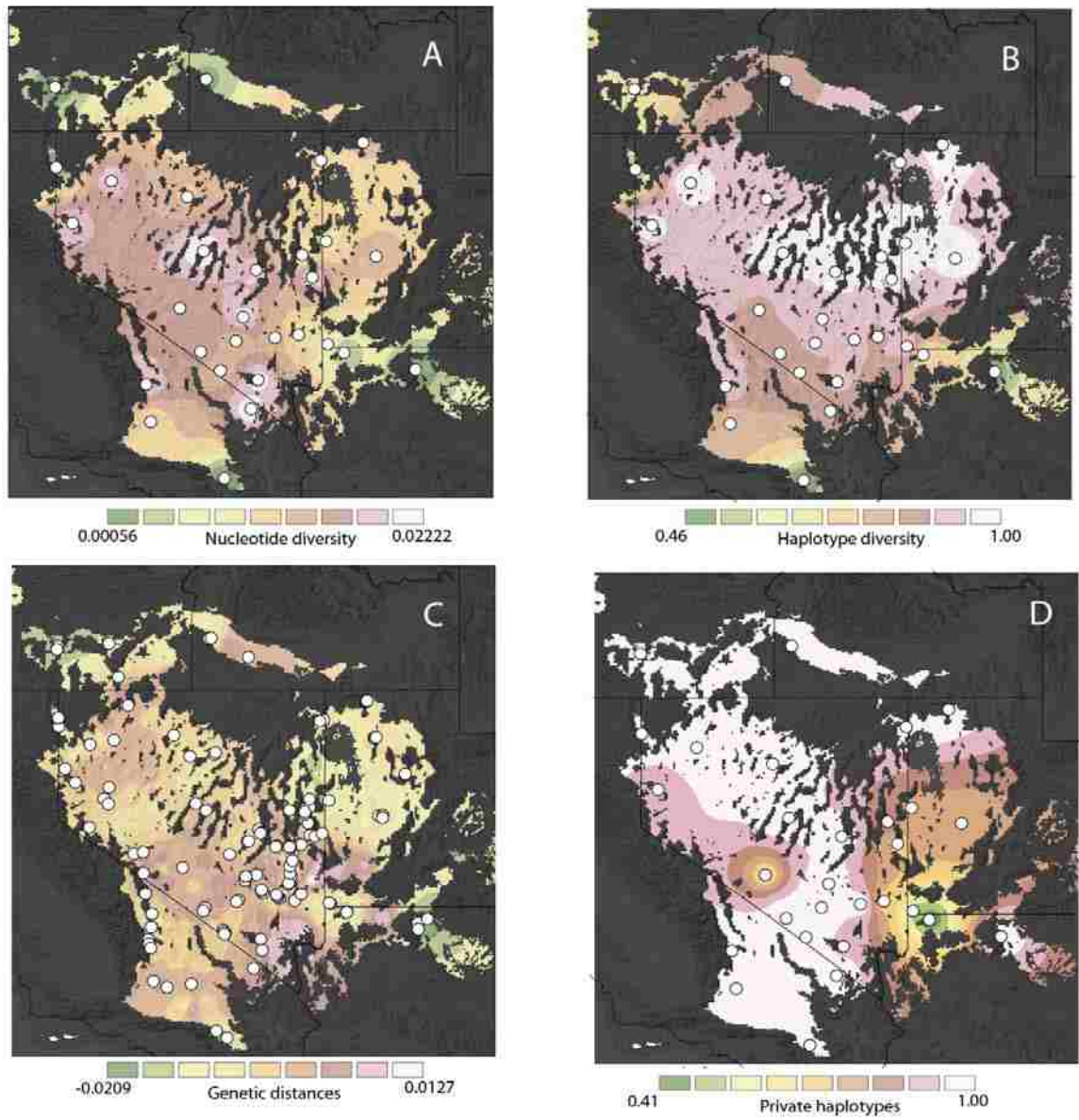
Figure 2.6

Figure 2.7

Figure 2.8

Frequency

Pairwise Differences ■ Observed ── Simulated
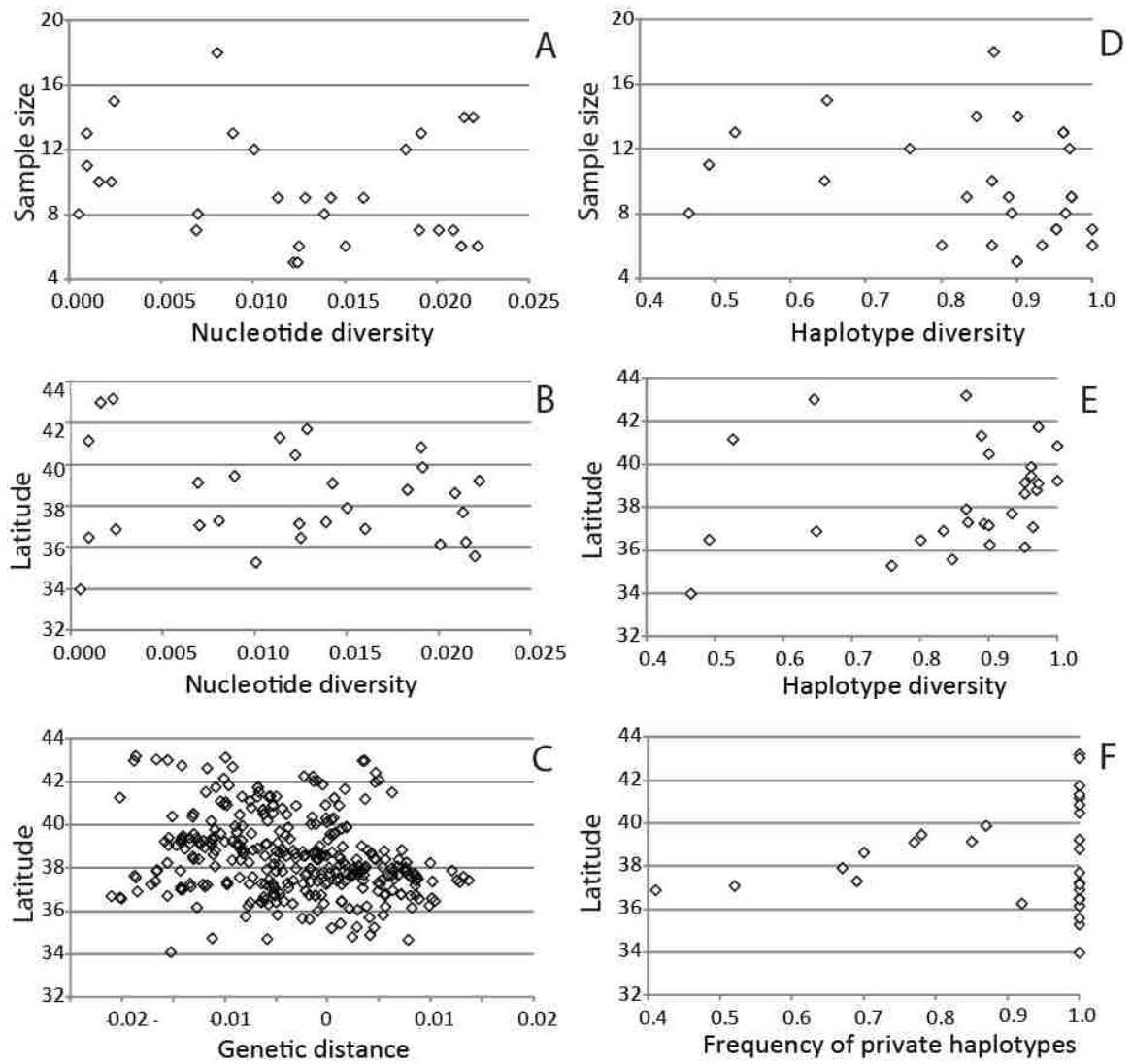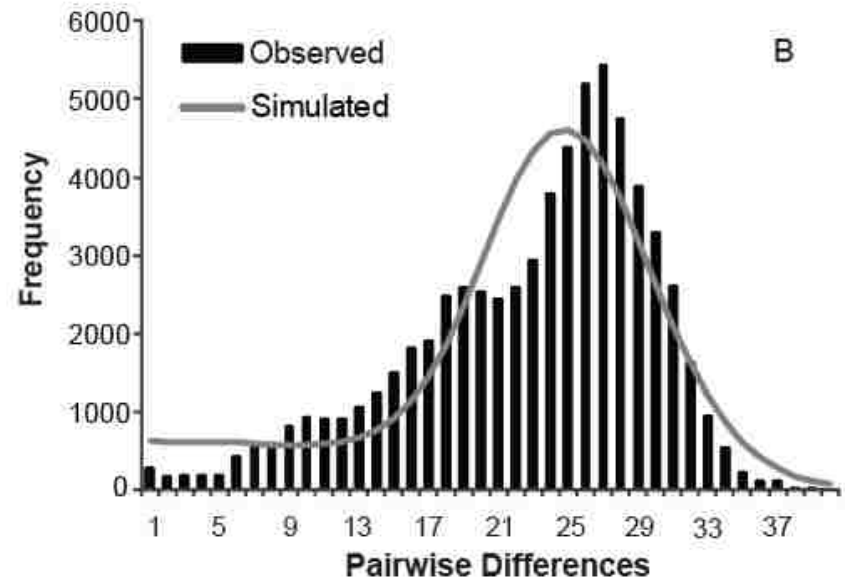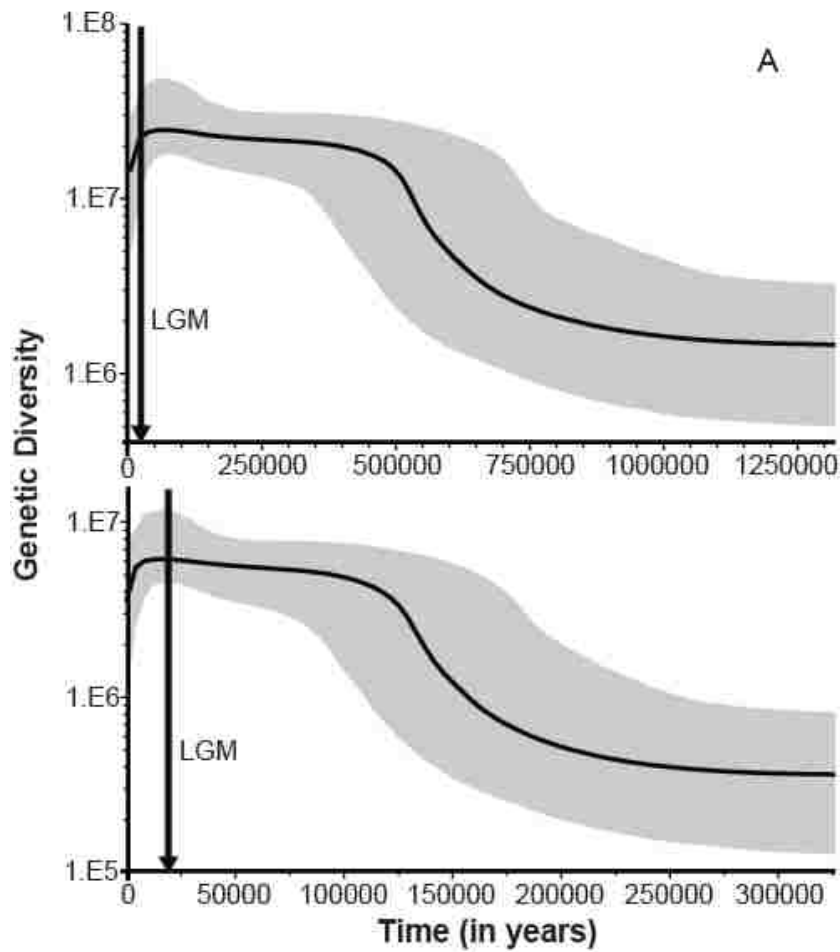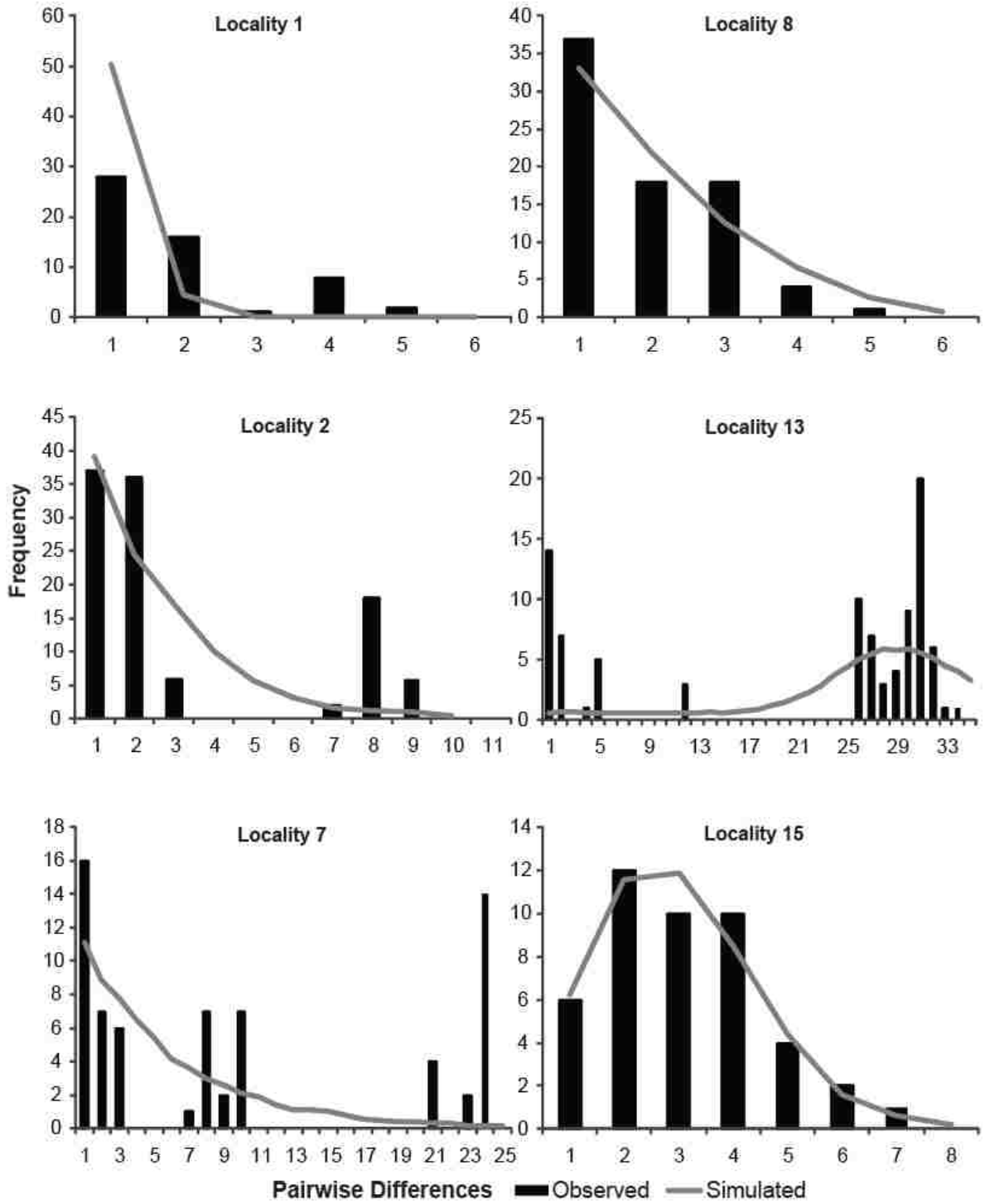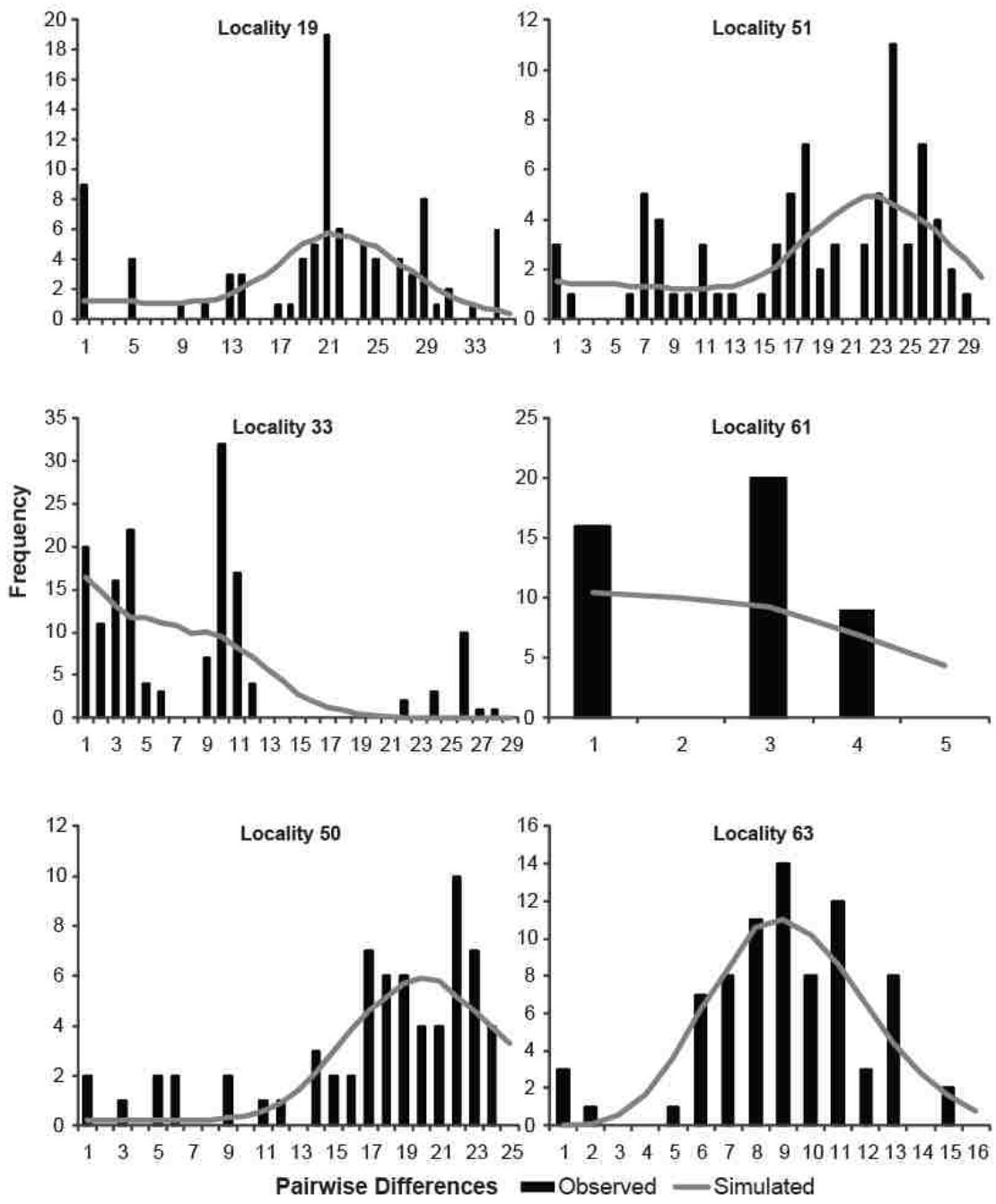
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CHAPTER 3

CLIMATIC PROMOTION OF NICHE SHIFTS: A CASE STUDY OF THE DESERT HORNED

LIZARD (*PHRYNOSOMA PLATYRHINOS*).

Abstract

During climate change, species are often assumed to shift geographic distributions

by tracking environmental conditions to which they are adapted while maintaining their

niches, generally referred to as niche conservatism. To test this assumption, I used

mitochondrial DNA and climatic niche assessments to evaluate response to climate

changes following the Last Glacial Maximum (LGM) in the desert horned lizard

(*Phrynosoma platyrhinos*). The phylogeographic analysis indicated persistence of *P.

platyrhinos* through climate changes within the southern Mojave and Sonoran deserts

and a recent expansion from these deserts into the Great Basin in western North

America, likely following warming climate after the LGM. Assessment of climatic niche

similarity revealed that populations within the Great Basin occupy a different climatic

niche (colder and wetter) with respect to the southern, persistent populations.

Additionally, my assessment inferred that the climatic niche within the southern regions

during the LGM did not reach the temperature and precipitation extremes that *P.

platyrhinos* experiences within the Great Basin today. I hypothesize that climatic

changes at the end of the LGM opened novel niche space within the Great Basin that

promoted a niche shift in these lizards.

Introduction

The burgeoning awareness of global climate change has focused the attention of

biologists on species responses to past, current, and potential future climatic changes

(Coetzee *et al.* 2009; Galbreath *et al.* 2009; Peterson *et al.* 2004; Thuiller *et al.* 2008;

Waltari *et al.* 2007). A general assumption underlying the interplay between current and

past models of species response has been that during climate change, the climatic niche

of a species (the range of climate conditions utilized by the species) remains relatively

stable and thus its geographic range 'shifts' by tracking the climate to which it is

adapted (Davis & Shaw 2001; Pearman *et al.* 2008; Wiens & Graham 2005). Such niche

conservatism *sensu stricto*, also called niche identity (Warren *et al.* 2008), has been a

working assumption for climatic niche assessments at time scales across the Last Glacial

Maximum, Middle Holocene, the pre-industrial era, and into the foreseeable future. The

departure from niche conservatism is a niche shift, a response that has been implicated

in episodes of rapid species diversification (i.e., upon entering a new geographic space

or adaptive zone), but that has often been considered negligible in species responses to

recent climatic changes (Ackerly 2003b).

In general, a niche shift can result from a shift in the fundamental niche (the full

spectrum of environmental factors that can be potentially utilized by an organism) or

the realized niche (a subset of the fundamental niche actually used by the organism,

restricted by historical and biotic factors; Araujo & Guisan 2006; Pearman *et al.* 2008).

Niche shifts resulting from an alteration of the realized niche (Jackson & Overpeck 2000;

Rodder & Lotters 2009) do not require evolutionary adaptation as species responses

may result from shifts in the realized environment , plasticity of traits (e.g. physiological,

behavioral) or through spatial segregation of individuals with certain functional traits

into populations following a process of ecological sorting (Ackerly 2003a, b).

Alternatively, the fundamental niche of a species can be shifted or broadened to meet

new environmental conditions through evolutionary adaptation (Davis & Shaw 2001;

Davis *et al.* 2005; Urban *et al.* 2007). The shift of fundamental niche (evolutionary

adaptation) can be difficult to distinguish from realized niche shift (plasticity or spatial

segregation) as both can arise from the same underlying processes and may even

accompany each other (Csuti 1979).

   Niche shifts (either realized or fundamental) have been shown to be triggered by

changes in biotic interactions through time or space, such as ecological release from

predators or competitors (Holt *et al.* 2005) or by access to novel combinations of

environmental variables (Ackerly 2003b; Jackson & Overpeck 2000; Nogues-Bravo 2009;

Rodder & Lotters 2009). Invasive species often undergo niche shifts, which may result

from differences in biotic and abiotic conditions experienced between native and

introduced ranges (Broennimann *et al.* 2007; Rodder & Lotters 2009; Urban *et al.* 2007).

Niche shift has also been shown in native populations responding to climatic changes

(Davis & Shaw 2001; Davis *et al.* 2005). Novel environmental conditions with no known

historical analog are often formed during climate change, creating a spectrum of new

habitats to individuals capable of exploiting the novel environment through shifts in

their realized or fundamental niches. Environmental changes resulting from glacial-

interglacial climatic oscillations throughout the Late Pleistocene are known to have had

pronounced impacts on species ranges and genetic structure (Hewitt 1996, 2000);

however, little is known about whether these climatic changes promoted niche shifts,

and whether certain areas, time periods, or taxa are more or less prone to such

responses in a predictable fashion.

In this study, I evaluate whether climatic changes at the end of the Last Glacial

Maximum (LGM; ca. 21,000 years ago; Harrison 2000), which expanded arid habitats

within the western deserts of North America, promoted a climatic niche shift in the

desert horned lizard (*Phrynosoma platyrhinos*). I follow up on two previous studies of

this species in which recent (post-LGM) northward range expansion into the Great Basin

was indicated from the more southern Mojave and Sonoran deserts (Jones 1995;

Mulcahy *et al.* 2006). I assess the phylogeography of *P. platyrhinos* to evaluate the

extent of population persistence within regions throughout the LGM and to detail the

recent expansion northwards. I then conduct a climatic niche analysis based on

temperature and precipitation variables to explore whether the recently expanding

populations occupy a different climatic niche than more southern populations that likely

persisted throughout climatic changes. Importantly, *P. platyrhinos* could have expanded

its range from areas of the Mojave and Sonoran deserts into the Great Basin without a

niche shift, if its current climatic niche within the Great Basin existed in the south during

the LGM and then expanded northward at the end of this major climatic event. This

would have allowed *P. platyrhinos* to expand its geographic range by tracking the

climate to which it was already adapted. To explore this possibility, I project climatic

niche models (CNMs) of recently expanding populations to climatic simulations of LGM

conditions (Harrison 2000), and evaluate the prospect that current climatic niches in the

Great Basin was mirrored by equivalent conditions during the LGM within more

southern latitudes. Finally, I compare climatic niches of persistent and expanding

populations of *P. platyrhinos* to the parapatric congeneric species, *P. douglasii* and *P.*

hernandesi, that also occupy portions of the Great Basin. I predict that when novel

environmental conditions form new potential habitat after a major climatic event,

species inhabiting the ecologically closest, and geographically most proximal, niche

would be most likely to exploit the new space. In other words, I predict that the current

CNMs of the northward expanding populations of *P. platyrhinos* will be more similar to

the CNM of the persistent, southern populations of *P. platyrhinos* than to those of *P.*

douglasii and *P. hernandesi.* In this study, I generally do not distinguish between shifts in

fundamental niche from shifts in realized niche; however, I do discuss and propose

hypotheses about both types of a niche shift when appropriate.

Methods

Study organism

Phrynosoma platyrhinos is one of 17 currently recognized species within the horned

lizard genus (Luxbacher & Knouft 2009), all of which occur in western North America. In

general, species of *Phrynosoma* tend not to occur in sympatry (Dumas 1964; Leache &

McGuire 2006; Luxbacher & Knouft 2009; Montanucci 1981). *Phrynosoma platyrhinos*

appears to be part of a species complex with taxa distributed from the northwestern

Sonoran Desert through the Mojave and Great Basin deserts (Fig. 3.1). Based on

60

mitochondrial (mtDNA) sequence data and morphology, Mulcahy *et al*. (2006) found

that southeastern populations of *P. platyrhinos* south of the Gila River represented a

distinct lineage, which they referred to as *P. goodei.* Mulcahy *et al.* (2006) also identified

another population quite divergent from *P. platyrhinos* from the Yuma Proving Grounds

(La Paz County, Arizona) along the east side of the Lower Colorado River Valley, but this

lineage was not assigned any particular taxonomic status. *Phrynosoma goodei* was

shown to hybridize with the flat-tailed horned lizard, *P. mcallii,* and as *P. goodei* appears

morphologically intermediate between *P. mcallii* and *P. platyrhinos,* Mulcahy *et al.*

(2006) speculated on a potential ancient hybrid origin for *P. goodei.*

<u>Taxon sampling</u>

For genetic assessments I acquired samples from 216 individuals of my target taxa

from 104 localities: 198 samples from 96 localities of *P. platyrhinos*, five samples from

one locality of the divergent lineage at the Yuma Proving Grounds, and 13 samples from

seven localities of *P. goodei* (Fig. 3.1A; Appendix 2). I included a sample of *P. mcallii* as

an outgroup based on its mtDNA similarity to *P. platyrhinos* (Leache & McGuire 2006;

Mulcahy *et al.* 2006). Overall, 30 samples were represented by sequences from

GenBank (Mulcahy *et al.* 2006), 19 samples came from museums, and the remaining

samples were obtained from specimens specifically captured for this study or accessed

from the previous study of Jones (1995). I mostly obtained samples from tail- or toe-

clips and then released the animals at the capture site (following a protocol approved by

the Animal Care and Use Committee, University of Nevada, Las Vegas).

For niche assessments and niche modeling, I compiled additional occurrence information for *P. platyrhinos* as well as the parapatric species *P. douglasii,* and *P. hernandesi* (Fig. 3.1A, B). Museum records for the occurrence of *P. platyrhinos* were obtained (on 12 February 2009) from HerpNET (http://herpnet.org) and the Collections Database of the Museum of Vertebrate Zoology, University of California (http://mvzarctos.berkeley.edu). All records missing geographic coordinates and records with geographic uncertainty greater than 5 km were excluded. Occurrence records for *P. hernandesi* and *P. douglasii* followed those reported by Jezkova *et al.* (2009a). Because *P. hernandesi* is widespread and occupies a range of different habitats, the dataset was restricted to samples from a monophyletic mtDNA clade occurring in the Great Basin and Colorado Plateau as identified by Zamudio *et al.* (1997).

<u>Laboratory methods</u>

I isolated total genomic DNA from tissues following a phenol-chloroform protocol or using a DNeasy Extraction Kit (Qiagen Inc.). I amplified and sequenced the mitochondrial NADH dehydrogenase subunit 4 (ND4) gene and adjacent tRNA for all samples using primers ND4 and Leu (Arevalo *et al.* 1994). For the phylogenetic analyses, I also amplified and sequenced a portion of the Cytochrome B (cytB) for a subset of samples using primers MVZ 49 and MVZ 14 (Roe *et al.* 1985). I updated amplification protocols through time, but most were accomplished at a 55°C annealing temperature using Takara Ex Taq Polymerase Premix (Takara Mirus Bio, Inc.) followed by purification using ExoSap-IT (USB Corp.). I conducted double-stranded cycle sequencing using fluorescence-based chemistry (BigDye Terminator v. 3.1 Cycle Sequencing Kit) with

electrophoresis and visualization on an ABI Prism 3130 automated sequencer (Applied

Biosystems, Inc.). I aligned sequences using SEQUENCHER (v. 4.6; Gene Codes Corp.) and

verified the alignment visually.

<div align="center">Phylogenetic analyses</div>

I conducted phylogenetic analyses using Maximum likelihood (ML) and Bayesian

inference (BI) on a combined dataset of 1089 base pairs (bp) of cytB, 684 bp of ND4, and

128 (or 129) bp of adjacent tRNA for a subset of samples including 21 *P. platyrhinos*, 3

specimens from the Yuma Proving Grounds, 2 *P. goodei,* and a sample of *P. mcallii*.

These samples were chosen to represent the major nested clades of *P. platyrhinos*

identified from the haplotype network (see below). Prior to BI and ML analyses, I

partitioned the dataset variously by gene and codon position (including unpartitioned)

and identified best-fitting models for each partition using MRMODELTEST (v. 2.2(Nylander

2004)under the Akaike Information Criterion (Posada & Buckley 2004). To evaluate

partitions, I ran each partition in MRBAYES (v. 3.1.2; Ronquist & Huelsenbeck 2003) for 5

million generations and compared marginal likelihood scores using Bayes factors (Kass &

Raftery 1995; Table 3.1). For final analyses of BI and ML, I used the HKY+I+Γ model for

the 1st+2nd codon positions of ND4 and cytB, GTR+ Γ model for the 3rd codon position of

ND4 and cytB, and the HKY+I model for the tRNA regions. I assessed the tree topology

and clade support in MRBAYES from consensus trees and posterior probabilities of 3 final

runs of 10 million generations each, sampled every 100 generations, with the first 2.5

million generations (25,000 trees) discarded as burn-in after assessing stationarity by

plotting log-likelihood scores against generations (Leache & Reeder 2002). I conducted

ML analyses in TREEFINDER (Jobb *et al.* 2004) using the "Bootstrap Analysis" option with

1,000 replicates and consensus level 50 to assess nodal support.

I constructed a median-joining network (a maximum parsimony approach) on the

concatenated data (812 bp) of partial ND4 and adjacent partial tRNA using the program

NETWORK (v. 4.5.1.0; Bandelt *et al.* 1999) for 216 sequences of *P. platyrhinos* including

samples from the Yuma Proving Grounds and *P. goodei*. To construct the final network, I

weighted transversions twice as high as transitions. After generating the network, I

employed the MP option (Polzin & Daneshmand 2003) to remove excessive links from

the network. For visualization purposes, I nested the haplotype network (Templeton *et

al.* 1987; Templeton & Sing 1993). I also calculated haplotype and nucleotide diversity

for the clades of *P. platyrhinos* using ARLEQUIN (v. 3.11; Excoffier *et al.* 2005).

<u>Historical demography</u>

I defined the 'core clade' of *P. platyrhinos* to exclude the more distantly related

samples from the Yuma Proving Grounds and *P. goodei* (see Phylogenetic analyses

results), and then analyzed past demographic changes. I assessed the concatenated ND4

and tRNA data using the Bayesian skyline plot (BSP) coalescent model (Drummond *et al.*

2005) implemented in the program BEAST (v. 1.5.3; Drummond & Rambaut 2007). I

employed the Bayes factor test (Newton *et al.* 1994; Suchard *et al.* 2001) implemented

in TRACER (v. 1.5; Rambaut & Drummond 2007) to assess partitioning and chose to

partition by genes and codon positions. Following assessment in MRMODELTEST, I

selected substitution models GTR+I+ Γ for the 1st+2nd codon positions of ND4, GTR+ Γ

for the 3rd codon position of ND4, and HKY+I for the tRNA. I used a strict molecular clock

after assessing for clock-like behavior (Drummond *et al*. 2007), a general mtDNA

substitution rate of 1% /lineage/million years available from the literature (Macey *et al.*

1999), 5 skyline groups, and a 2-year generation time (Pianka & Parker 1975). I

conducted several independent Markov Chain Monte Carlo (MCMC) runs of 80 million

generations, each with sampling every 8000 generations and a burn-in of 10%. For final

analysis, four MCMC runs (all with similar results) were combined using LOGCOMBINER

(distributed with BEAST). I checked convergence (effective sample sizes > 200) and

visualized the median and 95% highest posterior density intervals using TRACER.

Niche similarity comparisons between persistent and expanding populations

I conducted climatic niche comparisons following the methodology of Rissler and

Apodaca (2007) and Kozak and Wiens (2006) among geographically persistent versus

recently expanded populations of *P. platyrhinos* in order to evaluate whether the latter

exhibit a significantly different climatic niche. I assigned each sampling locality to

persistent or expanding groups of populations based on genetic patterns (see Results for

patterns). I also used museum records, assigning specimens to a particular persistent or

recently expanded group if the record was geographically located within the minimum

convex polygon of all genetically sampled localities that belonged to that group.

Museum records that fell outside all polygons were discarded from the analysis.

Minimum convex polygons for groups partly overlapped (Fig. 3.1B), thus not all localities

were independent in the analyses. From each occurrence record I extracted values from

19 bioclimatic variables (Kozak & Wiens 2006; Waltari *et al*. 2007) derived from the

WorldClim dataset (v. 1.4) with resolution of 2.5 minutes (Hijmans *et al.* 2005).

In Systat (v.12; Hilbe 2008), I conducted a Principal Component Analysis (PCA) to reduce the 19 bioclimatic variables, some of which are correlated (Kozak & Wiens 2006), to principal components (PCs). Factor scores of PCs with eigenvalues >1 were saved. After confirming that PC scores were normally distributed, I ran unbalanced ANOVA based on Type III sums of squares with PCA axis scores as dependent variables and the groups as fixed factors to test for the separation of population groups into different climatic niches. I used Post hoc Tukey tests to compare the least square means of each PC.

<u>Evaluation of a niche shift in *P. platyrhinos*</u>

In order to evaluate whether range shifts in *P. platyrhinos* were accompanied by niche shifts, I used climatic niche modeling (more broadly referred to as ecological niche modeling) to assess whether the climatic niche currently occupied by the expanding populations of *P. platyrhinos* had an equivalent during the LGM within the more persistent southern areas. This analysis was conducted under the assumption that the modeling approach was capturing climatic niches at a scale of resolution sufficiently relevant to species biology and ecology (see Discussion). I used the software package Maxent (v. 3.2.1; Phillips *et al.* 2006) to reconstruct current climatic niches and project those onto the climatic reconstructions of the LGM. Maxent implements a maximum entropy algorithm to model the niche of a species from data on species occurrence (presence-only data) and environmental variables. For occurrence records, I used the same persistent and expanding groups as in the climatic niche similarity assessment. For environmental layers of current climatic conditions, I started with the same 19

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bioclimatic variables used in the previous assessment that were clipped to the extent of

western North America. Because some of the 19 bioclimatic variables are correlated

(Kozak & Wiens 2006), I evaluated pairwise correlations on values extracted from the

presence records, and considered any two variables highly correlated when the

correlation coefficient was ≥ 0.9. Subsequently, I selected the following 13 variables for

building the CNMs: Bio2 - mean diurnal range, Bio3 - isothermality, Bio4 - temperature

seasonality, Bio5 - maximum temperature of warmest month, Bio6 - minimum

temperature of coldest month, Bio8 - mean temperature of wettest quarter, Bio9 -

mean temperature of driest quarter, Bio10 - mean temperature of warmest quarter,

Bio13 - precipitation of wettest month, Bio15 - precipitation seasonality, Bio17 -

precipitation of driest quarter, Bio18 - precipitation of warmest quarter, Bio19 -

precipitation of coldest quarter. I also explored selection of variables based on

perceived biological relevance to *P. platyrhinos* and model importance, but overall

model predictions were similar in all cases.

For environmental layers representing the climatic conditions of the LGM, I used the

current set of coupled ocean-atmosphere simulations (Harrison 2000) available through

the Paleoclimatic Modelling Intercomparison Project (PMIP; Braconnot *et al.* 2007).

PMIP has established a protocol followed by participating modeling groups for LGM

simulations regarding concentration of greenhouse gases, ice sheet coverage,

insolation, or change in topography caused by lowering sea levels. Of more than 15

available climatic models, I used the following two: Community Climate System Model

(CCSM v. 3; Otto-Bliesner *et al.* 2006) with a resolution of 1°, and the Model for

Interdisciplinary Research on Climate (MIROC v. 3.2; Hasumi & Emori 2004) with an

original spatial resolution of 1.4° x 0.5° (Braconnot *et al.* 2007). The original climatic

variables used in these models have been downscaled to the spatial resolution of 2.5

minutes under the assumption of high spatial autocorrelation and converted to

bioclimatic variables (Hijmans *et al.* 2005; Peterson & Nyari 2008).

I used the default parameters of MAXENT (i.e. 500 maximum iterations, convergence

threshold of 0.00001, regularization multiplier of 1, 10,000 background points) with the

following user-selected features: application of random seed, duplicate presence

records removal, logistic probabilities for the output (Phillips & Dudik 2008). Since I

were interested in the extent of analogous climates during two time periods, I used the

'do not interpolate' option in MAXENT. This option insures that the probability values for

the LGM variables are not going to be extrapolated beyond the range of values used for

model calibration. Therefore, my LGM models should not be interpreted as areas of

persistence for *P. platyrhinos*, but only as the extent of specific climatic combinations

during two time periods. I ran 10 replicates in MAXENT for each group (projected 10

times on each of the CCSM and MIROC climatic reconstructions), but present an average

model. Because the analyses are greatly dependent on the chosen threshold cut-off

values used for interpreting the CNMs, I evaluated across two extreme thresholds

corresponding to 0 and 10% omission error.

<u>Niche overlap between *P. platyrhinos* and parapatric species</u>

I used ENM tools (Warren *et al.* 2008) to assess the niche overlap between

persistent and expanding populations of *P. platyrhinos* with respect to *P. douglasii,* and

parapatric populations of *P. hernandesi*. The CNMs for all species were generated in

MAXENT as described above. I measured niche overlap among CNMs of taxa pairs using

the coefficient of niche similarity *D*, a metric for quantifying similarity of CNMs (Warren

et al. 2008). Values of *D* range from zero to one, where zero represents no overlap

between the CNMs of two taxa and one represents total (absolute) overlap. I then

conducted randomization tests of 50 pseudoreplicates where the records of each pair

are randomly partitioned and overlap is calculated using D. From the 50

pseudoreplicates, I built a null distribution of D that was compared to the observed

value of D. A one-tailed test was used to evaluate the hypothesis that observed D is

drawn from a statistical population that has a mean that is significantly different than

that of the random D.

Results

Phylogenetic and network analyses

Assessments using ML and BI methods based on a subset of haplotypes produced

identical tree topologies with similar nodal support based on posterior probabilities and

bootstrap values (Fig. 3.2). The inferred topology shows a strongly supported core clade

of *P. platyrhinos* with *P. goodei* as the sister clade, and samples from the Yuma Proving

Grounds appearing as a clade outside this group. The basal position of the Yuma Proving

Grounds clade, however, was not strongly supported, and the relationship could be

interpreted as a polytomy of three strongly supported clades. These results are

consistent with patterns identified by Mulcahy *et al.* (2006) for the same taxa. Within

the core clade of *P. platyrhinos*, I identified three well-supported subclades which I refer to as the Western, Northeastern, and Southeastern clades (Fig. 3.2, 3.3).

I identified 120 unique haplotypes from 216 sequences (812 bp of ND4+tRNA) representing *P. platyrhinos, P. goodei*, and samples from the Yuma Proving Grounds. Most haplotypes were represented by 1–4 samples with the exceptions of the abundant and widespread haplotypes Hw1, Hw2, He1, and He2 which give rise to numerous satellite (newly evolved) haplotypes (Fig. 3.3). Using nesting rules, I identified 15 four-step clades (Fig. 3.4). Clade 1 corresponds to the 5 animals collected from the Yuma Proving Grounds, and clades 2 and 3 correspond to individuals of *P. goodei*. Clade 4 represents all other samples from Arizona east of Colorado River with the exception of the sample from locality 12 (Fig. 3.1A, 3.4). Clades 5, 7–10, 12–14 are mainly distributed within the Mojave and northwestern Sonoran deserts, west of the Colorado River, in California, Nevada, Utah and northern Baja California (Fig. 3.4). Clade 15 was represented by one individual from the House Rock Valley in Arizona. The clades in the Mojave and northwestern Sonoran deserts overlap geographically and each clade exhibits numerous diverse and geographically restricted haplotypes. Within the southern deserts, haplotype and nucleotide diversities were relatively high (0.992 and 0.022, respectively) indicative of long-term persistence within the area (Hewitt 1996, 2000).

Clade 6 can be found within the northern Mojave Desert and within the western Great Basin. The haplotype Hw2 in clade 6 and its satellite haplotypes comprise all individuals from the southwestern Great Basin, and Hw1 and its satellite haplotypes

comprise all individuals in the northwestern Great Basin (Fig. 3.4). Similarly, clade 11

extends from the eastern Mojave Desert into the eastern Great Basin with widespread

haplotypes He1 and He2, and their satellite haplotypes, comprising those in the

northeastern and southeastern Great Basin respectively (Fig. 3.4). This structure is most

often indicative of a recent range expansion, when a subset of haplotypes (in this case

Hw1, Hw2, He1, He2) expands across large areas from the source haplotype group

followed by emergence of new mutations (see Discussion). Accordingly, these areas

dominated by one of the four abundant and widespread haplotypes were likely

colonized by *P. platyrhinos* only recently. Across the Great Basin, haplotype and

nucleotide diversities were lower (0.877 and 0.016, respectively), despite the presence

of the two quite divergent clades (6 and 11) within this overall region.

Historical demography

To estimate the starting time for growth of genetic diversity relative to the last

glacial period (Late Pleistocene) I used the BSP analysis and a general mutation rate of

1% /lineage/million years. The plot (Fig. 3.5) indicates a rapid and recent increase in

genetic diversity, which is consistent with recent population expansion. This increase in

genetic diversity appears to have begun accumulating sometime during the latest glacial

period, but I cannot rule out a post-glacial expansion.

Niche similarity comparisons between persistent and expanding populations

I assessed climatic niche similarity between areas occupied by persistent populations

and the areas that exhibit signals of recent range expansion. I analyzed the eastern and

western expanding populations separately as each represents a different genetic clade

(Fig. 3.4). In the expanding western (Ew) group, I included haplotypes Hw1, Hw2 and

their satellite haplotypes from clade 6, and in the expanding eastern (Ee) group, I

included haplotypes He1, He2 and their satellite haplotypes from clade 11 (Fig. 3.1B).

Although satellite haplotypes can be identified visually as they cluster around ancestral

nodes, I also used a star contraction method in NETWORK to confirm such clusters

(Forster *et al.* 2001). Other haplotypes in clades 6 and 11 from more southern areas

were excluded from the analysis, as these did not exhibit a clear signal of range

expansion. The remaining clades from the southern deserts that exhibit high genetic

diversity were assigned to the Persistent group (excluding clades 1-3, as these represent

more distantly related *P. goodei* and Yuma Proving Grounds animals). The final

occurrence dataset included 165 records in the Persistent group, 65 occurrence records

in the Ew group, and 25 occurrence records in the Ee group.

PCA reduced the 19 bioclimatic variables to four PCs with eigenvalues ≥1 that

explained 50.9, 25.0, 9.6, and 5.8 percent of the total variance, respectively. The

scatterplot for the first two PCs shows separation between the persistent and the

expanding groups with the latter experiencing (on average) lower temperatures, greater

temperature seasonality, greater annual range in temperature, higher precipitation, and

lesser seasonality in precipitation (Fig. 3.6A). The ANOVA showed significant differences

in least square means for all four PCs (for all tests, $P < 0.05$; Fig. 3.6B), and the pairwise

Tukey tests (Table 3.2) revealed that the PCs could be used to easily differentiate among

the groups.

Evaluation of a niche shift in *P. platyrhinos*

The CNM for the Persistent group in general did not over-predict the current climatic niche into areas now occupied by the expanding populations, although some areas within the southwestern Great Basin were predicted as suitable using the more liberal (0% omission) threshold (Fig. 3.7A). The model based on a zero omission threshold also over-predicted into areas currently occupied by congeneric species (i.e. P. goodei, P. mcallii, and P. blainvillii; Fig. 3.7B). For the expanding groups within the Great Basin (Ew and Ee), the thresholds used resulted in little difference in overall outcomes of the models. The CNM for the Ew group captures the distribution of the group within the western part of the Great Basin (Fig. 3.7B). The CNM based on the Ee group correctly captures the eastern Great Basin, but over-predicts across the western Great Basin, as well as to the east into the Colorado Plateau where P. platyrhinos is not known to occur (Tanner 1999).

The LGM projections for the Persistent group (Fig. 3.7D,G) show retention of the climatic niche within areas of current range, although the overall extent is substantially restricted, especially in the MIROC model (Fig. 3.7G). The LGM projections of climatic niches for the Ew and Ee groups were greatly reduced in size (Fig. 3.7E,F,H,I). The LGM projections for the Ew group shows retention of the current climatic niche only within small patches in the western Great Basin (CCSM, Fig. 3.7E) and Columbia Plateau (MIROC, Fig. 3.7H). Only the CCSM model projects the Ew climatic niche to a small area in the Sonoran Desert currently occupied by the Persistent group, but within the area covered by the Pleistocene Lake Cahuilla (Fig. 3.7E). The LGM projections for the Ee

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group shows displacement of the current climatic niche to the western Great Basin (CCSM, Fig. 3.7F) and some additional areas within the northeastern Great Basin (MIROC with the less conservative threshold only), although this area was covered predominately by the pluvial Lake Bonneville. The Ee climatic niche does not project to the areas currently inhabited by the Persistent group.

<u>Niche overlap between *P. platyrhinos* and parapatric species</u>

Using the measure D, I could reject the hypothesis of niche identity ($P < 0.001$) for all pairs of taxa. In general, the climatic niche overlaps (Table 3.3) between the persistent and expanding groups of *P. platyrhinos* were relatively low ($D = 0.11$ and 0.24), indicating dissimilarity in climatic regimes. Niche overlap between the two expanding groups of *P. platyrhinos* was relatively high ($D = 0.44$), despite the fact that there is no geographic overlap between the ranges. The overlaps of the expanding groups with parapatric *P. hernandesi* were also high ($D = 0.53$ and 0.32), while overlaps with *P. douglasii* were slightly lower ($D = 0.27$ and 0.32).

Discussion

<u>Phylogeographic analyses</u>

Within areas of the Mojave and Sonoran deserts, *P. platyrhinos* exhibits pronounced genetic structuring and high genetic diversity (Fig. 3.4) consistent with population persistence. The levels of genetic diversity and structure in *P. platyrhinos* appear higher in comparison to genetic patterns documented in several other warm-desert taxa that were interpreted as an evidence of geographically restricted glacial refugia in northern

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regions during the Late Pleistocene (Castoe *et al.* 2007; Douglas *et al.* 2006; Jezkova *et al.* 2009b; Murphy *et al.* 2006). The genetic patterns of *P. platyrhinos* indicate that the species probably remained quite widespread throughout much of the northern Sonoran Desert and maintained populations within portions of the Mojave Desert despite the climatic changes of the Late Pleistocene.

Populations of *P. platyrhinos* within the Great Basin exhibit low genetic diversity and little genetic structure indicative of recent range expansion from areas of persistence in the south. Within the Great Basin, the haplotype network shows a few central, abundant, and widespread haplotypes surrounded by numerous, low frequency haplotypes separated by one or a few mutational steps (Fig. 3.3), with the satellite haplotypes being geographically restricted. This pattern is consistent with leading edge colonization where the range expansion involves random subsets of individuals from the populations at the colonization front (Excoffier *et al.* 2009; Hampe & Petit 2005; Hewitt 1993; Hewitt 2000). The genetic evidence suggests that *P. platyrhinos* expanded along two different low elevation colonization routes into the Great Basin, one along an eastern corridor into the Bonneville Basin and the other along a western corridor into the Lahontan Basin. These expansions involved individuals from two different clades, with clade 6 expanded along the western front and clade 11 along the eastern front. As envisioned for leading edge colonization, genetic diversity typically decreases in the direction of expansion due to loss of haplotypes through founder effects (thinning of haplotypes; Hewitt 1996). The northward expansion in *P. platyrhinos* clearly exhibits this pattern with only haplotypes from clades 6 and 11 evident in samples from above 38° of

latitude and only single ancestral haplotypes, Hw1 and He1, found above 39° of latitude

along each of the two expansion routes (Fig. 3.4). Under this expansion scenario,

populations grow exponentially and private mutations typically become fixed with

higher frequency in the newly invaded areas. Such newly evolved satellite haplotypes

are evident around each of the four ancestral haplotypes associated with the range

expansions (Fig. 3.3). Recent population expansion in *P. platyrhinos* is also consistent

with the pattern exhibited in the coalescent assessment of the sequence data presented

in the BSP (Fig. 3.5).

The expansion of *P. platyrhinos* into the Great Basin likely followed warming climate

and desiccation of pluvial lakes at the end of the LGM. Such northward expansion of

warm-desert organisms is not unique to *P. platyrhinos* as similar patterns have been

documented or proposed in several plant and animal taxa (Hockett 2000; Mulcahy 2008;

Pavlik 1989). My coalescent assessment of the sequence data under the presumed

mutation rate estimates the timing of the expansion to the latest glacial period (Fig.

3.5), but prior to the LGM time frame. Only a slightly faster mutation rate, however,

would need to be assumed for the assessment to be consistent with post-Pleistocene

expansion (Galbreath *et al.* 2009).

Niche similarity comparisons between persistent and expanding populations

Climatic niche comparisons revealed that the recently expanding populations of *P.

platyrhinos* within the western and eastern Great Basin occupy a different climatic niche

than that of the persistent populations in the Mojave and Sonoran deserts. Individuals

from the expanding populations within the Great Basin experience on average higher

precipitation and lower temperatures than individuals from the southern populations

(Fig. 3.6; 3.8). *Phrynosoma platyrhinos* within the eastern Great Basin experience the

most extreme conditions with the lowest temperatures, largest annual temperature

range, and highest precipitation (Fig. 3.8). These climatic differences likely impact

latitudinal shifts in ecological, behavioral, and physiological traits. For example, northern

animals may compensate for a colder climate behaviorally (Kearney *et al.* 2009) by

shifting activity periods and occupying microhabitats with suitable thermal conditions

(e.g. basalt formations), or physiologically by lowering active body temperatures

(Monasterio *et al.* 2009). Changes in mean body temperature may in turn affect life

history traits such as growth rate, body size, and reproductive rate (Sears & Angilletta

2004). Indeed, there is evidence that populations of *P. platyrhinos* in the Great Basin

exhibit increased sexual size dimorphism, shorter breeding season, smaller number of

clutches per season, and possibly larger clutch size than populations within the southern

deserts (Pianka & Parker 1975). Such latitudinal shifts in natural history traits are not

unique and have been documented in many reptilian taxa (Fitch 1985; Iverson *et al.*

1993).

Whether *P. platyrhinos* has reached its tolerance limits for climatic variables is not

entirely clear. Interestingly, I found *P. platyrhinos* near Elko, NV (Fig. 3.1, locality 58),

although only *P. hernandesi* has been reported from this higher elevation area in the

past (Jezkova *et al.* 2009a). I speculate that *P. platyrhinos* has invaded this area only

within the last few decades, either following a further shift in tolerance limits for

climatic variables or in response to a subtle but favorable shift in regional climate. The

haplotype (He1) identified in the two samples from Elko belong to the eastern clade,

even though the area is geographically closer to known occurrence records for *P.

platyrhinos* from lower elevations to the west that are likely occupied by individuals

from the western clade (Fig. 3.1, locality 68 and occurrence records between localities

58 and 68) and that are connected to the Elko site by a potential dispersal corridor along

the Humboldt River. I speculate that the individuals from the eastern clade, which on

average inhabit the most regionally extreme climatic conditions for the species (see

above), might have been better suited to invade the cold Elko area.

<u>Evaluation of a niche shift in *P. platyrhinos*</u>

The LGM models presented herein could possibly be interpreted as indicating areas

of potential persistence for *P. platyrhinos* within the Great Basin assuming that the

climatic niche between the two time periods was conserved. My genetic data, however,

indicate that *P. platyrhinos* did not persist within the northern regions during the LGM. I

use these models unconventionally to evaluate whether climatic conditions currently

occupied by the expanding populations of *P. platyrhinos* in the Great Basin had

equivalents during the LGM within the southern areas currently occupied by persistent

populations. If such patterns were found, then *P. platyrhinos* could have expanded its

range from the Mojave and Sonoran deserts into the Great Basin without a niche shift.

My projections, however, indicate that the climatic niches within the Great Basin

currently occupied by *P. platyrhinos* do not appear to have been predominately shifted

southwards during the LGM (Fig. 3.7). These results are in agreement with paleo-

environmental reconstructions, based on pollen and macrofossil data from packrat

middens, indicating that temperature and precipitation averages within large areas of the southern deserts never reached the climate extremes that *P. platyrhinos* currently experiences within the Great Basin. The paleo-environmental reconstructions suggest that the temperature in the Mojave Desert was on average 6°C colder and precipitation 40 % higher during the LGM than today (Spaulding 1990). In comparison, my niche assessment indicates that the current average annual temperature experienced by populations within the Great Basin is roughly 9°C lower than that of populations in the Mojave and Sonoran deserts, and annual precipitation within the areas occupied in the eastern Great Basin (Ee group) is almost 70 % higher than that for the areas occupied by the persistent populations (2.8). These patterns further support my interpretations from the CNMs and the hypothesis that *P. platyrhinos* did not just shift range in response to warming climate but that some *P. platyrhinos* experienced a niche shift in certain climatic variables that allowed the northward range expansions.

An important question to ask here is whether the postulated niche shift experienced by populations invading the Great Basin is biologically meaningful? As mentioned above, variability in ecological traits has been recorded between the northern and southern populations of *P. platyrhinos* (Pianka & Parker 1975) indicating that the species could have adapted to novel conditions through genetic differentiation and thereby expand its fundamental niche (Csuti 1979; Davis & Shaw 2001; Urban *et al.* 2007). Rapid climatic shifts at the end of the LGM are similar to conditions that species encounter during invasions to new areas. Novel niches with less competition promote rapid dispersal and expansion of populations, possibly followed by directional selection favoring those

individuals that are better adapted to the new environment (Ackerly 2003b; Broennimann *et al.* 2007; Davis & Shaw 2001; Pearman *et al.* 2008). Climatic changes at the end of LGM indeed appear to have produced new combinations of climatic variables within areas of the Great Basin, which had no substantial analog in southern regions during the previous glacial period. Therefore, these developing novel habitats may have promoted adaptation (Ackerly 2003b; Davis & Shaw 2001).

Alternatively, *P. platyrhinos* may exhibit phenotypic plasticity in various life history traits and could have simply expanded its realized niche to take advantage of changing environmental conditions that may well be within its existing range of tolerances (Jackson & Overpeck 2000; Rodder & Lotters 2009). Such a shift could also have been intertwined with a shift in realized environment (i.e. environmental conditions available at any given time; Ackerly 2003a,b; Hoffmann 2005; Jackson & Overpeck 2000). These shifts would not have necessarily required any significant adaptive changes in the biology of the species; common garden and reciprocal transplant experiments could be used to test between these alternatives. In any case, the niche shift in *P. platyrhinos* is interesting as several currently sympatric lizards within the Mojave and Sonoran deserts have not expanded into the Great Basin (e.g. *Dipsosaurus dorsalis*, *Sauromalus obesus*, *Heloderma suspectum*), and while there may be several factors related to these more limited distributions, possibly some species simply were not capable of the scale of niche shift documented in *P. platyrhinos*.

In this study, I focused on the niche shift of *P. platyrhinos* within the Great Basin; however, the niche of persistent populations within the Mojave and Sonoran deserts

has also likely shifted. In particular, following the end of the last glacial period, *P. platyrhinos* did not disappear from the low elevation valleys that now represent the hottest and driest parts of western North America. These areas are currently dominated by novel plant communities, creosote bush-white bursage desertscrub, that did not develop until Holocene times (Hunter *et al.* 2001; Spaulding 1990). This combination of extreme desert climate and novel plant communities apparently had no equivalent during the LGM (Spaulding 1990), although these areas now represent prime habitat occupied by *P. platyrhinos*, as well as many other warm-desert species.

The niche shift assessments conducted here critically depend on accurate climatic reconstructions of the LGM. The differences in the two LGM simulation models (CCSM and MIROC) generate quite different projections, indicating that current understanding of LGM climate as applied broadly is limited. The MIROC model predicts higher precipitation than the CCSM model (which appears to generate a more restricted climatic niche for the Persistent group within the Mojave Desert) but warmer temperatures (which appear to generate more extensive climatic niches for the expanding groups within the Great Basin). In general, interpolations and downscaling of the originally coarse climatic datasets may have produced severe errors or inaccuracies in the base data layers, especially in topographically diverse terrains such as the Great Basin. Further, neither the CCSM nor MIROC models take into account impacts of the large pluvial lakes on local or regional temperature and precipitation. Despite these potential inaccuracies, my interpretations of the overall results are consistent regardless of the model used, which indicates some robustness in my general findings.

Unfortunately, my approach only searches for the presence of climatic variable

combinations available during calibration and does not reveal which variables may have

actually shifted, to what extent, and the biological relevance of the shifts on *P.*

platyrhinos.

Niche overlap between *P. platyrhinos* and parapatric species

When a novel niche space opens up after a major climatic event, I might expect

the species inhabiting the ecologically closest and geographically most proximal niche to

be most likely to colonize the new environment. I predicted that the climatic niche of

the recently expanding populations of *P. platyrhinos* would be more similar to the

persistent southern populations than to *P. douglasii* and *P. hernandesi* from the Great

Basin. Conversely, my results indicate that the climatic niches currently occupied by the

expanding populations are more similar to that of *P. hernandesi* and *P. douglasii* than to

that of the persistent populations of *P. platyrhinos* (Table 3.3). In other words, given my

prediction, *P. hernandesi* and *P. douglasii* should have been more likely than *P.*

platyrhinos to populate parts of the Great Basin currently occupied by *P. platyrhinos*.

I do not have a direct explanation for this seeming contradiction, but offer

several (not mutually exclusive) hypotheses. First, it is possible that *P. platyrhinos*

directly outcompetes these other lizards. Competitive exclusion between *P. platyrhinos*

and *P. hernandesi*, and *P. douglasii* has not been tested, but some studies suggest that

competition between *Phrynosoma* species might exist despite different reproductive

strategies or diet preferences (Montanucci 1981; Pianka & Parker 1975). Second,

genetic constraints on adaptation (Davis *et al.* 2005) could possibly prevent *P.*

hernandesi and *P. douglasii* from adapting to warming climate or to some other (non-measured) factors that may favor *P. platyrhinos*. Lastly, ranges of many species expand at high latitudes and elevations, but contract at the warm margins in response to warming climate (Hewitt 2000; Merrill *et al.* 2008). The northward expansion of *P. platyrhinos* at the end of the LGM placed the northern populations on the leading edge of novel habitat where adaptation may be enhanced by the increased variability facilitated by gene flow from the centers of the range (Davis & Shaw 2001). Conversely, *P. hernandesi* and *P. douglasii* within the Great Basin were on the trailing edge during warming climate, where adaptation to the changing environment depends predominantly on variation within local populations (Davis & Shaw 2001). As has been hypothesized, changing environment could have produced deteriorating conditions for the trailing-edge populations, leading to population contraction or even extirpation (Davis & Shaw 2001; Hampe & Petit 2005). This leading versus trailing edge effect could have been most pronounced during the warm Middle Holocene when climate would have favored expansion of warm-desert species moving northward along the latitudinal gradients or upward along elevational gradients (Grayson 2000).

Conclusions

My analyses indicate that *P. platyrhinos* likely persisted within areas of the Mojave and Sonoran deserts through climatic oscillations of the Late Pleistocene. Conversely, this species only recently expanded into the Great Basin, likely following the warming climate along two low elevation corridors at the end of the LGM. The expanding populations did not just track expansion of suitable habitat, but appear to have

experienced niche shift that allowed populations of *P. platyrhinos* to exploit novel

(colder and wetter) environmental conditions. The biological mechanisms behind the

niche shift, however, remain unclear.

Table 3.1. Bayes factors for partitionings of the ND4+cytB+tRNA sequences of *Phrynosoma* taxa calculated in MRBAYES.

Partition	*N* of partitions	Model	Mean Marginal Likelihood Score	Bayes Factor
All together	1	GTR+I+ Γ	5919.62	
By gene	3	GTR+I+ Γ (cytB)	5914.47	10.3
		HKY+I+ Γ (ND4)		
		HKY+I (tRNA)		
By $1^{st} + 2^{nd}$, 3rd codon (tRNA unpartitioned)	3	HKY+I+ Γ ($1^{st} + 2^{nd}$)	5709.16	410.62
		GTR+ Γ (3rd)		
		HKY+I (tRNA)		
By gene and by $1^{st} + 2^{nd}$, 3rd codon(tRNA unpartitioned)	5	HKY+I ($1^{st} + 2^{nd}$ cytB)	5760.04	-101.76
		GTR+ Γ (3rd cytB)		
		HKY+I ($1^{st} + 2^{nd}$ ND4)		
		GTR+ Γ (3rd ND4)		
		HKY+I (tRNA)		

Table 3.2. Significant differentiation of the climatic niche represented by four principal components based on Tukey tests between the Persistent, expanding eastern (Ee) and expanding western (Ew) groups of *Phrynosoma platyrhinos*. Significant values are indicated in bold.

	Persistent				East expanding (Ee)			
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
East expanding (Ee)	**0.000**	**0.000**	0.956	**0.001**				
West expanding (Ew)	**0.000**	**0.000**	**0.000**	0.923	**0.000**	0.358	**0.003**	**0.001**

Table 3.3. Niche overlap measure using the index *D* between evaluated *Phrynosoma* taxa, with those of *P. platyrhinos* shown for the Persistent, expanding eastern (Ee), and expanding western (Ew) groups. *N* represents the number of occurrence records used to build climatic niche models.

	N	P. douglasii	P. hernandesi	Ee	Persistent	Ew
P. douglasii	17	x				
P. hernandesi	41	0.49	x			
Ee	25	0.27	0.53	x		
Persistent	165	0.12	0.07	0.11	x	
Ew	65	0.32	0.32	0.44	0.24	x

Figure 3.1. (A) General sample sites of *Phrynosoma platyrhinos*, *P. goodei* (localities 7, 13–17, 102) and *P. platyrhinos* from Yuma Proving Grounds (locality 2); closely situated samples without intervening physical barriers are grouped for visual interpretation and discussion. Grey circles represent occurrence records based on museum specimens and grey shadings represent ecoregions as adapted from (Olson *et al.* 2001). (B) Occurrence records used in the niche similarity comparison of *P. platyrhinos* and parapatric species *P. douglasii* and *P. hernandesi*. The shaded polygons represent Persistent, expanding western (Ew), and expanding eastern (Ee) groups of *P. platyrhinos* (see text for details).

Figure 3.2. Maximum likelihood tree for combined ND4, tRNA and cytB sequences for 22 unique haplotypes of *Phrynosoma platyrhinos*, 2 haplotypes of *P. goodei,* and 3 haplotypes of *Phrynosoma platyrhinos* from Yuma Proving Grounds. *Phrynosoma mcallii* was used as an outgroup. The three major clades of *P. platyrhinos* (Western, Southeastern, and Northeastern) are indicated. Nodal support from nonparametric bootstrap values are shown (numbers above), as are posterior probabilities from Bayesian inference (numbers below). The locality number for each sample is in parentheses.

Figure 3.3. Median-joining network of concatenated ND4 and tRNA sequences for *Phrynosoma platyrhinos*, *P. goodei,* and *P. platyrhinos* from Yuma Proving Grounds. Circle size and shading reflect the number of samples exhibiting a given haplotype ranging from 1 to 4, with several abundant haplotypes indicated by large circles labeled

internally with the number of samples. The length of connection lines between haplotypes is proportional to the number of mutational changes, with the shortest connection line representing a single mutational change.

Figure 3.4. Distribution of major nested clades (left) identified from the median-joining network (right) of the concatenated ND4 and tRNA sequences for *Phrynosoma platyrhinos*, *P. goodei,* and *P. platyrhinos* from Yuma Proving Grounds. Pie graph sizes in the map reflect the sample size at each location progressing from smallest (N = 1) to largest (N = 6). The clade numbers and color correspond to those on the median-joining network. The polygons represent the extent of the contracted expanding haplotypes in the western Great Basin (Hw1 and Hw2 indicated in green), and those in the eastern Great Basin (He1 and He2 indicated in pink).

Figure 3.5. Bayesian skyline plot derived from concatenated ND4 and tRNA sequences of *Phrynosoma platyrhinos.* The x-axis shows the time and the y-axis shows an index of genetic diversity assuming a 2-year generation time. The black line is the median for genetic diversity and the grey area represents the 95% upper and lower highest posterior density limits. The plot is presented truncated on the right as the extended region showed no evidence of change in genetic diversity.

Figure 3.6. (A) Scatter plot for the first two principal components derived from 19 bioclimatic variables for the Persistent group (white dots), expanding eastern (Ee) group (black dots), and expanding western (Ew) group (grey dots) of *Phrynosoma platyrhinos*.

(B) Least square means for the first four principal components derived from 19 bioclimatic variables for the three groups of *P. platyrhinos*.

Figure 3.7. Climatic niche models of the climatic niche for the Persistent group (left column), expanding western (Ew) group (center column) and expanding eastern (Ee) group (right column) of *Phrynosoma platyrhinos.* Rows represent the current climatic condition (first row), and two reconstructions of climatic conditions at the Last Glacial Maximum — CCSM (second row) and MIROC (third row). The light areas represent predicted suitable habitats using the minimum presence threshold (light green) and 10% omission (darker green). Dark blue areas represent the extent of pluvial lakes (Raines *et al.* 1996).

Figure 3.8. Least square means of four bioclimatic variables for the expanding western, expanding eastern and Persistent groups of *Phrynosoma platyrhinos*.

Figure 3.1

Figure 3.2

Figure 3.3

Western clade

Hw2

14

Hw1

26

He1

18

He2

Northeastern clade

Southeastern clade B

— 1 mutational step

○ 1 haplotype
◔ 2 haplotypes
◑ 3 haplotypes
● 4 haplotypes
(n) n haplotypes

Southeastern clade A

P. goodei

Yuma Proving Grounds
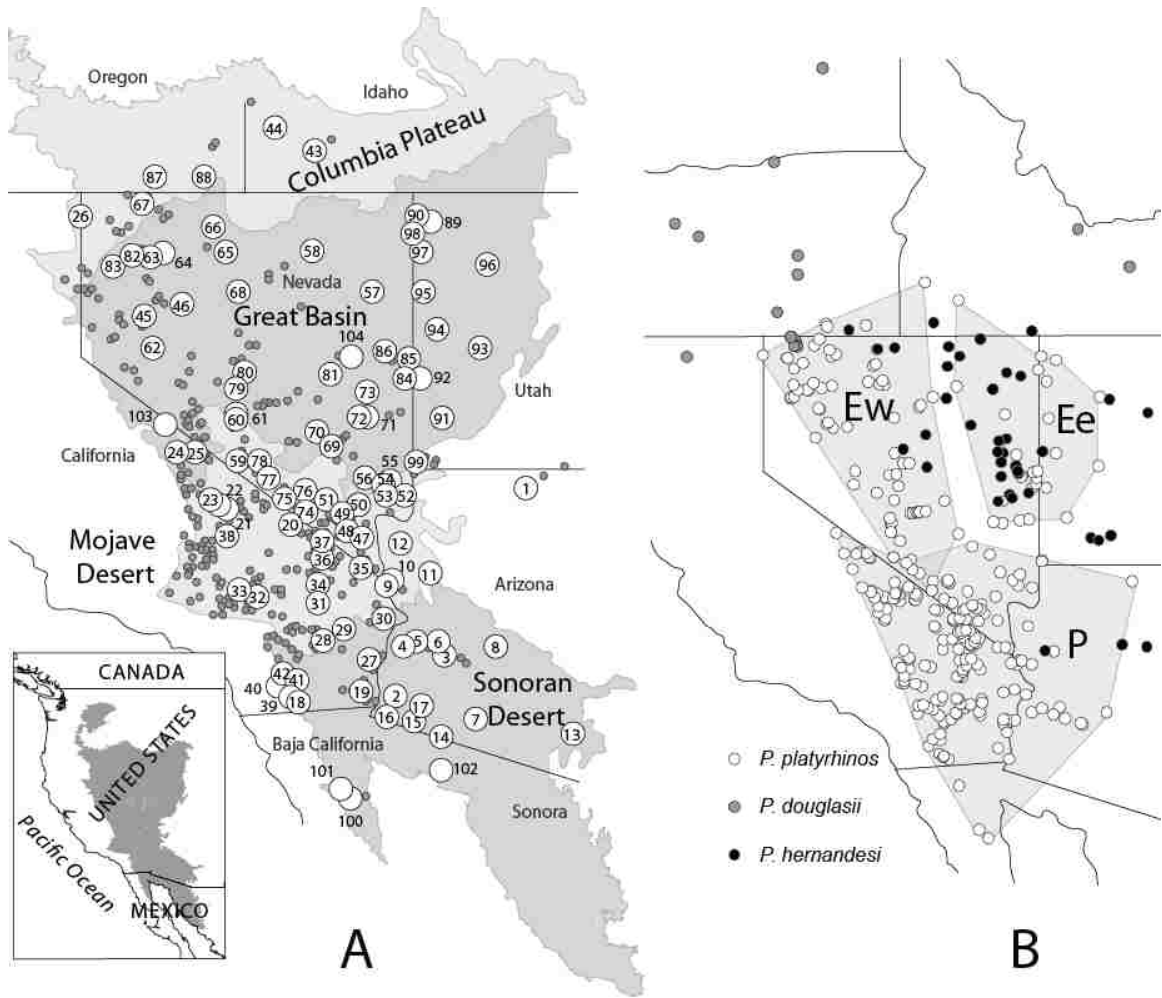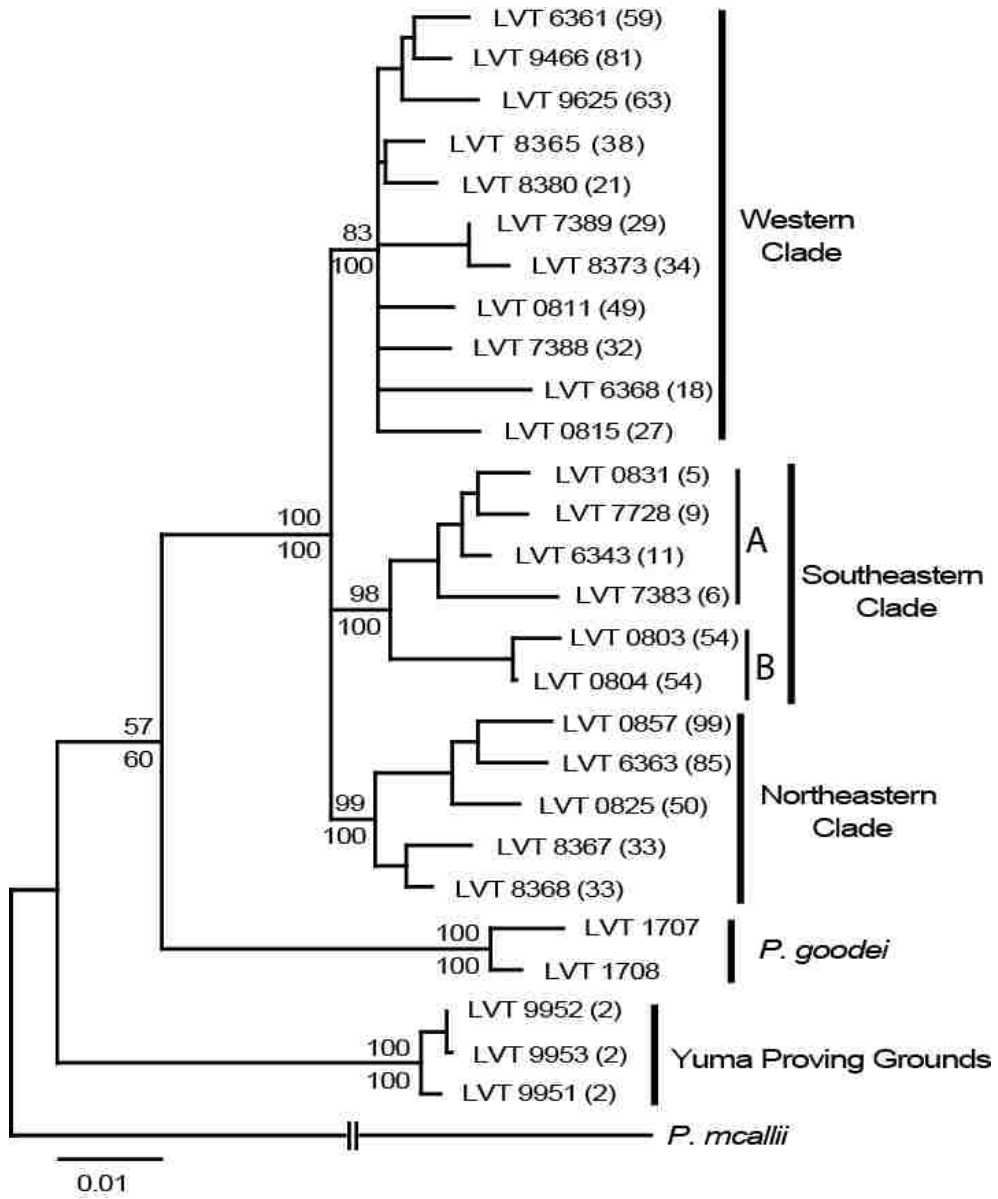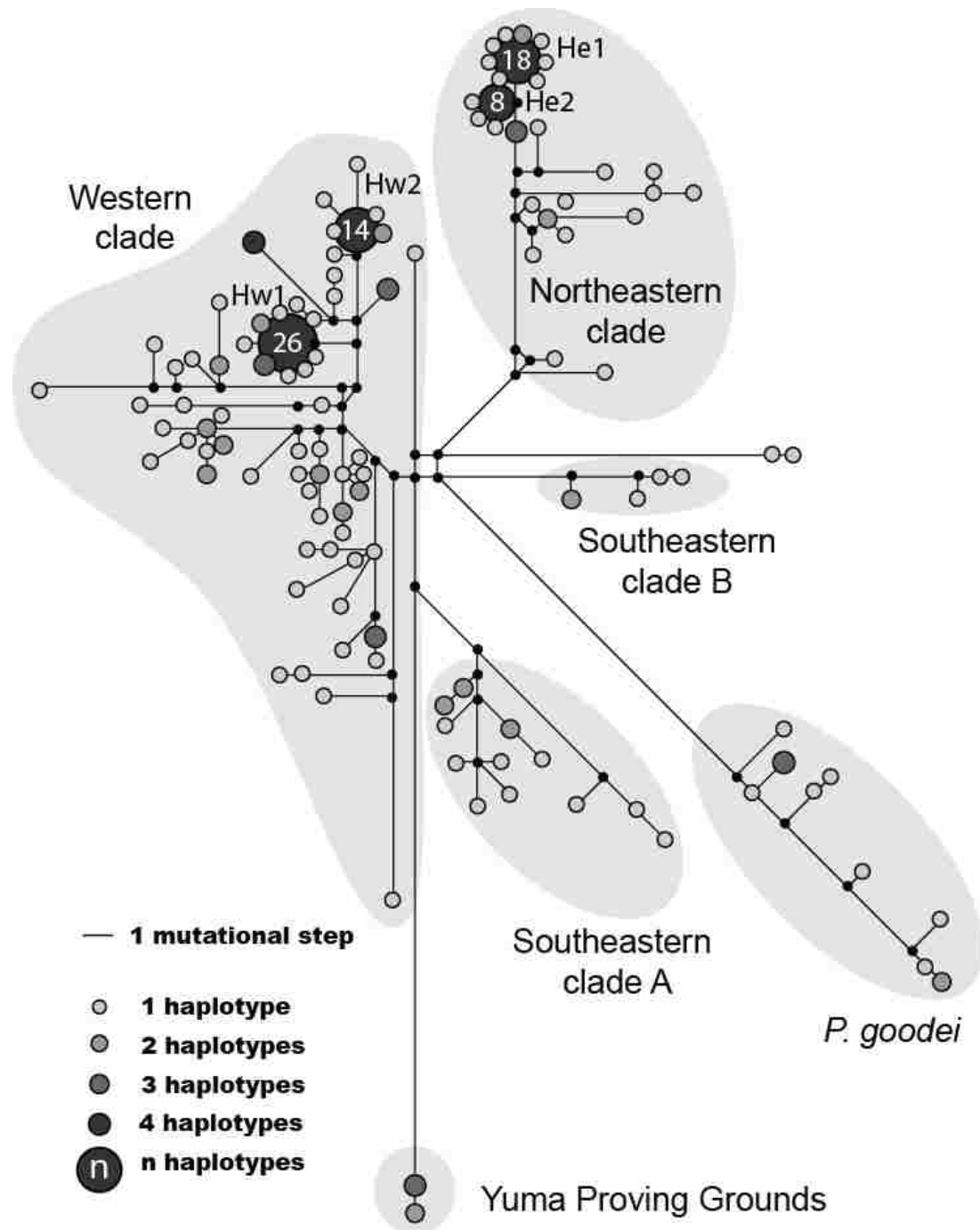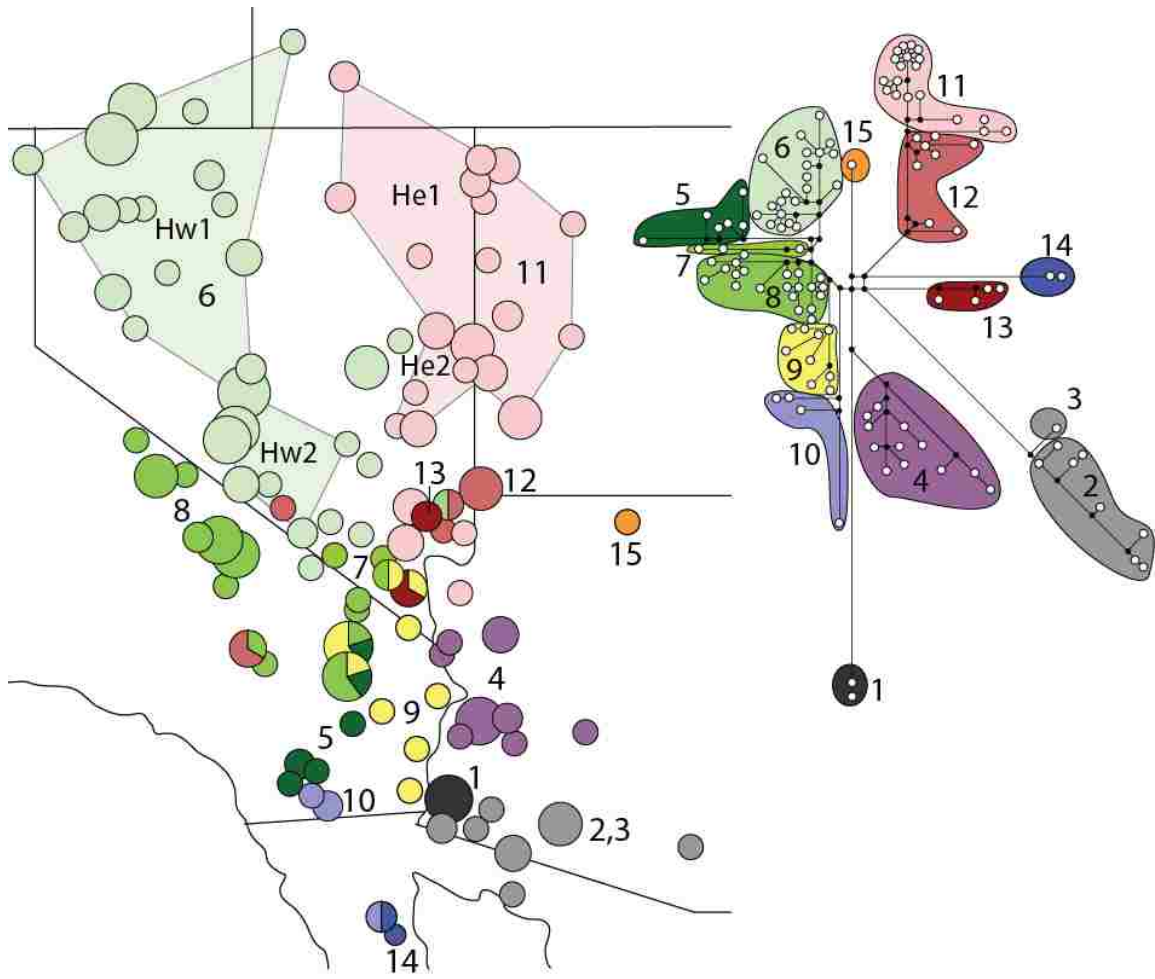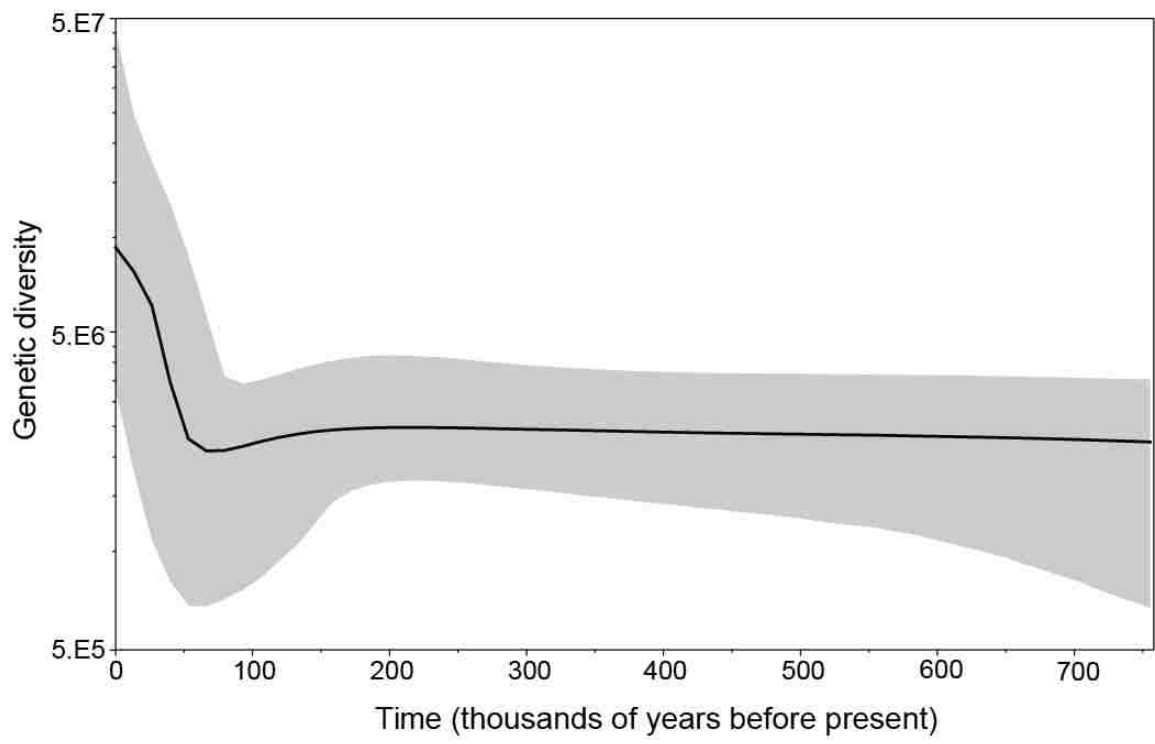
Figure 3.4

Figure 3.5

Figure 3.6
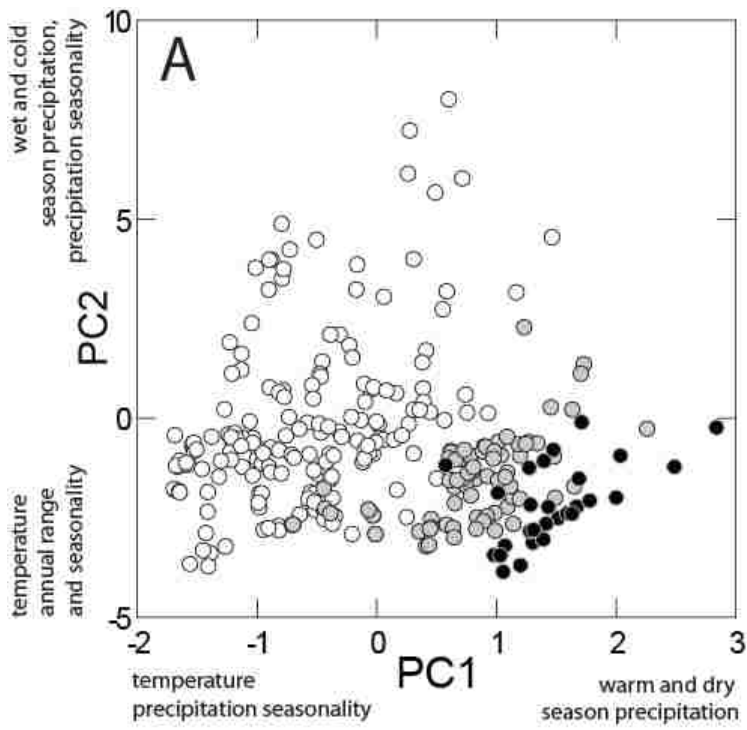
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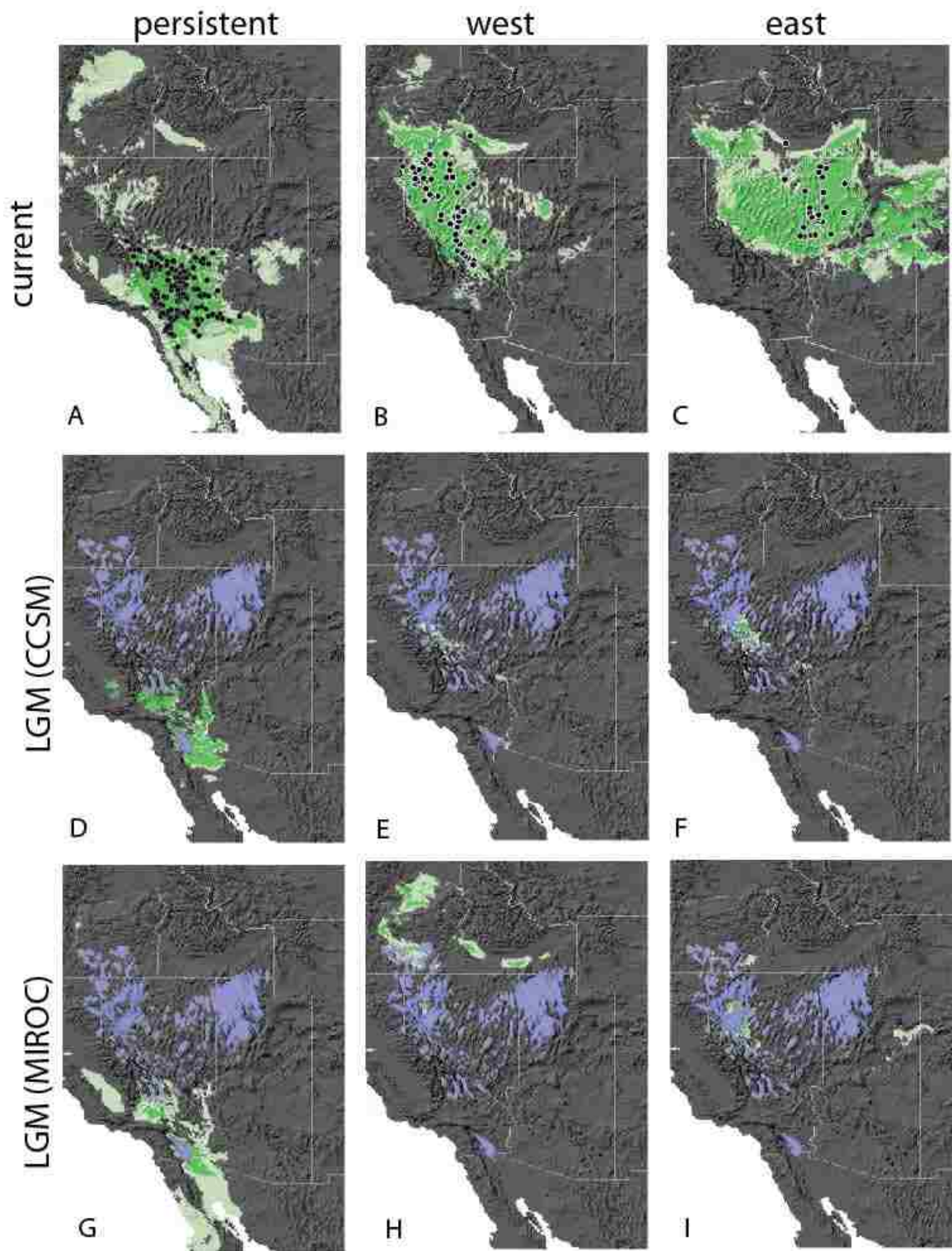
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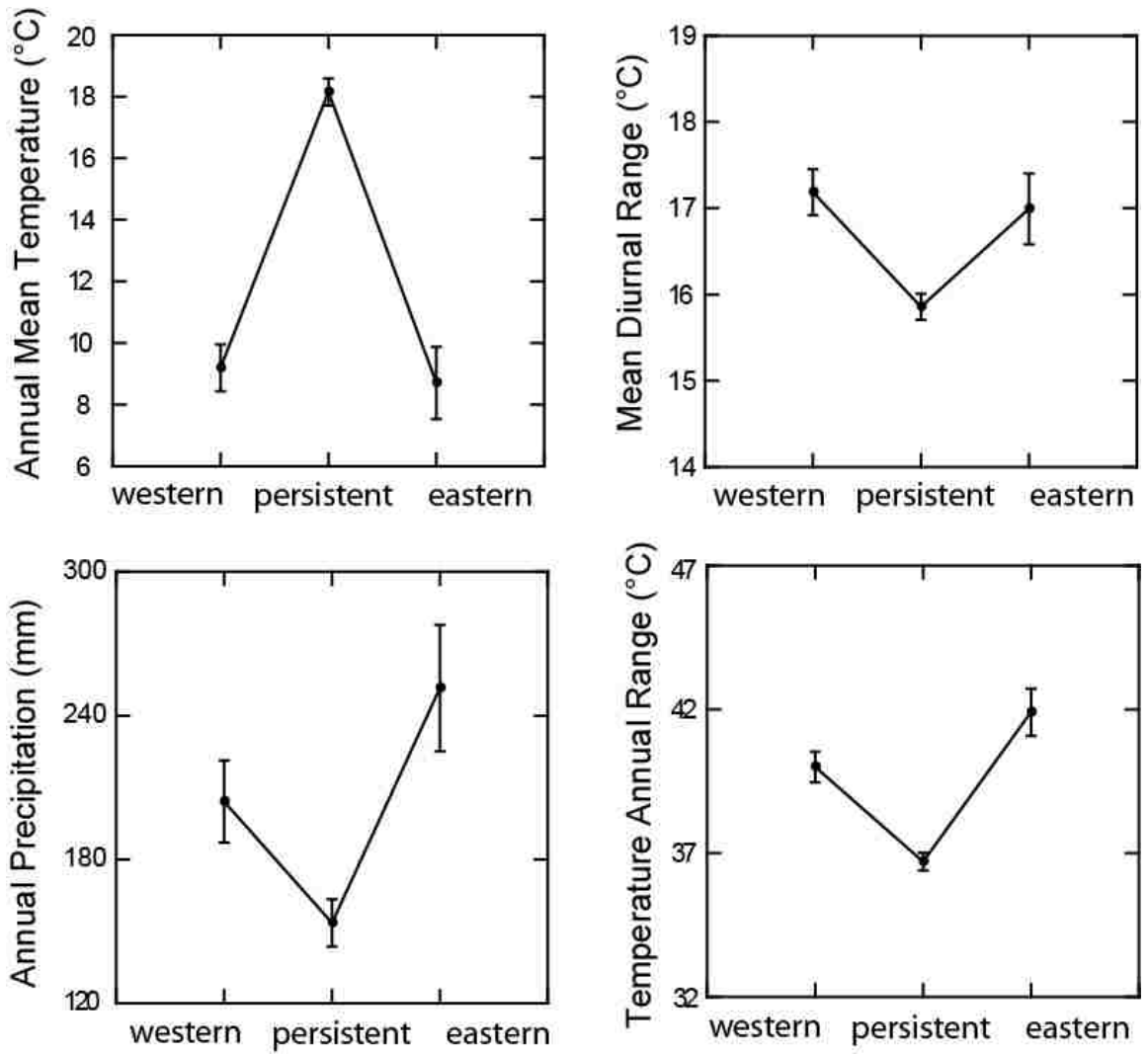
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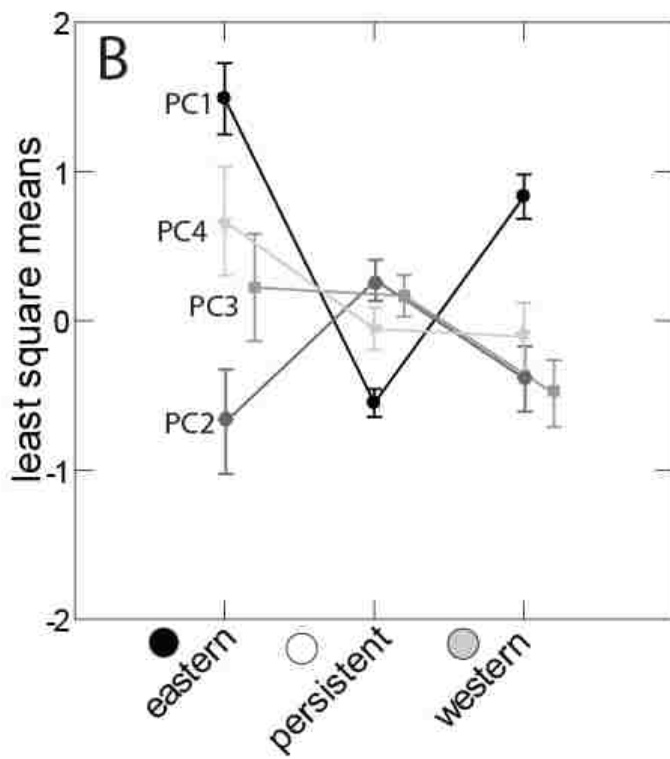
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CHAPTER 4

SOME MORE CHALLENGES FOR ECOLOGICAL NICHE MODELS: EXPLORING THE

CHALLENGES OF TRANSFERAL MODELING IN BIOGEOGRAPHY

Abstract

I expand on challenges for ecological niche modeling (ENM) discussed by Araújo &

Guisan (2006) into the realm of transferal modeling. Transferal modeling involves

projecting ecological niche models (ENMs) onto different geographic areas or different

time periods and has been used for predicting species responses to global warming,

reconstructing palaeo-ranges of organisms, or modeling the spread of invasive species.

Transferability of models in time and space however has been widely questioned

because of conceptual and algorithmic assumptions and uncertainties associated with

the methodology. Herein, I discuss several high-priority challenges in transferal

modeling: (1) model-based variability in climatic reconstructions; (2) selection of

variables; (3) projection outside the calibration range; (4) niche shifting; and (5)

transferal model evaluations. Through theoretical background and sets of experiments, I

demonstrate how these challenges can affect resulting models and, when possible, offer

suggestions on how uncertainties might be diminished. I focus mainly on projections in

time to climatic conditions of the last glacial maximum, but most of the issues are

applicable when projecting to other time periods or in space. Our intent is to provide

better understanding of conceptual and algorithmic methodology behind transferal

modeling in order to facilitate critical evaluation of existing models, and to stimulate

further exploration of these and other challenges associated with transferal modeling.

Ultimately, I hope our experiments and discussion will provide for general

improvements in the development of transferal models.

Introduction

Ecological niche models (ENMs, also referred to as climate envelope models [CEMs],

species distribution models [SDMs], or bioclimatic models) are important tools for

biogeographers (Araujo & Guisan 2006; Elith *et al.* 2006; Guisan & Zimmermann 2000;

Jeschke & Strayer 2008; Peterson & Soberon 2005). Araújo & Guisan (2006) explored

several of the fundamental challenges inherent in use of ecological niche modeling,

including: (1) niche concepts; (2) data sampling and model building; (3) model

parameterization; (4) model selection and predictor contribution; and (5) model

evaluation. An additional topic not explored by Araújo & Guisan (2006) concerns the use

of ENMs to predict species distributions across geographic space or under changing

environmental conditions through time. Herein, I address the challenges related to use

of ENMs in the realm of *transferal modeling*.

Transferal modeling involves projecting ENMs onto different geographic areas, *i.e.*

transferal in space, often used for modeling invasive species (Fitzpatrick *et al.* 2007;

Peterson *et al.* 2003; Randin *et al.* 2006) or onto a focal geographic area under past or

future environmental conditions, *i.e.* transferal in time, often used for studying species

responses to global climate change, or reconstructing palaeo-ranges of organisms

(Carnaval & Moritz 2008; Carstens & Richards 2007; Martinez-Meyer *et al.* 2004;

Pearson *et al.* 2006; Peterson *et al.* 2004; Peterson & Nyari 2008; Waltari & Guralnick

2009; Waltari *et al.* 2007). A typical approach to transferal modeling entails building (calibrating) an ecological niche model (ENM) using one of the available statistical methods (e.g. logistic regression, climatic envelope, neural network, or generic algorithms) that utilize presence-only or presence-absence records of species occurrence and a set of environmental variables [for summary see Elith *et al.* (2006) and Jeschke & Strayer (2008)]. Using the rules developed during *calibration*, the ENM is then projected onto a set of environmental variables representing a different area or time period.

Transferability of models in space and time has been widely questioned because of real or perceived obstacles, including: *extrapolation* of environmental variables, *transferability* of variables, existence of non-analogous climates between two time periods, existence of ecotypes or phenotypic plasticity within a modeled taxon, changes in biotic interactions in space and time, or inconsistencies among modeling approaches (Araujo & New 2007; Fitzpatrick *et al.* 2007; Jeschke & Strayer 2008; Nogues-Bravo 2009; Pearman *et al.* 2008; Pearson *et al.* 2002; Randin *et al.* 2006). Below, I discuss several of these high-priority challenges and show how they might affect (or bias) resulting models. I mainly focus on *projections* in time, in particular to climatic conditions of the last glacial maximum (LGM), but most of the issues I address are applicable when projecting in space or to other time periods. When possible, I offer suggestions on how particular uncertainties might be diminished, although I make no claim that such approaches will suffice for any particular dataset or question. I do not address general ENM challenges or comparisons among different modeling approaches,

as these issues have been reviewed elsewhere (Araujo & Guisan 2006; Elith *et al.* 2006; Peterson *et al.* 2007; Phillips 2008; Phillips *et al.* 2006). Although most of our analyses were done using the program Maxent 3.2 (Phillips *et al.* 2006; Phillips & Dudik 2008; Phillips *et al.* 2004), which has been reported to have better predictive accuracy than other current approaches (Elith *et al.* 2006; Phillips 2008; Phillips *et al.* 2006; Phillips & Dudik 2008), most issues discussed herein are applicable, or at least relevant to, other modeling methods, e.g., Desktop GARP (Stockwell & Peters 1999), BIOCLIM (Hijmans *et al.* 2005b).

Methods

The ENMs (used in Challenges 1-4) were built in the software package MAXENT v. 3.2.1 (Phillips *et al.* 2006), a program that calculates relative probabilities of the species' presence in the defined geographic space (Phillips *et al.* 2004). I used the default parameters in MAXENT (500 maximum iterations, convergence threshold of 0.00001, and regularization multiplier of 1, 10,000 background points) with the application of random seed and logistic probabilities (approximating niche suitability) for the output (Phillips & Dudik 2008). Occurrence records for individual species were obtained from HerpNET (http://herpnet.org) or MaNIS (http://manisnet.org). All records missing geographic coordinates, lacking a value for geographic uncertainty, and records with geographic uncertainty greater than 5 km were excluded. Current climate was represented (unless otherwise stated) by 19 bioclimatic variables (herein referred to as Bio 1 - 19) from the WorldClim dataset v. 1.4 with resolution of 2.5 minutes

(http://www.worldclim.org/; Hijmans *et al.* 2005a). The bioclimatic variables are derived

from monthly temperature and precipitation data, and represent biologically

meaningful aspects of climate (Jezkova *et al.* 2009; Waltari *et al.* 2007). For

environmental layers representing the climatic conditions of the LGM, I used the

Community Climate System Model v. 3 (CCSM) and the Model for Interdisciplinary

Research on Climate v. 3.2 (MIROC; see below for more details).

Challenge 1: Model-based variability in climatic reconstructions

When projecting in space, the environmental variables used in the new area are

usually of a similar quality to those used for calibration, *i.e.* the same global dataset can

be used for calibration on one continent and projected onto another continent.

However, when projecting to a different time period (past or future) the projection

variables are often derived very differently from those used for calibration. For example,

current climatic (temperature and precipitation) conditions are derived directly from

data recorded at numerous worldwide weather stations (Hijmans *et al.* 2005a) and then

interpolated over the study region, while the past (and future) climatic conditions are

derived using sophisticated simulations under specific assumptions. The current set of

coupled ocean-atmosphere simulations for the climatic conditions of the last glacial

maximum (LGM: ca 21,000 calendar yr B.P., equivalent to ca 18,000 14C yr B.P.;

Harrison 2000) is available through the Paleoclimatic Modeling Intercomparison Project

(PMIP phases II; Braconnot *et al.* 2007). PMIP has established a protocol followed by

participating modeling groups for LGM simulations regarding concentration of

greenhouse gases, ice sheet coverage, insolation, change in topography (mainly caused by lowering sea levels), etc. Based on this general protocol, more than 15 different climatic models for the LGM are currently available from various modeling groups (http://pmip2.lsce.ipsl.fr/; Braconnot *et al.* 2007).

Simulation of the LGM started as an experiment to examine climate response to the presence of ice sheets and lowered greenhouse gas (mainly CO_2) concentrations in order to provide a credibility test for different future scenarios of increased CO_2 (Otto-Bliesner *et al.* 2006). Increasingly, climatic variables derived from these simulations are being used to reconstruct species paleo-distributions and evaluate range shifts, contractions, and expansions associated with climatic changes since the LGM (Carstens & Richards 2007; Jezkova *et al.* 2009; Martinez-Meyer *et al.* 2004; Peterson *et al.* 2004; Peterson & Nyari 2008; Rodriguez-Robles *et al.* 2010; Waltari *et al.* 2007). Of the 15 commonly available climatic models, the following two are most often utilized for transferal modeling: Community Climate System Model Version 3 (CCSM; Otto-Bliesner *et al.* 2006) with a resolution of 1°, and the Model for Interdisciplinary Research on Climate Version 3.2 (MIROC; Hasumi & Emori 2004) with an original spatial resolution of 1.4° x 0.5° (Braconnot *et al.* 2007). The original climatic variables used in these models have been downscaled to the spatial resolution of 2.5 minutes (Peterson & Nyari 2008; Waltari & Guralnick 2009; Waltari *et al.* 2007) under the assumption that changes in climate are relatively stable over space (high spatial autocorrelation; Hijmans *et al.* 2005a).

The CCSM and MIROC climatic models provide quite different reconstructions of the climatic conditions for the LGM. For example, Figure 4.1 shows a single bioclimatic variable, Annual Precipitation, reconstructed under each climatic model over a portion of western North America (Fig. 4.1A,B), and the absolute difference for this variable between these two models (Fig. 4.1C). The greatest inconsistencies between models are centered within the southern Sonoran Desert (northwestern Mexico) and western Sierra Nevada. Differences between these two climatic models might explain why resulting transferal models of species climatic niches are often quite different. For example, Figure 4.1 also shows a ENM for Merriam's kangaroo rat (*Dipodomys merriami*) projected onto the CCSM (Fig. 4.1D) and MIROC (Fig. 4.1E) models (calibration model and data not shown) using the 19 bioclimatic variables (Hijmans *et al.* 2005a; Waltari *et al.* 2007). The absolute difference in logistic probabilities between these two models (Fig. 4.1F) shows a major area of inconsistency in the Sonoran Desert, in the same region as the area of inconsistency for Annual Precipitation (Fig. 4.1C).

Previous studies that used more than one climatic model for transferal modeling approached these inconsistencies differently. Some authors reconciled discrepancies by summing, intersecting, or averaging all models (e.g.; Waltari & Guralnick 2009; Waltari *et al.* 2007); whereas others presented each model separately (e.g.; Peterson & Nyari 2008; Rodriguez-Robles *et al.* 2010). I currently have no information about the accuracies of the past and future climatic models, and it is likely that model accuracy varies across space. I suggest that the purpose of each specific study should drive the decision on how the model-based variability is treated. For example, if the purpose of

the study is to identify "hotspots" for conservation purposes based on species

persistence through time, the intersection of all ENMs can be used to increase

confidence in area selection, but when assessing the area of impact for an emerging

pathogen or invasive species, all possibilities (sum of all models) might be of interest.

Additionally, if the generation of testable hypotheses is the objective (e.g., for

evolutionary or phylogeographic studies) models might be considered separately and

each tested using independent approaches.

Challenge 2: Selection of variables

Selection of environmental variables to be used in ecological niche modeling has

been a center of debate, with concerns about how to target environmental variables

that actually define a species range, the number of environmental variables that should

be used, and the influence of over-parameterization (too many variables) on model

performance (Nogues-Bravo *et al.* 2008; Peterson *et al.* 2007; Stockwell 2006). In

transferal modeling, variable selection faces an additional challenge since some

variables are less transferable than others because of unstable covariation with other

variables through time (Nogues-Bravo 2009). For example, elevation (which is known to

limit the current distributions of many species) correlates with temperature and

precipitation differently at different time periods. In particular, certain elevations in the

Great Basin of North America were associated with cooler temperatures and higher

precipitation during the LGM relative to current conditions. As a result, these *non-

analogous climatic conditions* (i.e. variable combinations nonexistent during the

calibration) might not be correctly projected simply because I have no information in terms of presence/absence of the species under these conditions during the calibration. The presence of non-analogous climates likely results in the underestimation of suitable habitat in transferal models (Nogues-Bravo 2009).

To document this effect, I built ENMs for the Great Basin pocket mouse (*Perognathus parvus*), an endemic species from the Great Basin that in the fossil record shows elevational shifts as a response to late Pleistocene/Holocene climatic changes (Grayson 2000). The models were created using the 19 bioclimatic variables, first without elevation included as a variable, and then with elevation included. While the 0K (calibration) models built with and without elevation do not differ substantially (Fig. 4.2A,B), the two transferal LGM models (MIROC) were very different from each other. The inclusion of elevation (Fig. 4.2C) resulted in approximately a two-third reduction in predicted suitable habitat from the model with elevation omitted (Fig. 4.2D). Additionally, histograms of predicted suitable elevations throughout the area (in this example with logistic probabilities higher than 0.2) revealed that only the model excluding elevation predicted species shift to lower elevations during the LGM, in accord with evidence from the fossil record (Fig. 4.3). Although this example might seem trivial, the lack of transferability in other variables might not be so obvious.

The transferability of variables can be partly evaluated in Maxent using the jackknife plot of *test gain* and area under curve (AUC) on test data (see the Maxent manual for better understanding of these methods) because variables that do not perform well on the test data (test data being occurrence points set aside during calibration for

subsequent evaluation of the model) are not likely to perform well when transferred in space or time. Covariance among variables at different time periods can also be compared using standard statistical approaches (Nogues-Bravo 2009). Finally, program algorithms that utilize covariance between environmental variables for deriving ENMs often can be modified and certain features can be excluded (e.g. Product features in Maxent may be one of these) when non-analogous climatic conditions are of concern (Steven J. Phillips, personal communication).

Challenge 3: Projection outside the calibration range (Extrapolation)

A common issue associated with transferal modeling and is that the calibration layers often have a different range of values than the transferal (projection) layers (Randin *et al.* 2006; Thuiller *et al.* 2004). For example, the climatic conditions of the LGM in western North America are believed to have been colder and wetter than those of today. Under such conditions, I would expect the values of associated climatic variables to be shifted towards lower temperatures and higher precipitation. In particular, 17 of 19 bioclimatic variables within western North America have projection (LGM) values outside the *calibration* (0K) *range* (Table 4.1). Consequently, the habitat suitability across values absent from the calibration dataset cannot be directly projected and some extrapolation method must be employed to complete the projection.

Figure 4.4 shows how different extrapolation methods, as well as the shape of a response curve within the calibration range, effect probability values (representing occurrence probability) within the *projection range*. Both graphs in this figure represent

a unimodal response of a hypothetical organism to a particular environmental variable.

In the left graph, the calibration layer captures the unimodal distribution of the

response curve but is missing the right tail (high values) of the projection layer. To

complete the projection, I employ three different extrapolation methods. Line A

represents a nonlinear regression method and results in an extrapolated curve

approximate to the real response curve. Line B represents a method employed by

Maxent that truncates the projection layer to the same extent as the calibration layer,

with all values outside the calibration range set to the maximum or minimum value of

the calibration layers. This latter method results in an overestimate (although not

severe) of the probability values outside the calibration range. Line C is the most

conservative approach, where probability is set to zero outside the calibration range,

which results in an underestimate of occurrence probability. Overall, however, none of

these extrapolation methods resulted in severe errors under the hypothetical conditions

shown.

A more severe concern is shown in the right graph of Figure 4.4. This scenario shows

a unimodal response curve within the calibration range that does not reach the peak,

giving the illusion during the calibration that the response to this variable is linear (when

in reality it is unimodal). A nonlinear regression (line A) results in a monotonic increase

of suitability throughout the projection range, whereas the truncation method (line B)

maintains equally high suitability. Both these methods result in increasing overestimates

of habitat suitability towards maximum values of the variable. In Maxent, this case can

be detected as large areas of unrealistically high probabilities, often in areas with

extreme climatic conditions. Setting the probability to zero outside the calibration range

(Line C) has an opposite trend and underestimates values close to the calibration range.

This method avoids the strong monotonic increase of probabilities described above

(Randin *et al.* 2006), but overall, none of these extrapolation methods was able to

approximate the true response of our hypothetical variable.

One way to decrease the amount of extrapolation in transferal modeling is to

maximize the range of each variable during the calibration process. This can be achieved

when the area for calibration is larger than the area used for projection (Pearson *et al.*

2002). For example, only 7 (for CCSM) and 9 (for MIROC) out of 19 bioclimatic variables

will have a projection range outside the calibration range when models are calibrated

using climatic variables extending across the entire world and projected onto the

variables clipped to an area of western North America (Table 4.1B). The extrapolation

differences between calibrating and projecting on the same extent versus calibrating

using a much broader area can be evaluated in Maxent. As mentioned above, Maxent

restricts the projected variables to the range of values encountered during training (i.e.

a technique called *clamping*). The clamping values generated in Maxent give the

absolute change in logistic probability caused by the clamping process. To demonstrate

how maximizing the range of each variable during the calibration affects clamping

values, I generated ENMs for the striped whipsnake (*Masticophis taeniatus*). Figure

4.5A shows where clamping occurred when calibration and projection variables were

clipped to western North America. Figure 4.5B shows how clamping values decreased

when the model was calibrated using bioclimatic variables from the entire world and

then projected on the truncated western North American dataset. However, large

commission errors can be a problem with maximizing the area during calibration when

utilizing pseudo-absences (the method utilized in Maxent) because the absence data are

randomly taken from the entire calibration area (Pearson *et al.* 2002; Randin *et al.* 2006;

Thuiller *et al.* 2004). For example, when I modeled the striped whipsnake for LGM using

the information reflected in Figure 4.5B (World to western North America) the resulting

predicted suitability area was over 40% larger than that modeled using information

reflected in Figure 4.5A (western North America to western North America; data and

models not shown).

Another option to decrease the amount of extrapolation is to exclude variables that

have a projection range that extends extensively beyond the calibration range. In our

example, when I exclude all variables that have a projection range for the MIROC model

more than 10% beyond the calibration range (Bio 1, 5, 6, 8, 9, 10, 11, 13, 14, 17, 18, and

19; Table 4.1A), the remaining seven variables do not require any extrapolation and

consequently clamping values remain zero. The disadvantage is that in many cases, too

many variables are often discarded (in our example, 12 from the MIROC model and 16

from the CCSM model).

Importantly, the level and extent of clamping does not necessarily equal the error in

the ENM caused by extrapolation. As shown in Figure 4.4, a variable with a unimodal

response curve that is captured within the calibration range will likely not result in a

severe error. I experienced this while developing models for the common side-blotched

lizard (*Uta stansburiana*). Figure 4.6 shows a set of response curves from 19 bioclimatic

variables for this species produced by Maxent (model shown in Figure 4.7). Five

variables (Bio 1, 3, 4, 6, and 11) have a unimodal response curve and all values outside

the calibration range will have a probability value close to zero. Six variables (Bio 2, 5, 8,

9, 10, and 18) have a non-zero probability value (herein referred to as an *open end*) on

the upper end of the value ranges. The remaining nine variables (Bio 7, 12, 13, 14, 15,

16, 17, 18, and 19) have non-zero probability values on the lower end. Extrapolation of

these variables can result in overestimates of probabilities (as seen in Fig. 4.4); however,

when these response curves are compared with the CCSM value ranges in Table 4.1,

only a single variable (Bio 2) has an open-end where extrapolation is needed (*i.e.* upper

values). Figure 4.7 shows CCSM models for the common side-blotched lizard when all 19

bioclimatic variables were included (Fig. 4.7A, and associated clamping values 7b) and

with the variable Bio 2 (mean diurnal temperature range) excluded (Fig. 4.7C, and

associated clamping values 4.7D). The model (Fig. 4.7A) shows high probabilities within

the northern and north-eastern areas that are biologically unrealistic (these areas were

under ice during the LGM and could not have been habitat for this species); also notice

the high clamping values in Fig. 4.7B. Excluding Bio 2 improves the model considerably

with the large overpredicted areas disappearing (Fig. 4.7C) and clamping values reduced

(Fig. 4.7D).

To assess and minimize the problems of extrapolation, I recommend exploring a

range of values and response curves for the calibration and projection variables. If

necessary, I suggest decreasing the need for extrapolation by excluding problematic

variables, using asymmetrical geographic extent of variables (as described above), or

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masking the models to the area of interest. If extrapolation is still required, I suggest

exploring various extrapolation methods (which are usually unique to each modeling

algorithm) and deciding on which method is most appropriate given the response curves

for the variables under consideration.

Challenge 4: Ecological niche shift

The vast majority of transferal models are built under the assumption of niche

conservatism (Warren *et al.* 2008; Wiens & Graham 2005), which means that the niche

currently occupied by a species is identical to the niche that was occupied in the past

and that will be occupied in the future. In reality, the assumption of niche conservatism

will almost always be violated as species niches shift even over short periods of time

(Nogues-Bravo 2009). Evolutionary adaptations in response to the changing

environment can be responsible for niche shifts, in which case the fundamental niche of

the species is altered (Fig. 4.8). Not all niche shifts, however, result from evolutionary

adaptations. In many cases, the realize niche of a species shifts through time while the

species fundamental niche remains stable (Fig. 4.8; Pearman *et al.* 2008). As indicated

above, realized niche shifts can result from shifts in the realized environment, when

non-analogous climatic conditions occur between two time periods (Ackerly 2003a;

Ackerly 2003b; Hoffmann 2005; Jackson & Overpeck 2000; Nogues-Bravo 2009). Such

niche shifts do not require plastic or evolutionary adaptive change but non-analogous

climatic conditions may be omitted during model projection. A species may also occupy

different portions of its fundamental niche (i.e. shift their realize niche) because of

varying biotic interactions through time or because of plasticity in various (behavioral,

phonological, morphological physiological) traits that allow them to adjust to changing

environments and persist in place despite environmental changes (Gibbs & Breisch

2001; Huppop & Huppop 2003; Post *et al.* 1999; Smith & Betancourt 2003).

Niche shifts have been documented from fossil records as well as from direct

observations of species responses to recent climatic change. For example, only 14 out of

28 species showed elevational shifts in response to warming climate within the last

century in California (Moritz *et al.* 2008), and only 3 out of 19 in northern Nevada (Rowe

et al. 2010). Fossil records show that cooling climates lead to larger body mass in

woodrats (genus *Neotoma*), consistent with Bergman's Rule, that allowed them to

persist *in situ* throughout the oscillating climate of the late Pleistocene, rather than

track their niche up and down in elevation, or north and south, as would be predicted if

their niches remained conserved (Smith & Betancourt 2003). Similarly, fossil records of

spotted hyena dated to the last interglacial were discovered within areas that exhibited

substantially different environmental conditions than those the species inhabits today

(Varela et al. 2009). Niche shifts have been documented in several species that

expanded northwards after the LGM and that show novel adaptations to the newly

encountered environment (Davis & Shaw 2001; Davis *et al.* 2005) and niche shifts are

also quite common in invasive species where the environmental conditions and biotic

interactions often differ between native and introduced ranges (Broennimann *et al.*

2007; Colautti *et al.* 2010; Rodder & Lotters 2009; Urban *et al.* 2007). Species currently

occupying the driest and hottest areas within the Mojave desert of western North

America (e.g. Death Valley) likely experienced a niche shift at the end of the last glacial

period as the current extreme conditions apparently had no equivalents during the LGM

(Spaulding 1990). The average annual temperature within the low elevational parts of

the Mojave desert is currently 7-8° C warmer than during the LGM and these areas are

currently dominated by novel plant communities, including the dominant and

widespread creosote bush - white bursage (*Larrea-Artemisia*) desertscrub, that did not

develop until Holocene times (Hunter *et al.* 2001; Spaulding 1990). Following the

warming climate at the end of the last glacial period, the species living on the valley

bottoms of the Mojave desert did not shift upwards as would be predicted under the

assumption of niche conservatism, but rather persisted and adapted to the newly

developing, water-stressed environment, possibly through changes in their physiology,

diet, and behavior (Tracy & Walsberg 2002).

As an example, I demonstrate the problem of niche shifts on four species

(*Lemmiscus curtatus*, *Marmota flaviventris*, *Neotoma lepida*, *Tamias minimus*) by

reconstructing their current and LGM climatic niches using ENMs. I used fossil records of

the target species from Faunmap (Graham *et al.* 1994) identified as Full Glacial (ca.

14,500-20,500 14C yr B.P.) that should roughly correspond to the climatic conditions of

the LGM (Waltari & Guralnick 2009). Values from19 bioclimatic variables were extracted

from both the CCSM and MIROC LGM models and compared with extracted variables

from current observation records. The dimensionality of the dataset was reduced using

principal component analysis (PCA) and the factor scores from the first two principal

components were plotted (Fig 4.9). The results show that some historical records (LGM)

for three of the species (*L. curtatus*, *M. flaviventris*, and *T. minimus*; Fig . 4.9A,B,D) fall

outside the ranges for current conditions (0K) for at least one principal component.

Furthermore, the LGM records of *N. lepida* as well as one record of *T. minimus* are

characterized by principle component scores on the very edge of those derived from

current climatic niches (Fig. 4.9C,D). Only two LGM records of *M. flaviventris* fall well

within the values representing the current climatic niche (Fig. 4.9B). When ENMs for

these four species were constructed and projected on reconstructions of the LGM, many

of the fossil occurrence records were outside or on the edge of the climatic niche

interpreted as suitable during LGM (in agreement with the PCA analysis; Fig. 4.10).

Niche shifts are tied directly to the previous two challenges and in some cases can

be alleviated by extrapolation. Extrapolation, however, is not necessarily biologically

meaningful and can result in nonrealistic predictions as seen in Fig. 4.7. Nogues-Bravo

(2009) strongly suggested that researchers always test for presence of non-analogous

climates between the two evaluated time periods. Fossil records from different time

periods can also be reviewed and a potential niche reconstructed by summing the

niches occupied during all time slices (Nogues-Bravo *et al.* 2008). Finally, presence of

niche shifts may be revealed from genetic data as populations that shifted their niche *in

situ* and persisted in place will exhibit a different genetic signal than populations that

shifted their distributions in concert with the oscillating climate (see chapter 2).

Challenge 5: Transferal model evaluations

Model evaluation is important (Jeschke & Strayer 2008; Nogues-Bravo *et al.* 2008)

but unlike current models (and to some extent transferal models in space) that can be

evaluated by splitting the data into training and testing datasets, evaluation of models

projected in time must be done using independent and often surrogate data. Herein I

discuss three evaluation approaches and their possible drawbacks – (1) population

genetic data, (2) direct fossil records, and (3) indirect pollen and plant macrofossil

records representing biome changes.

<u>Genetics</u>

Genetic signals imprinted in species genomes has been shown to trace species

geographic and demographic histories (Excoffier *et al.* 2009; Hewitt 2000; Hewitt 1996;

Hewitt 2004), and various molecular markers have been used to evaluate processes

such as range shift, range expansion, range contraction, population expansion or

population bottlenecks (Avise 2000). Recently, genetic markers also have been used to

evaluate *a priori* hypotheses based on transferal models (Carstens & Richards 2007;

Waltari *et al.* 2007). Although genetic analyses can be valuable for assessing transferal

models, there are several issues that must be considered to validate this approach.

First, pronounced phylogeographic structure, in the form of genetic divergence

among geographically separated populations dated to the mid or late Pleistocene, often

has been attributed to climatic changes, providing evidence that during certain climatic

periods (e.g. glacial periods) populations have been fragmented in two or more isolated

refugia that persisted long enough to generate a phylogeographic signal (Knowles 2001).

In such cases, the transferal model is expected to predict isolated patches of suitable habitat for the climatic conditions representing the glacial period. Genetic divergence, however, can originate without any obvious geographic or ecological barriers (Graham *et al.* 2006; Irwin 2002; Jansson 2003; Losos *et al.* 2006; Neigel & Avise 1993), even when habitat remains relatively contiguous through time. This is particularly true for mtDNA which may exhibit rapid and stochastic lineage sorting (Avise 2000). Divergence without geographic barriers can be particularly pronounced in species with low mobility and small effective population sizes, where genetic drift can override gene flow (Irwin 2002; Rodriguez-Robles *et al.* 2010). Consequently, genetic divergence (especially when only a single molecular marker is being evaluated) does not necessarily indicate former presence of a barrier of unsuitable habitat among isolated refugia. To distinguish between stochastic divergence and that caused by past habitat fragmentation, multiple independent molecular markers and, ideally, multiple co-distributed taxa with similar ecological niches should be evaluated in search of congruent patterns of molecular and geographic divergence.

Second, extinction of clades is almost impossible to track using genetic information from extant taxa (Calvignac *et al.* 2008) which can complicate the use of genetic data. Let us assume a situation (Fig. 4.11) where a transferal model suggests presence of a hypothetical organism during an initial time period in the past (T1) in two separate refugia (Areas 1 and 2). The genetic analysis at current time (T3), however, recovers relatively high genetic diversity within Area 1 (indicative of some persistence of the organism within this area) while that for Area 2 exhibits very low genetic diversity with

most (all) individuals possessing genotypes that are also present in Area 1. One possibility (Fig. 4.11, scenario A) is that the transferal model incorrectly predicts persistence of the species within Area 2 which was in reality not suitable during the initial period (T1) – Area 2 was consequently colonized (during T2) from the genotypes present in Area 1. The second possibility (Fig. 4.11, Scenario B) is that the Area 2 was occupied during the past (T1) by the species (as suggested by a transferal model) but subsequently the original population (or at least the genotypes) went extinct and Area 2 was, again, colonized from Area 1 during some subsequent time (T2). In both cases, the genetic structure recovered currently (T3) would be similar (identical) but the histories (and consequently the suitability of Area 2 at T1 - which is of interest) would be different. In summary, an extinction event can destroy a genetic signal of species persistence and can be incorrectly interpreted as an error in the transferal model.

The third issue with using genetic data to evaluate transferal models is pseudo-congruence between the models and genetic data. Persistence of a taxon within an area, divergence of populations into refugia, as well as new colonization of a species into a previously uninhabited area can seemingly be supported by genetic data, while the genetic structure could have been generated during different times and for different reasons. Time of divergence among and within populations can be calculated from genetic data based on genetic divergence (typically percent sequence divergence) and a known, or estimated, mutation rate (Bromham & Penny 2003). These time estimates can then allow genetic patterns to be equated to the time period represented by the transferal model. Genetic divergence, however, greatly depends on effective population

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sizes and on population size fluctuations through time (Edwards & Beerli 2000) and is

highly stochastic due to the stochastic nature of genetic drift (Carstens *et al.* 2005;

Knowles & Maddison 2002; Maddison & Knowles 2006). Also, mutation rate can be

difficult to estimate as it is variable among different genes, among organisms (Spradling

et al. 2001), and through time (Ho *et al.* 2005). As a result, confidence intervals around

divergence times derived from genetic data often widely span the time period for which

the transferal model was built.

<div align="center">Fossil record</div>

When appropriately dated, direct fossil records of the target organisms can

document presence, or imply absence, of a species and can be used in the evaluation of

transferal models (Martinez-Meyer *et al.* 2004; Waltari & Guralnick 2009). There are

several drawbacks and challenges that should be considered when using fossil records

for evaluation. First, fossils records can be dated with precision from few hundred to

thousands, or tens of thousands, of years, while transferal models usually represent a

climatic state for a particular time period (e.g. height of the LGM). Under the periods of

time represented by the fossil record, an area could have experienced significant

climatic fluctuations (Grootes & Stuiver 1997; Thompson *et al.* 1993) and a particular

fossil might not represent presence of the species exactly at the time during which the

environmental conditions are reflected in the transferal model.

Second, fossil identification may represent a substantial problem. Some species are

difficult to identify to species level. For example, pocket mice in the family

Heteromyidae comprise two reciprocally monophyletic and deeply divergent genera,

Perognathus and *Chaetodipus*, yet are not recognized as separate genera in the fossil record (Alexander & Riddle 2005; Hafner *et al.* 2007). Furthermore, extinct taxa that morphologically resemble extant studied organisms but occupied different niches could exist cryptically in the fossil record (Varela *et al.* 2009).

Finally, local versus regional shifts in species distributions can be difficult to distinguish from the fossil record. Small patches of suitable habitat available locally to the organism may not be recovered in coarse transferal models. In such cases, the fossil record documents presence while the transferal models predict absence of the organisms within a particular area. This can also be a problem when evaluation of the transferal model is based on species absence from the fossil record. For example, while a species can be locally extinct within the small area from which the fossil records originated (e.g. within the home range of the raptor that deposited pellets with prey remains), it could persist regionally within the resolution of the transferal model. In such cases, the fossil record seemingly does not support the transferal model.

<u>Palaeo-environmental reconstructions</u>

The PMIP experiments of simulated past climates have been evaluated using palaeo-environmental reconstructions. Several global palaeo-environmental datasets have been used for PMIP experiment evaluation (Farrera *et al.* 1999; Harrison 2000; Kohfeld & Harrison 2000; Prentice & Jolly 2000; Prentice & Webb 1998; Qin *et al.* 1998). For western North America, BIOME 6000 (Thompson & Anderson 2000) represents a pollen and plant macrofossil dataset, with the latter primarily derived from numerous packrat middens (*i.e.* woodrats, rodent species within the genus *Neotoma*). Interestingly, the

pollen and macrofossil data do not necessarily provide the same information. The fossil pollen generally represents a larger, regional picture of the palaeo-vegetation but with less detail (lower species richness), while the packrat middens provide more detailed information (higher species richness) but only locally, within the home range of a woodrat (Mehringer & Wigand 1990). Consequently, attention must be paid when comparing palaeo-vegetation from two areas reconstructed from these different data sources. Packrat midden data should also be interpreted with caution because different species of woodrats (which are difficult to identify by their middens) have different preferences for collection of plant material and consequently their midden contents can be different even within the same environment. This problem may be exacerbated through time if one woodrat species replaces another within the same midden, which could result in an incorrect interpretation of environmental change when none occurred (Dial & Czaplewski 1990).

Concluding remarks

In this paper, I identified several general challenges, both algorithmic and conceptual, that can complicate the use of transferal modeling. Our major goal was to stimulate more objective evaluations of transferal models with better understandings of the assumptions and uncertainties. I hope that our experiments and discussion will motivate researchers to further explore these and other challenges associated with transferal modeling, as our list was certainly not intended to be complete nor have I provided complete solutions to the challenges I describe. While some of the challenges

are substantial, and should raise concerns regarding the accuracy of this approach, I

believe that transferal modeling offers strong potential to provide biogeographers with

an important approach for increasing my understanding of evolutionary and

biogeographic processes.

Table 4.1. Range of values of 19 bioclimatic variables for the 0K and LGM (CCSM and Miroc) datasets, when (A) both the 0K and LGM variables are clipped to the geographic extent of the western North America, and (B) the 0K dataset represents the entire world while the LGM variables are clipped to the extent of western North America. Highlighted are LGM values that are outside the 0K range (light grey < 10%, dark grey ≥ 10%).

A	0K (western)		CCSM (western)		MIROC (western)	
	Low	High	Low	High	Low	High
Bio01	-71	294	-314	277	-388	282
Bio02	32	213	-31	360	32	219
Bio03	19	86	-9	86	21	34
Bio04	449	14199	452	14195	436	14200
Bio05	60	456	-108	422	-128	389
Bio06	-295	215	-557	200	-667	205
Bio07	118	522	99	628	99	549
Bio08	-135	332	-252	299	-341	293
Bio09	-196	328	-481	273	-553	278
Bio10	5	360	-143	299	-216	307
Bio11	-221	283	-507	267	-581	272
Bio12	35	4524	13	5990	59	3750
Bio13	7	881	4	1151	9	1059
Bio14	0	112	0	167	0	172
Bio15	5	138	5	141	5	138
Bio16	18	2378	9	3150	24	2401
Bio17	0	366	0	541	0	547

Bio18	1	1608	0	1854	5	2359
Bio19	1	1455	3	1350	0	1901

B	0K (world)		CCSM (western)		MIROC (western)	
	Low	High	Low	High	Low	High
Bio01	-278	319	-314	277	-388	282
Bio02	9	213	-31	360	32	219
Bio03	8	96	-9	86	21	34
Bio04	64	22704	452	14195	436	14200
Bio05	-86	489	-108	422	-128	389
Bio06	-559	258	-557	200	-667	205
Bio07	53	725	99	628	99	549
Bio08	-278	376	-252	299	-341	293
Bio09	-501	365	-481	273	-553	278
Bio10	-127	382	-143	299	-216	307
Bio11	-506	289	-507	267	-581	272
Bio12	0	2115	13	5990	59	3750
Bio13	0	2437	4	1151	9	1059
Bio14	0	697	0	167	0	172
Bio15	0	265	5	141	5	138
Bio16	0	6586	9	3150	24	2401
Bio17	0	2319	0	541	0	547
Bio18	0	5040	0	1854	5	2359
Bio19	0	4580	3	1350	0	1901

Figure 4.1. Difference between the two climatic models for the western region of North America: The left column represents Bio 12 (Annual Precipitation) for (A) the CCSM model, (B) MIROC model, and (C) the absolute difference between the two models. The values are divided using the natural (Jenks) breaks into five classes that maximize differences among classes**.** The right column represents the ENMs for the Merriam's kangaroo rat (*Dipodomys merriami*) using 19 bioclimatic variables projected on (C) the CCSM and (E) MIROC climatic reconstructions of the LGM, and (F) the absolute difference of logistic probabilities between these two models. Shading represents different categories of logistic probabilities.

Figure 4.2. ENMs for the Great Basin Pocket Mouse (*Perognathus parvus*) created using 19 bioclimatic variables and elevation for (A) current and (B) LGM conditions. ENMs with elevation excluded are shown for (C) current and (D) LGM conditions. While the models calibrated on current variables do not differ significantly whether the elevation was included or not, the LGM model with (B) elevation included has less than 1/3 of suitable habitat than (D) the model with elevation omitted.

Figure 4.3. Histograms of elevation for the areas with logistic probabilities higher than 0.2 extracted from the ENMs of *Perognathus parvus*. The current model was created using 19 bioclimatic variables and elevation (top). The LGM models were created using all bioclimatic variables (MIROC) but with elevation included or excluded (middle and bottom, respectively). While both LGM models predict extinction of the species at

higher elevations (blue rectangles), only the LGM model that excludes elevation predicts that the species shifted to lower elevations (red rectangle).

Figure 4.4. Schematic picture showing different approaches when projecting a model outside the calibration range (extrapolation). The curve represents a hypothetical unimodal response of organism to an environmental variable. In each picture, line A represents interpolation of values using a regression method; line B represents a method utilized by Maxent where the values outside the training range are assigned the probability value of the last (highest or lowest) value of the training range; and line C represents a method where all values of habitat suitability outside the calibration range are set to zero. Although both figures represent the same response of the organism, the extrapolation differs based on what part of the response curve is available during calibration (see text for details).

Figure 4.5. The clamping values for ENMs of the striped whipsnake (*Masticophis taeniatus*) when calibration and projection was performed on 19 bioclimatic variables (A) clipped to the western North America and (B) when the calibration of the model was performed using bioclimatic variables representing the entire world and then projected on the truncated dataset of the western North America. The clamping values range from 0 to 1 because they represent change in logistic probabilities caused by clamping (see text for details).

Figure 4.6. A set of response curves of 19 bioclimatic variables for the common side-blotched lizard (*Uta stansburiana*) produced by Maxent. The X-axis represents a range of values of each variable for the 0K climatic conditions, and the Y-axis represents the logistic probability value interpreted as occurrence probability or habitat suitability.

Figure 4.7. (A) ENM for the common side-blotched lizard (*Uta stansburiana*) for the LGM when all 19 bioclimatic variables are included, and (B) the associated clamping values. (C) The LGM model derived with variable Bio 2 (mean diurnal temperature range) excluded, and (D) the associated clamping values.

Figure 4.8. Representation of a niche shift in a hypothetical species from time T1 to time T2. The shift in T2A was due to an evolutionary adaptation that resulted in an expansion of the species fundamental niche, while in T2B, the fundamental niche remained conserved while the realized niche shifted (because of changes in biotic factors, plasticity of the organism that allowed it to persist in place, or because of the appearance of novel environmental conditions that were not available at time T1).
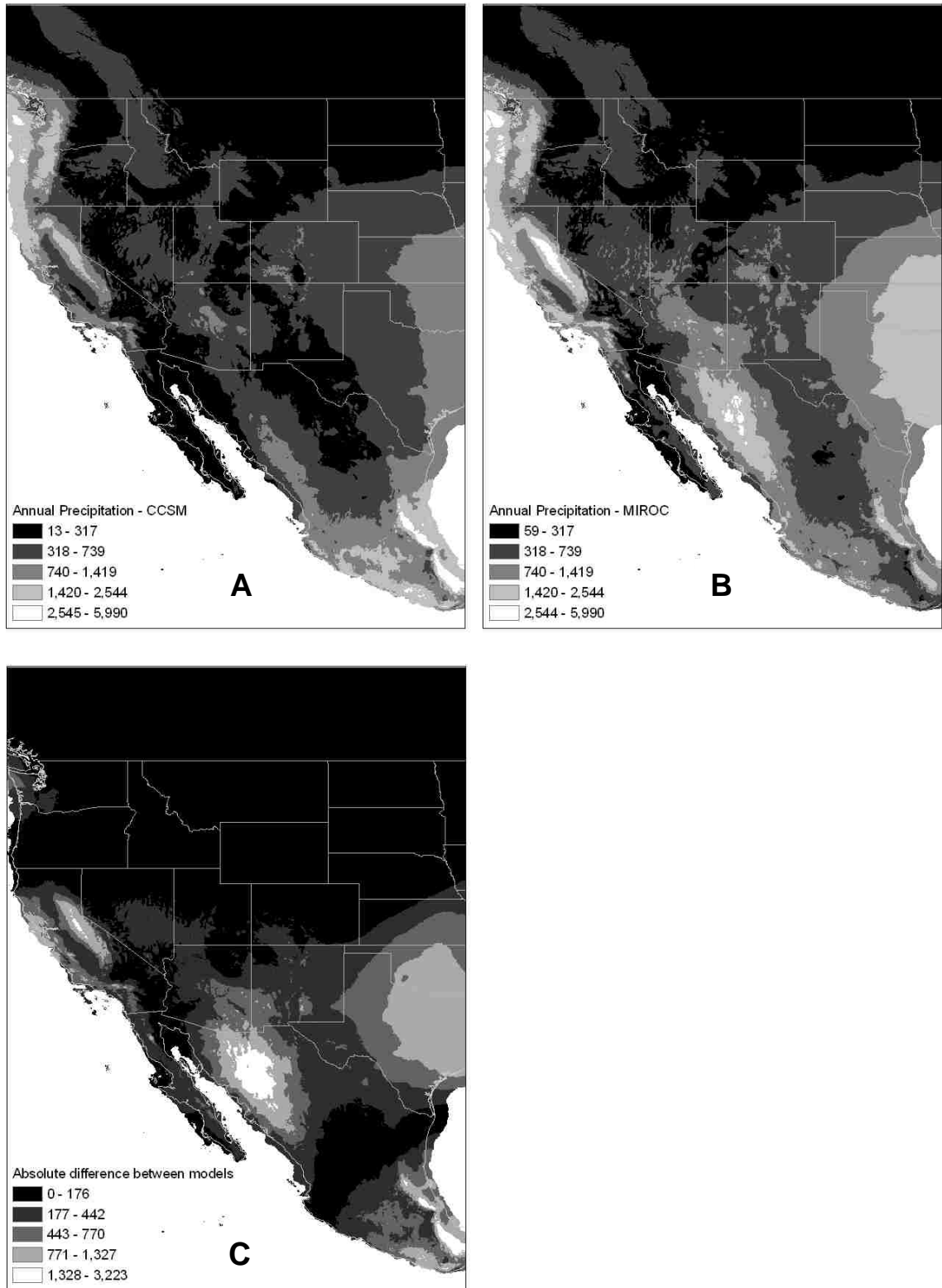
Figure 4.9. Comparison of principal components scores derived from bioclimatic niches occupied by four species of rodents at 0K (empty symbols) and during the LGM (red and green colored symbols). The axes represent the first two principal components of the 19 bioclimatic variables after data reduction using principal component analysis. The occurrence records representing the 0K climatic conditions were downloaded from

MaNIS while the occurrence records representing the LGM were obtained from the

Faunmap database, constrained to the full glacial (ca. 14,500-20,500 years B.P.).

Figure 4.10. Ecological niche models for four species of rodents using the LGM

reconstructions of CCSM (left column) and MIROC (right column). The red dots

represent fossil records dated to the full glacial (ca. 14,500-20,500 years B.P.) obtained

from the Faunmap database. The shades represent different categories of logistic

probabilities.

Figure 4.11. Two scenarios of a hypothetical species history leading to the same genetic

signal. In scenario A, the species persists only in Area 1 during an early time (T1),

generating high genetic diversity. When habitat becomes suitable at Area 2 during a

subsequent time (T2), a small subset of the genotypes from Area 1 colonizes Area 2. In

scenario B, both Areas 1 and 2 are suitable during T1. During T2, genotypes from Area 2

go extinct while a small subset of the genotypes from Area 1 colonizes Area 2. In both

cases, the genetic structure identified during current time (T3) is identical.
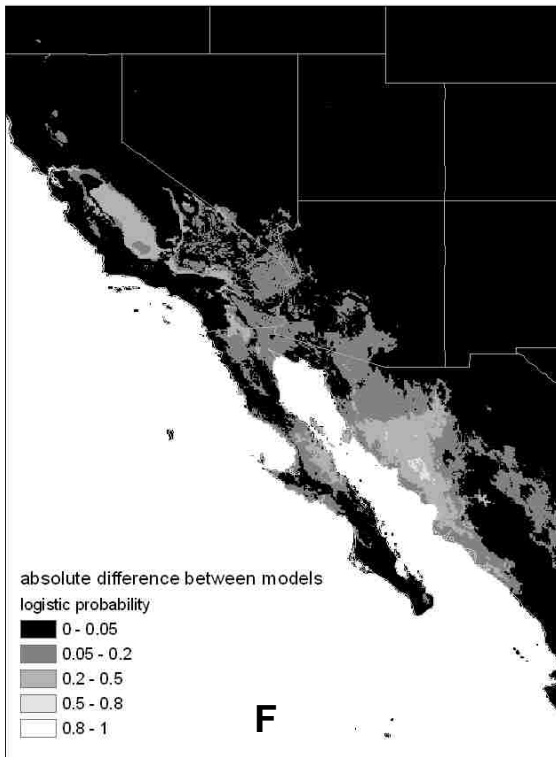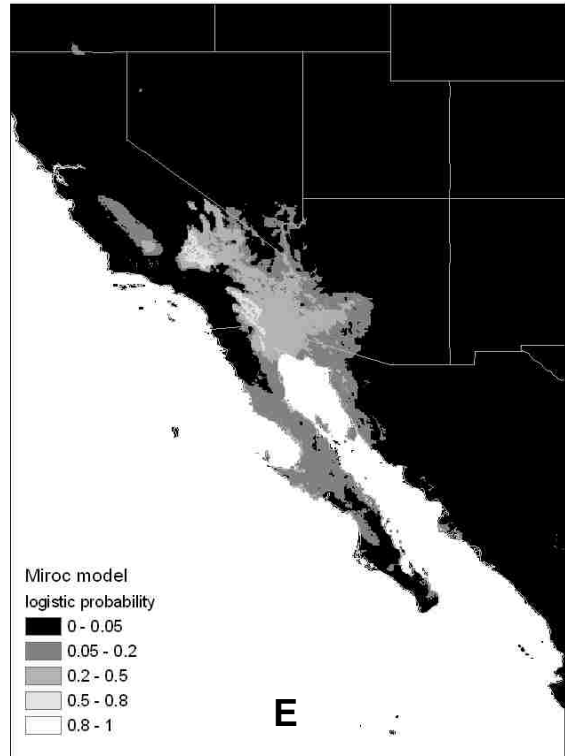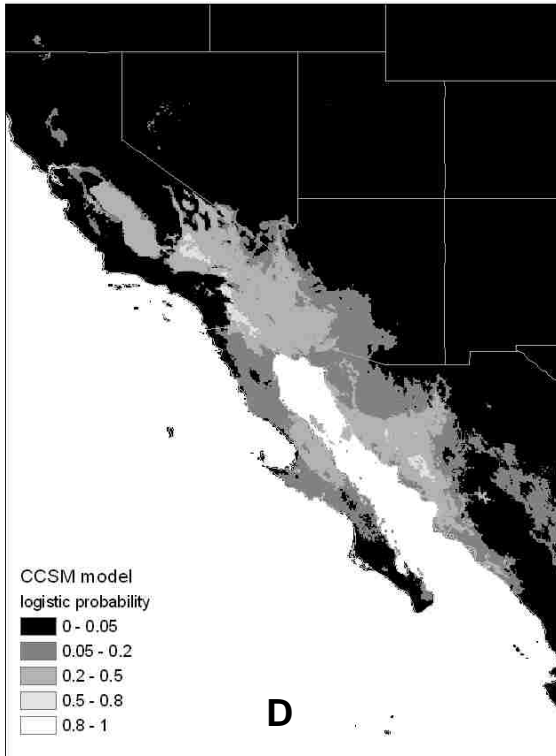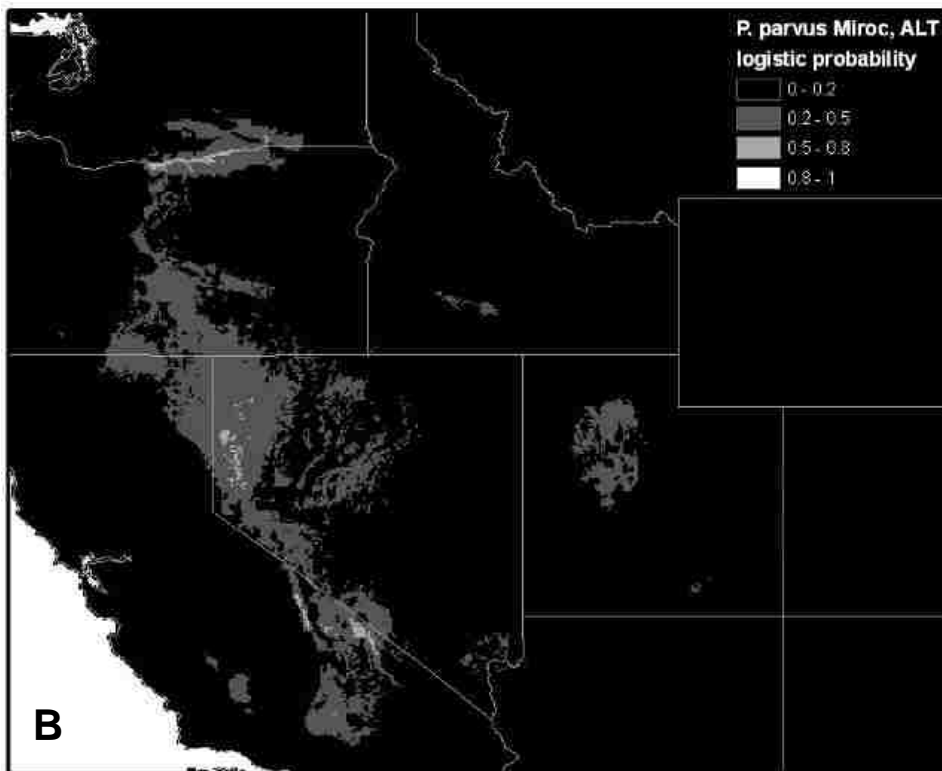
Figure 4.1

Annual Precipitation - CCSM
- 13 - 317
- 318 - 739
- 740 - 1,419
- 1,420 - 2,544
- 2,545 - 5,990

A

Annual Precipitation - MIROC
- 59 - 317
- 318 - 739
- 740 - 1,419
- 1,420 - 2,544
- 2,544 - 5,990

B

Absolute difference between models
- 0 - 176
- 177 - 442
- 443 - 770
- 771 - 1,327
- 1,328 - 3,223

C

CCSM model
logistic probability
- 0 - 0.05
- 0.05 - 0.2
- 0.2 - 0.5
- 0.5 - 0.8
- 0.8 - 1

D

Miroc model
logistic probability
- 0 - 0.05
- 0.05 - 0.2
- 0.2 - 0.5
- 0.5 - 0.8
- 0.8 - 1

E

absolute difference between models
logistic probability
- 0 - 0.05
- 0.05 - 0.2
- 0.2 - 0.5
- 0.5 - 0.8
- 0.8 - 1

F

Figure 4.2

P. parvus 0K, noALT
logistic probability
☐ 0 - 0.2
▨ 0.2 - 0.5
▨ 0.5 - 0.8
☐ 0.8 - 1

C

P. parvus Miroc, noALT
logistic probability
☐ 0 - 0.2
▨ 0.2 - 0.5
▨ 0.5 - 0.8
☐ 0.8 - 1

D

Figure 4.3

Figure 4.4

Figure 4.5

Clamping Values
- 0 - 0.05
- 0.05 - 0.2
- 0.2 - 0.5
- 0.5 - 0.8
- 0.8 - 1

A

Clamping Values
- 0 - 0.05
- 0.05 - 0.2
- 0.2 - 0.5
- 0.5 - 0.8
- 0.8 - 1

B
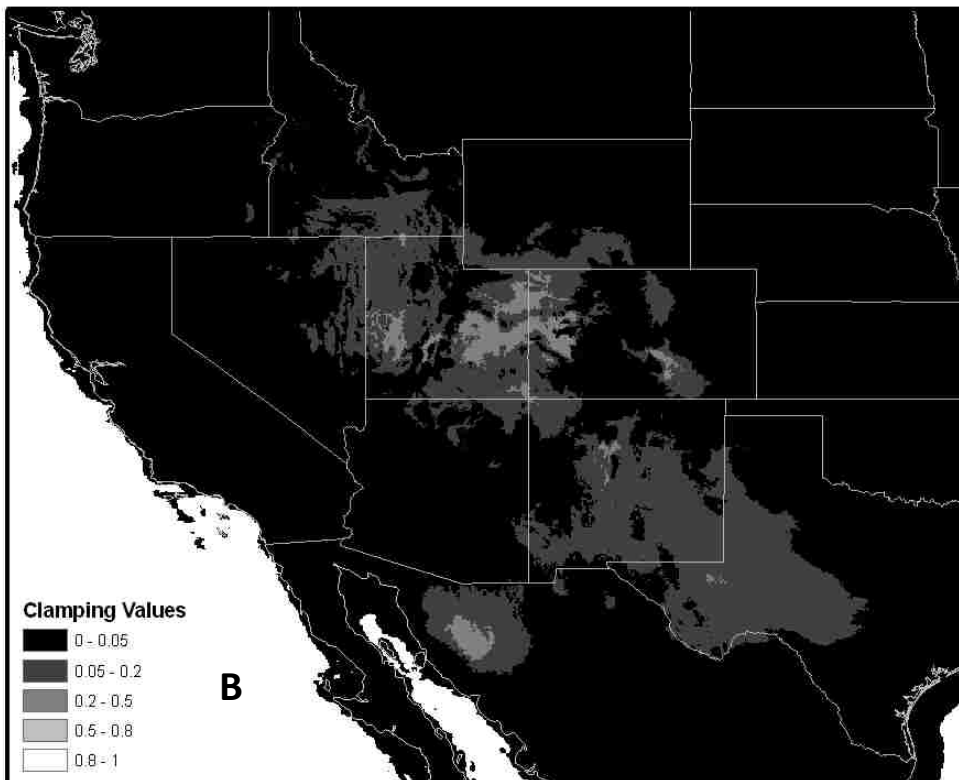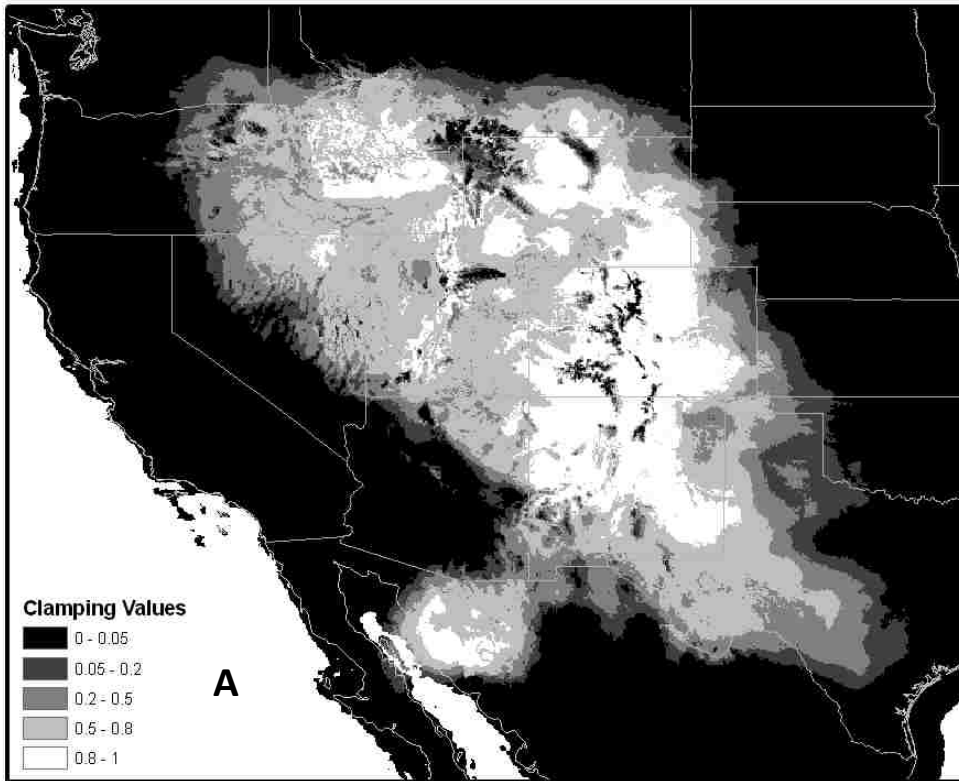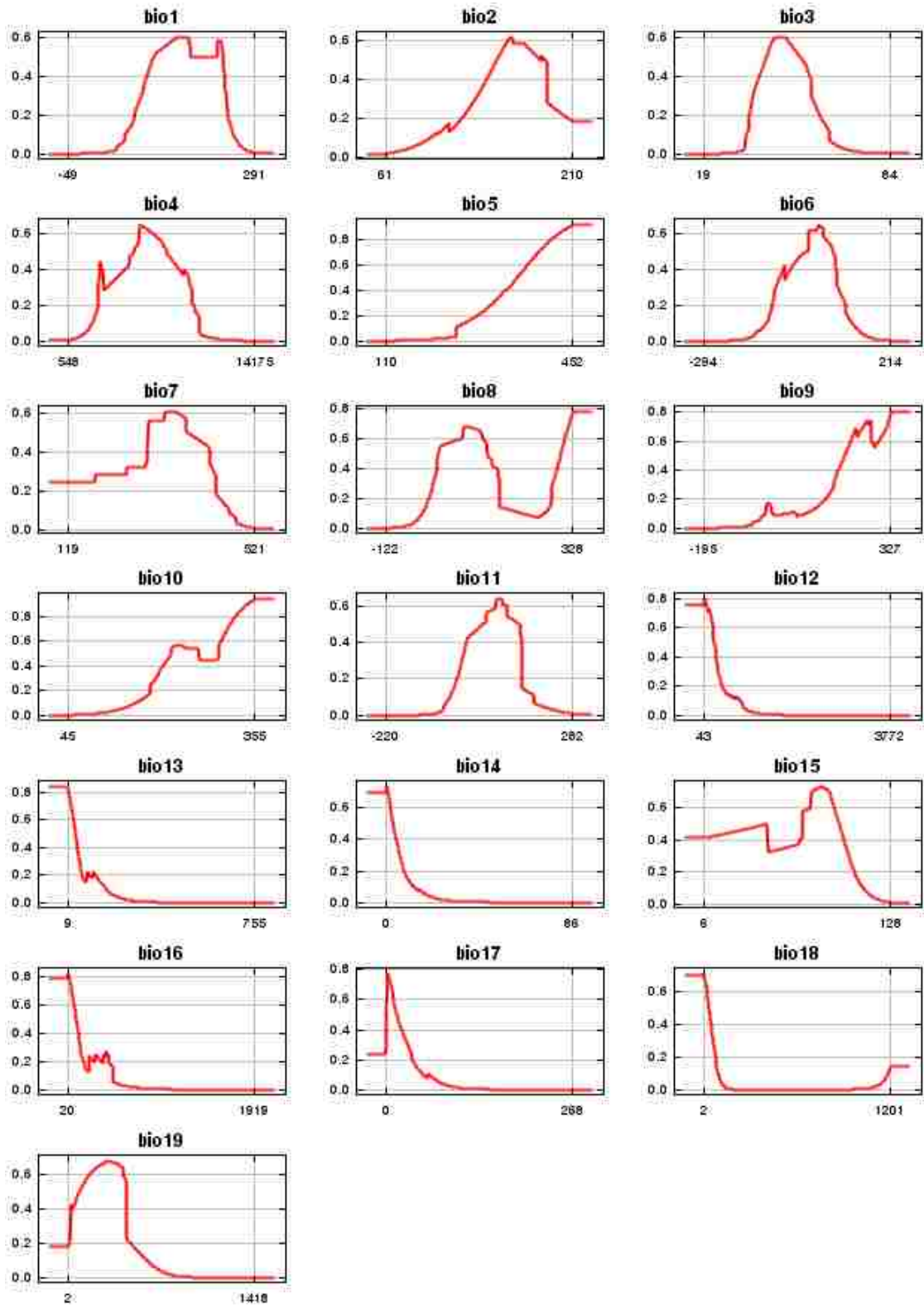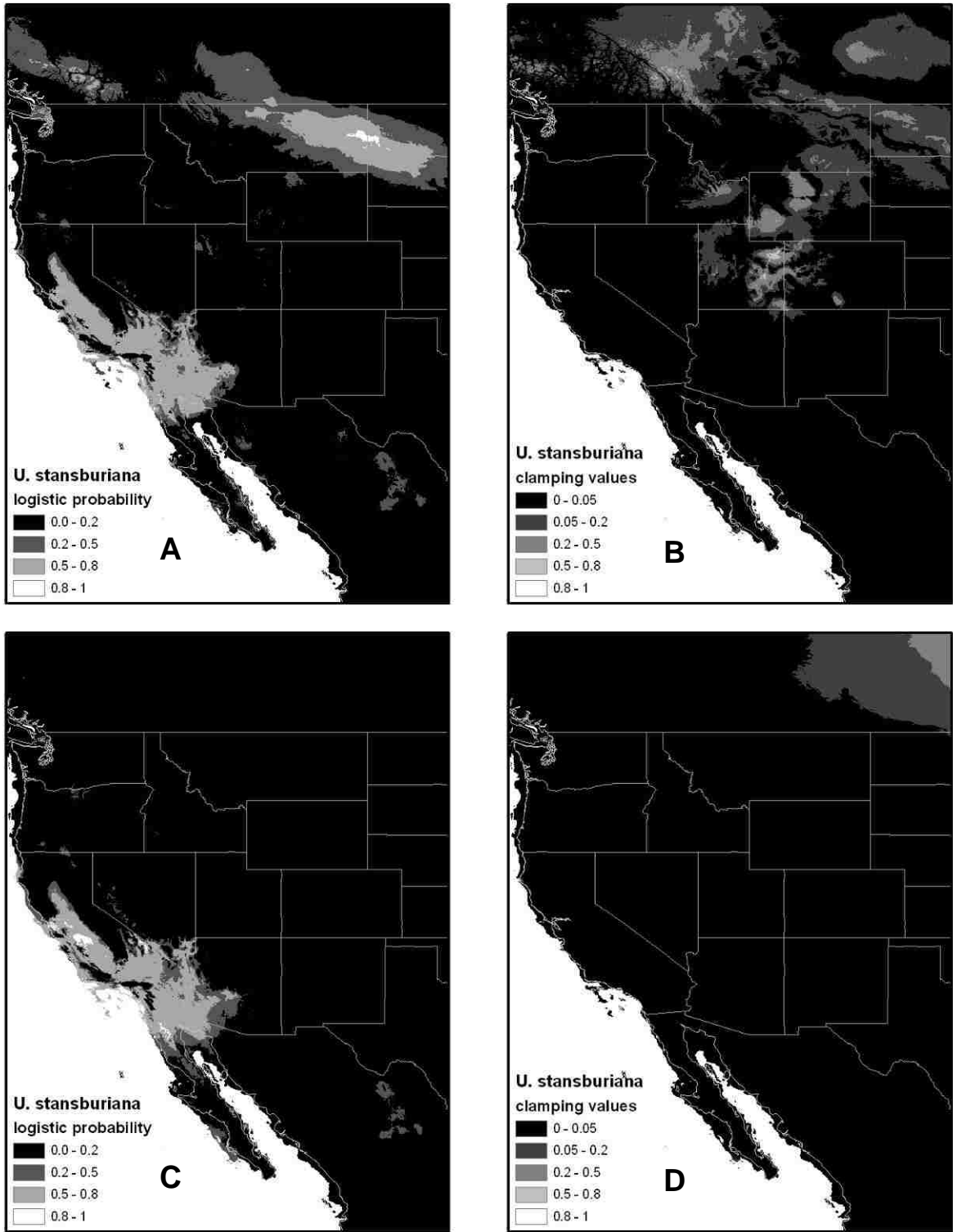
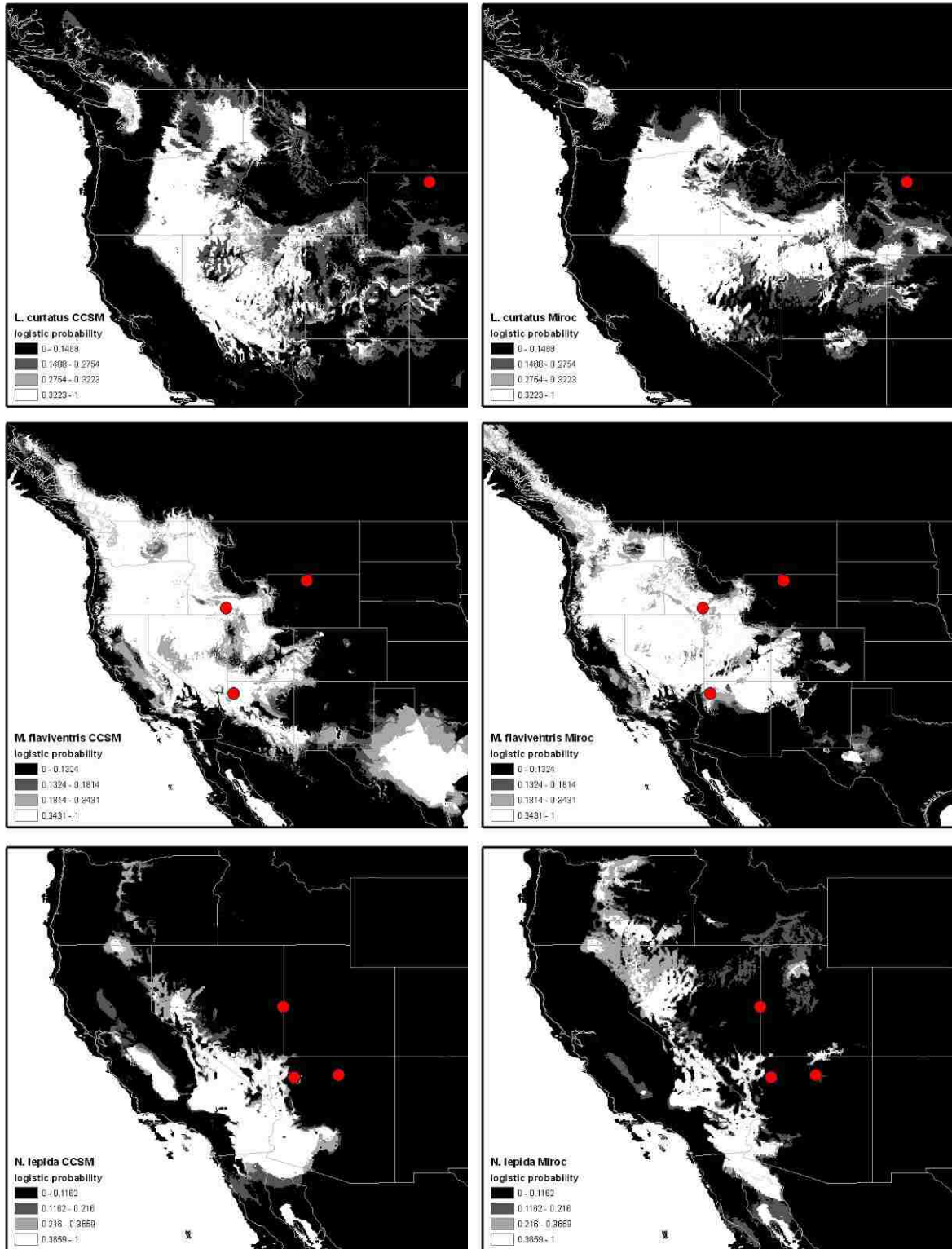**Figure 4.6**

Figure 4.7
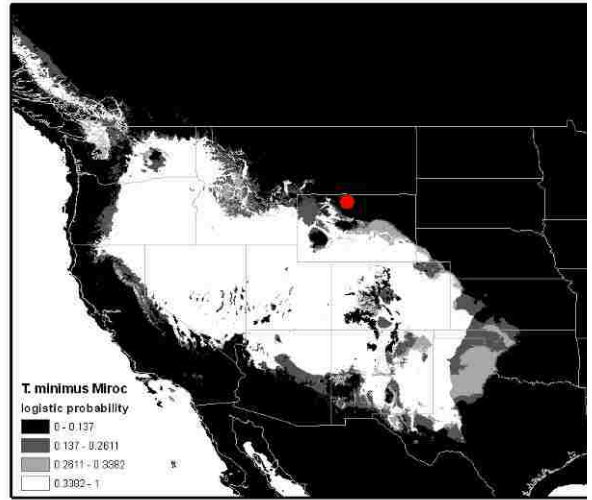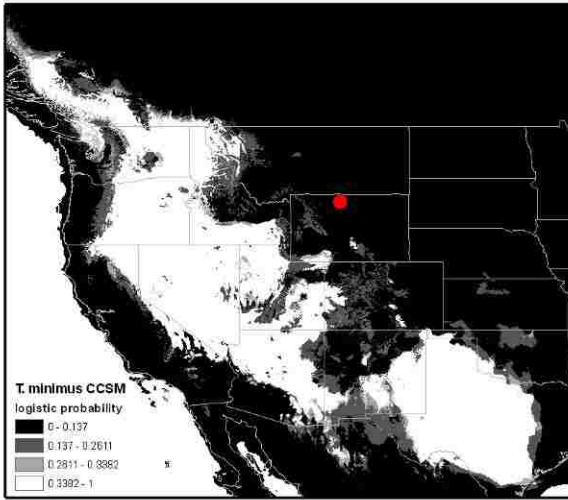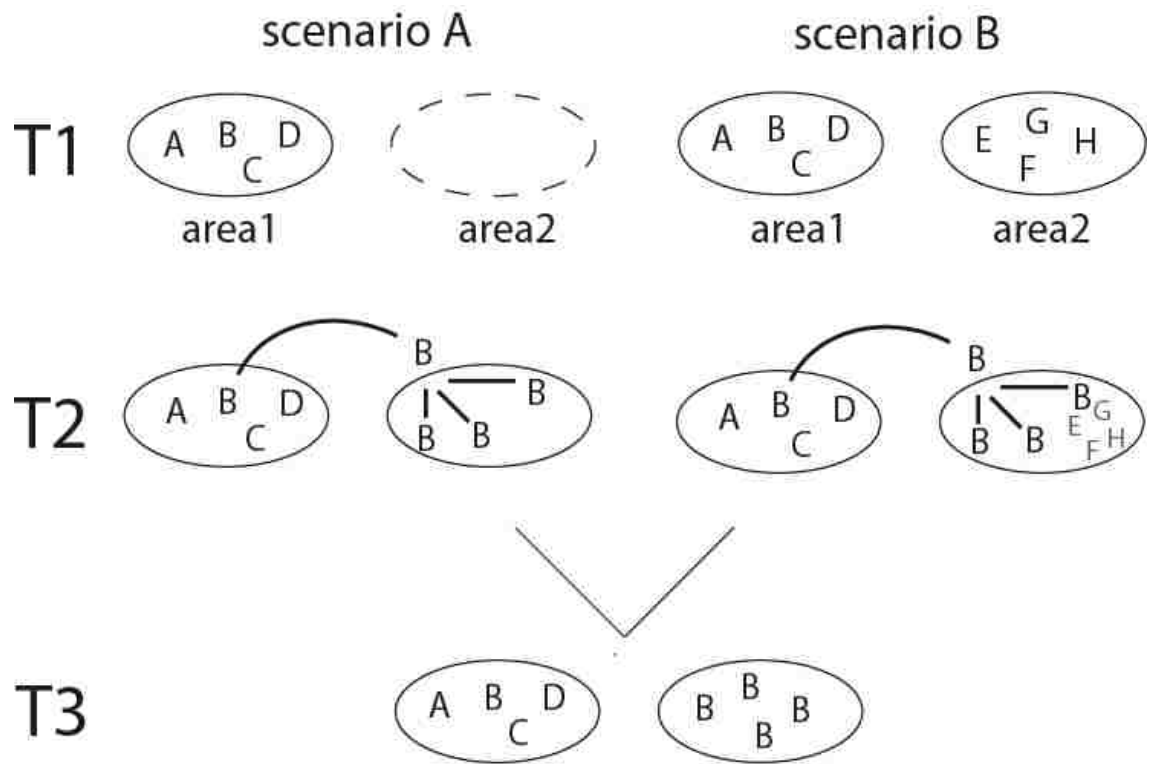
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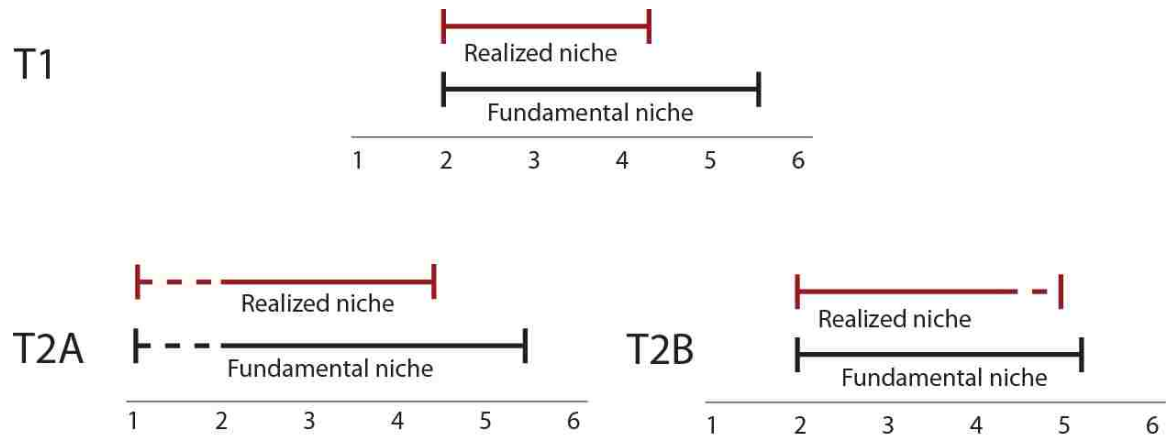
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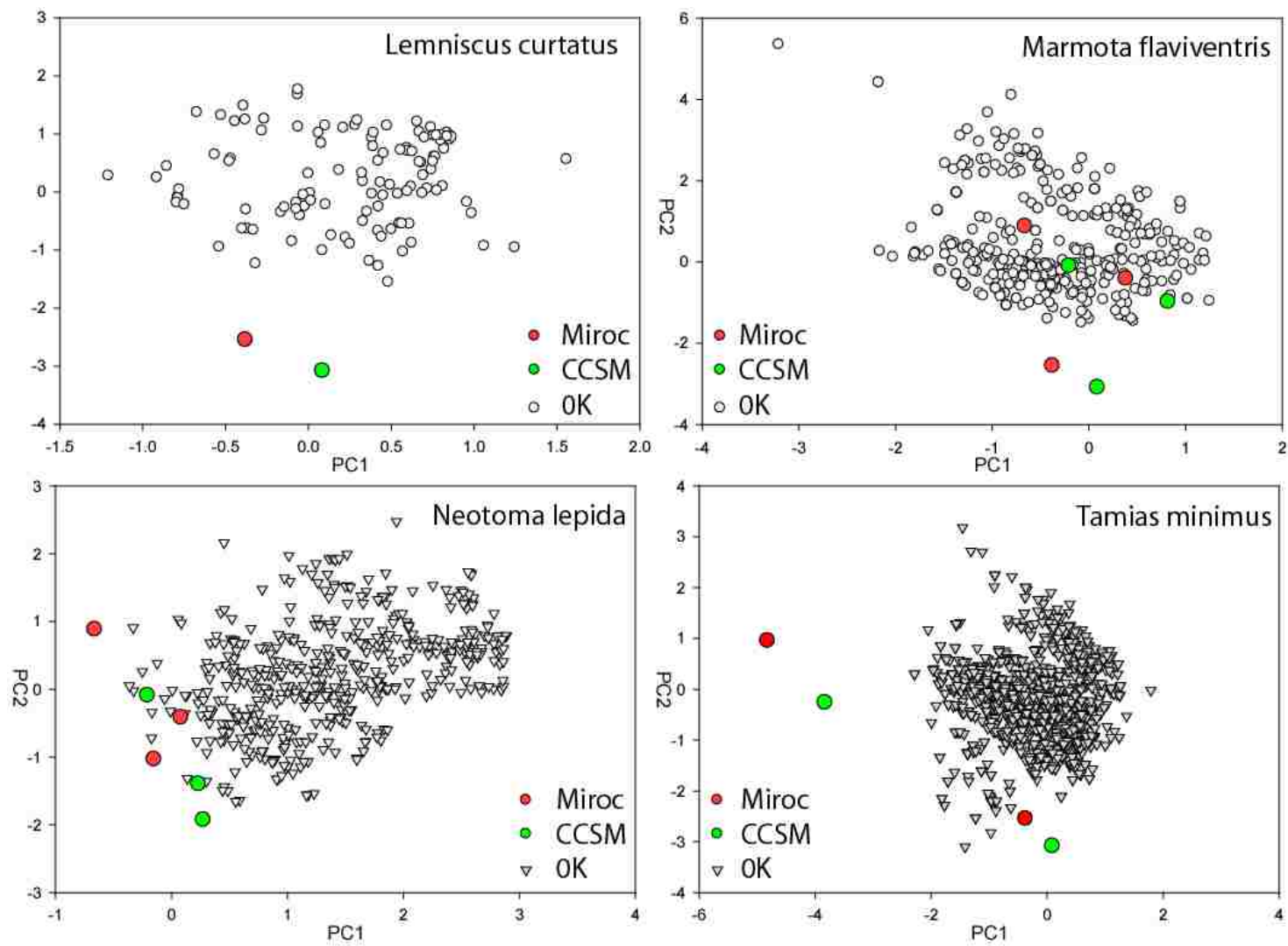
Figure 4.10

Figure 4.11

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APPENDIX 1

SAMPLES OF *DIPODOMYS MICROPS*

Samples of *Dipodomys microps* sorted by locality identification number. Ear-clips are identified by a tissue number (LVT – Las Vegas Tissues), vouchers are identified by a tissue and voucher number (MVZ – Museum of Vertebrate Zoology, TTU – Texas Tech University, NMMNH – New Mexico Museum of Natural History). Latitude and longitude are in decimal degrees and WGS 84 datum.

Arizona: Coconino County: **1** – House Rock Valley, 36.4940, -111.9623 [LVT-9375, LVT-9377, LVT-9380, LVT-9382, LVT-9383, LVT-9384 (NMMNH 5612)]; 36.6294, -111.9747 [LVT-9361, LVT-9363, LVT-9365, LVT-9368]; 36.7256, -111.7583 [LVT-9370]; Mohave County: **2** – 10 mi N Wolf's Hole, 36.8847, -113.5625 [LVT-10399, LVT-10400, LVT-10401, LVT-10402, LVT-10403, LVT-10404, LVT-10405, LVT-10406, LVT-10407]; 36.8939, -113.5615 [LVT-10392, LVT-10393, LVT-10394, LVT-10395, LVT-10396, LVT-10397]; California: Inyo County: **3** – Coso Junction, 36.0517, -117.9370 [LVT-8699 (NMMNH 5601)]; Haiwee, 36.1532, -117.9781 [LVT-8688, LVT-8689, LVT-8692, LVT-8695]; Olancha, 36.2516, -117.9867 [LVT-8683, LVT-8684 (NMMNH 5599)]; **4** – Owens Valley, 36.5364, -117.9256 [LVT-7795 (NMMNH 5519)]; **5** –Saline Valley, 36.8388, -117.9139 [LVT-9795]; **6** –Deep Spring Valley, 37.3038, -118.0562, [LVT-8133 (NMMNH 5580), LVT-8134, LVT-8135, LVT-8136); Kern County: **7** – Koehl Lake, 35.2890, -117.8800 [LVT-8700, LVT-8700, LVT-8701, LVT-8702, LVT-8703, LVT-8704, LVT-8705, LVT-8706, LVT-8707,

LVT-8708, LVT-8709, LVT-8710, LVT-8712, LVT-8713]; Modoc County: **8** – 8 mi S

Eagleville, 41.1621, -119.9928 [LVT-8900, LVT-8901, LVT-8903, LVT-8905]; 5 mi E, 3 mi N

Eagleville, 41.3649, -120.0007 [LVT-8911, LVT-8914, LVT-8915, LVT-8917, LVT-8918, LVT-

8919, LVT-8920, LVT-8921, LVT-8922]; Riverside County: **9** – Stubby Spring, 33.9863, -

116.2305 [MVZ-114058, MVZ-114059, MVZ-148434, MVZ-148435, MVZ-148436, MVZ-

149483, MVZ-149484, MVZ-149569]; San Bernardino County: **10** –12 mi NNE Boron,

35.1493, -117.5718 [LVT-2058]; **11** – Yucca Valley, 34.1450, -116.4684 [MVZ-159304,

MVZ-159305]; **12** – Superior Lake, 35.2259, -117.0300 [LVT 10465, LVT 10466]; **13** –

Clark Mountain, 35.5855, -115.6357 [LVT-10432, LVT-10433, LVT-10434, LVT-10435,

LVT-10436, LVT-10437, LVT-10438, LVT-10439, LVT-10440, LVT-10441, LVT-10442, LVT-

10443, LVT-10444, LVT-10445]; Idaho: Owyhee County: **14** – Bruneau Canyon, 42.7629, -

115.7564 (LVT-10368, LVT-10369, LVT-10370, LVT-10371); **15** –5 mi W Murphy, 43.1902,

-116.6445 [LVT-8969, LVT-8970, LVT-8972, LVT-8983); 2 mi W Murphy, 43.2012, -

116.5861 [LVT-8976, LVT-8978, LVT-8979, LVT-8980, LVT-8981, LVT-8985]; Nevada:

Churchill County: **16** – Fallon (Sand Creek Road), 39.3765, -118.8837 [LVT-9587]; 10 mi

W Fallon, 39.4988, -118.9875 [LVT-9573]; **17** – Hot Springs Mountains, 39.7581, -

118.8735 [LVT-10203, LVT-10204, LVT-10205]; Clark County: Cottonwood Valley,

36.0015, -115.4496; **18** – Cottonwood Valley, 36.0015, -115.4496 [LVT-10684, LVT-

10685]; **19** – Kyle Canyon, 36.2643, -115.4788 [LVT-10446, LVT-10448, LVT-10449, LVT-

10450, LVT-10451, LVT-10452, LVT-10453, LVT-10454, LVT-10455, LVT-10456, LVT-

10457, LVT-10458, LVT-10459, LVT-10460]; Elko County: **20** – Montello, 41.2886, -

114.1579 [LVT-9659, LVT-9660, LVT-9661, LVT-9662]; Tecoma, 41.3196, -114.0804 [LVT-

9653, LVT-9655, LVT-9656, LVT-9657, LVT-9658]; Esmeralda County: **21** – Fish Lake

Valley, 37.7805, -118.0980 [LVT-8128 (NMMNH 5577)]; **22** – 10 mi S Tonopah, 37.9120, -

117.2235 [LVT-10161, LVT-10162, LVT-10164, LVT-10165, LVT-10166, LVT-10167); **23** –

White River Valley, 38.3865, -115.1460 [LVT 08232 (NMMNH 5595), LVT 08234];

38.4084, -115.1199 [LVT 08231 (NMMNH 5594)]; Eureka County: **24** – 5 mi SSW

Beowawe, 40.5203, -116.5138 [LVT-9640, LVT-9641, LVT-9642]; 3 mi SSW Beowawe,

40.5614, -116.4881 [LVT-9646]; Humboldt County: **25** – 10 mi S Battle Mountain,

40.4751, -117.0621 [LVT-8986, LVT-8987, LVT-8988, LVT-8989, LVT-8990]; **26** – ~5 mi W

Sulphur Landing, 40.8432, -118.7577 [LVT-9610, LVT-9611, LVT-9612, LVT-9613, LVT-

9614, LVT-9615, LVT-9616]; **27** – 4 mi E Golconda, 40.9586, -117.4243 [LVT-9635, LVT-

9636]; **28** – 30 mi S Denio, 41.6474, -118.4404 [LVT-9635, LVT-9636]; Lander County: **29**

– Monitor Valley, 39.2288, -116.6990 [LVT-10175, LVT-10176, LVT-10177, LVT-10178,

LVT-10179, LVT-10180]; **30** – Big Smoky Valley, 39.3893, -116.9322 (LVT-10193); Lincoln

County: **31** – Coyote Spring, 37.1481, -114.7228 [LVT-9664, LVT-9665]; 7 mi E Coyote

Spring, 37.1481, -114.7228 [LVT-9785]; **32** – Pahranagat NWR, 37.2044, -115.0662 [TTU-

161809]; 37.2343, -115.1019 [TTU-161826, TTU-161827, TTU-161828]; 37.2343, -

115.1010 [TTU-148048]; 37.2415, -115.1144 [TTU-161832, TTU-161833]; 37.2829, -

115.1272 [TTU-161836]; **33** – Kane Spring Valley, 37.2993, -114.5806 [LVT-10536, LVT-

10537, LVT-10538, LVT-10539, LVT-10540, LVT-10541, LVT-10542, LVT-10543, LVT-

10544, LVT-10545, LVT-10546, LVT-10547, LVT-10548, LVT-10549, LVT-10550, LVT-

10551, LVT-10552, LVT-10553]; **34** – Tickaboo Valley, 37.3195, -115.4383 [LVT-8163];

37.3696, -115.4697 [LVT-9452]; 37.3969, -115.4625 [LVT-9458, LVT-9459]; **35** – Delmar

Valley, 37.5211, -114.8689 [LVT-7754]; 37.5572, -114.8600 [LVT-7771]; **36** – 6 mi N, 31 mi W Hiko, 37.6200, -115.8303 [LVT 05140]; Rachel, 37.7059, -115.8135 [LVT-8158, LVT-8159, LVT-8160, LVT-8161, LVT-8162]; **37** – Dry Lake Valley, 37.7119, -114.7976 [LVT-7757]; 37.7130, -114.8012 [LVT-7764]; 37.7784, -114.8301 [LVT-7773]; **38** – ~6 mi NE Tempiute, 37.7393, -115.5759 [LVT-1570 (NMMNH-5909)]; **39** – Dry Lake Valley, 37.9428, -114.8320 [LVT-7775]; 38.0694, -114.7744 [LVT-7780 (NMMNH-5511); **40** – Cave Valley, 38.3672, -114.8243 [LVT-8060 (NMMNH-5566)]; 38.3773, -114.8428 [LVT-8064 (NMMNH-5570)]; 38.3992, -114.8171 [LVT-8061 (NMMNH-5567)]; **41** – Lake Valley, 38.4299, -114.5834 [LVT-7822 (NMMNH-5533); 38.4515, -114.6098 [LVT-7821 (NMMNH-5532), LVT-7835 (NMMNH-5539)]; Mineral County: **42** – Marietta, Teels Marsh, 38.2294, -118.3136 [LVT-8498]; **43** – Tonapah Junction, 38.2670, -118.1085 [LVT-8505, LVT-8506, LVT-8507]; **44** – Smith Valley, 38.8371, -119.3057 [LVT-9571]; Nye County: **45** – Ash Meadows NWR, 36.3773, -116.2977 [TTU-161787, TTU-161788, TTU-161789]; 36.4037, -116.2754 [TTU-150485]; 36.4267, -116.3018 [TTU-161761]; 36.4708, -116.3235 [TTU-148008]; **46** – Beatty, 36.9086, -116.7583 [LVT-9201, LVT-9202, LVT-9203, LVT-9204, LVT-9205, LVT-9206, LVT-9207, LVT-9208]; 9 mi N Beatty, 36.9845, -116.7230 [LVT-4935 (NMMNH-5968)]; **47** – Nevada Test Site, Area 9, 37.1251, -116.0212 [LVT-10518, LVT-10519, LVT-105120]; Nevada Test Site, Area 10, 37.1561, -115.9720 [LVT-10516, LVT-10517]; **48** – Hot Creek Valley, 38.2100, -116.1800 [LVT-9493 (NMMNH-5613), LVT-9497]; **49** – Railroad Valley, 38.5115, -115.7829 [LVT-8649, LVT-8650]; 38.5209, -115.7533 [LVT-8651]; **50** – 2-8 mi SE Currant, 38.6980, -115.4861 [LVT-9482, LVT-9483]; 38.7203, -115.4624 [LVT-9478, LVT-9479, LVT-94780, LVT-9484];

38.7275, -115.4592 [LVT-9474, LVT-9475, LVT-9476]; 38.7934, -115.5254 [LVT-9469, LVT-9470, LVT-9471]; Washoe County: **51** – Mullen Pass, 39.8730, -119.6210 [LVT-10215, LVT-10216, LVT-10217, LVT-10218, LVT-10219, LVT-10220, LVT-10221, LVT-10222, LVT-10223, LVT-10224, LVT-10225, LVT-10226, LVT-10227]; **52** – Flanigan, 40.1891, -119.8490 [LVT-8525, LVT-8526, LVT-8527]; **53** – 5 mi NE Gerlach, 40.7469, -119.2875 [LVT-9599]; White Pine: **54** – Snake Valley, 38.6303, -114.2701[LVT-8166 (NMMNH-5587)]; 38.6967, -114.1146 [LVT-8173 (NMMNH-5585); LVT-8175, LVT-8176, LVT-8178]; Spring Valley, 38.6586, -114.3823 [LVT-7846 (NMMNH-5547), LVT-7899]; **55** – Spring Valley, 38.9378, -114.4176 [LVT-7850]; 38.9406, -114.4212 [LVT-7901]; **56** – Spring Valley, 39.1397, -114.4982 [LVT-7902, LVT-8054, LVT-8055]; 39.1975, -114.4983 [LVT-8053 (NMMNH-5563)]; 39.2885, -114.4635 [LVT-7903 (NMMNH 5553), LVT 08057]; 39.3026, -114.3890 [LVT-7906 (NMMNH-5556)]; **57** – Steptoe Valley, S of Ely, 39.2336, -114.8395 [LVT-9804]; **58** – Spring Valley, 39.4867, -114.3878 [LVT-8056]; OR: Harney County: **59** – Fields, 42.3067, -118.6598 [LVT-8958, LVT-8959, LVT-8960, LVT-8965]; **60** – 20 mi S Narrows, 43.0709, -118.8730 [LVT-8943, LVT-8944, LVT-8947, LVT-8948]; Lake County: **61** – Alkali Lake, 42.9433, -120.0274 [LVT-8936, LVT-8937]; 43.0107, -120.0114 [LVT-8925, LVT-8927, LVT-8928, LVT-8929, LVT-8930, LVT-8938, LVT-8940, LVT-8941]; Utah: Boxelder County: **62** – Kelton, 41.7260   , -113.1380 [LVT-8625, LVT-8628]; 41.7410, -113.1260 [LVT-8629, LVT-8630, LVT-8631], 41.7550, -113.1080 [LVT-8632, LVT-8633, LVT-8634, LVT-8635]; Juab County: **63** – Snake Valley, 39.4568, -113.9606 [LVT-8656, LVT-8657, LVT-8658, LVT-8659, LVT-8665, LVT-8666, LVT-8667, LVT-8670, LVT-8671, LVT-8672, LVT-8673, LVT-8675, LVT-8679]; Millard County: **64** – 10 mi S Delta,

39.0580, -112.7640 [LVT-8594]; White Sage Valley, 39.1030, -112.8500 [LVT-8587, LVT-8588, LVT-8603 (NMMNH-5597); Cricket Mountains, 39.1120, -112.7600 (LVT-8589, LVT-8590, LVT-8591, LVT-8592, LVT-8593); Tooele County: **65** – Rush Valley, 40.0780, -112.2560 [LVT-8621]; **66** – Puddle Valley, 40.8910, -112.9330 [LVT-8639]; 40.8950, -112.9460 [LVT-8638]; 40.9100, -112.9040 [LVT-8646, LVT-8647]; Washington County: **67** – 23 mi N Littlefield, 37.0784, -113.9237 [LVT-10409, LVT-10410, LVT-10411, LVT-10412, LVT-10413]; 24 mi N Littlefield, 37.0952, -113.9540 [LVT-10418, LVT-10419, LVT-10420].

APPENDIX 2

SAMPLES OF *PHRYNOSOMA PLATYRHINOS*

Descriptions of general sample areas for *Phrynosoma platyrhinos* by country, state,

county, site identification number (referenced in Fig. 2.1A), site reference name,

latitude, and longitude. Samples associated with the sample area follow in parentheses.

United States: Arizona: Coconino County: **1** – House Rock Valley, 36.6294, -111.9747

(LVT-9367); La Paz County: **2** – Yuma Proving Grounds, 32.8683, -114.3742 (CAS 228862-

3, LVT-9951-3); **3** – vicinity of Salome, 33.6379, -113.4419 (LVT-7381); **4** – Bouse-

Quarzsite Rd (CAS-228896); **5** – Bouse Dunes, 33.8578, -113.9480 (CAS-228895, LVT-

829-32); **6** – Wenden, 33.8819, -113.5475 (LVT-7382-3); Maricopa County: **7** – vicinity of

Ajo, 32.4902, -112.8621 (LVT-810, 817-9); **8** – Wittmann, 33.7764, -112.5285 (LVT-361);

Mohave County: **9** – vicinity of Golden Shores, 34.8038, -114.4966 (LVT-7728); **10** –

vicinity of Oatman, 34.9090, -114.4327 (LVT-6346); **11** – E of Kingman, 35.1059, -

113.6698 (LVT-6343-5); **12** – Dolan Spring Rd, 35.6407, -114.2424 (LVT-735); Pima

County: **13** – W of Tucson Mtn Park, 32.2231, -111.1143 (LVT-820); Yuma County: **14** –

Pinacate Lava Flow, 32.1017, -113.4621 (CAS-228867-9); **15** – vicinity of Copper Mtn,

BMG Airforce Range, 32.4375, -113.9663 (CAS-8874); **16** – BMG Airforce Range,

32.4873, -114.4577 (CAS_228841, 9922); **17** – Mohawk Dunes, 32.6947, -113.8083 (CAS-

228865); California: Imperial County: **18** – Ocotillo, 32.7764, -116.0695 (CAS-3601, LVT-

6368); **19** – Ogilby Rd, 32.9833, -114.8989 (CAS-228893); Inyo County: **20** – vicinity of

Shoshone, 35.9956, -116.2149 (LVT-6080); **21** – Panamint Valley Rd, 36.2804, -117.3712 (LVT-8379-83); **22** – vicinity of Darwin Falls, 36.3567, -117.5279 (LVT-8374-8); **23** – Saline Valley Rd, 36.4166, -117.6554 (LVT-7386-7); **24** – vicinity of Bishop, 37.2359, -118.2565 (LVT-851-4); **25** – Eureka Valley Rd, 37.2589, -117.9279 (LVT-7385); **103** – vicinity of Benton, 37.6878, -1184309 (LVT-10514); Modoc County: **26** – Surprise Valley, 41.5646, -120.0235 (LVT-6364-5); Riverside County: **27** – vicinity of Blythe, 33.5388, -114.7849 (LVT-816); **28** – near Joshua Tree NM, 33.8680, -115.6382 (LVT-815); San Bernardino County: **29** – Cadiz Valley, 34.0550, -115.2503 (LVT- 7389); **30** – Whipple Mtns, 34.2587, -114.5429 (LVT-7390); **31** – vicinity of Amboy, 34.5377, -115.7236 (LVT-812-4, LVT-6082-3); **32** – Ord Mtns, 34.7113, -116.8321 (LVT-7388); **33** – vicinity of Barstow, 34.8612, -117.1005 (LVT-8366-8); **34** – vicinity of Kelso Dunes, 34.9108, -115.7303 (LVT-8369-73); **35** – Arrowhead Junction, 35.1851, -114.9027 (LVT-7735); **36** – Cima Rd, 35.4108, -115.6418 (LVT-636); **37** – Spring Mtn, 35.5855, -115.6357 (LVT-9807); **38** – Trona, 35.7628, -117.3719 (LVT-8365); San Diego County: **39** – Carrizo Badlands, 32.8548, -116.1775 (DGM-804); **40** – Blair Valley, 33.0293, -116.4146 (DGM-549); **41** – Ocotillo Wells State Vehicle Recreation Area, 33.1544, -116.1675 (CAS-228891); **42** – Borrego Springs, 33.1834, -116.3257 (CAS-228880, 228894); Idaho: Owyhee County: **43** – Bruneau Canyon, 42.7629, -115.7564 (LVT-10373-4); **44** – vicinity of Murphy, 43.1471, -116.4998 (LVT-934); Nevada: Churchill County: **45** – Hot Springs Mtns, 39.7581, -118.8735 (LVT-10194-6); **46** – Stillwater Mtns, 39.9935, -118.1820 (LVT-867); Clark County: **47** – El Dorado Valley, 35.7727, -114.9104 (LVT-0473-5); **48** – S of Sloan, 35.9122, -115.2064 (LVT-801-2); **49** – vicinity of Las Vegas, 36.1256, -115.2612 (LVT-

811); **50** – vicinity of Apex, 36.2977, -114.9625 (LVT-824-6); **51** – Lee Canyon, 36.4085, -115.5668 (CAS-223435); **52** – Whitney Pockets, 36.4988, -114.1519 (CAS-223372); **53** – Overton, 36.5433, -114.4649 (LVT-465); **54** – Arrowhead, 36.6589, -114.5758, (LVT-803-5); **55** – Upper Mormon Mesa, 36.7774, -114.4281 (LVT-0471-2); **56** – Coyote Springs Valley, 36.8312, -114.8646 (LVT-476-8); Elko County: **57** – Currie, 40.2636, -114.7475 (LVT-924); **58** – Elko, 40.8884, -115.8083 (LVT-10382-3); Esmeralda County: **59** – vicinity of Bonnie Claire Lake, 37.1539, -117.1781 (CAS-223438, 8976, LVT-6361); **60** – vicinity of Gold Field, 37.8735, -117.2436 (LVT-6311-5); **61** – vicinity of Tonopah, 37.9120, -117.2235 (LVT-10168-72); **62** – Blow Sand Mtn, 39.1990, -118.7221 (LVT-10464); Humboldt County: **63** – vicinity of Sulphur Landing, 40.8432, -118.7577 (LVT-9625); **64** – Black Rock Desert, 40.8953, -118.5200 (LVT-919); **65** – Golconda Summit, 40.9210, -117.3915 (DGM-1775); **66** – vicinity of Winnemucca, 41.3463, -117.5984 (LVT-941-2); **67** – McGee Mtns, 41.7668, -118.9189 (LVT-10248-53); Lander County: **68** – vicinity of Battle Mtn, 40.1889, -117.1591 (LVT-916-8); Lincoln County: **69** – Tikaboo Valley, 37.3774, -115.4663 (LVT-9451); **70** – Rachel, 37.6715, -115.7578, (LVT-9461); **71** – Dry Lake Valley, 37.9054, -114.8152 (LVT-7760, 9958-9); **72** – vicinity of Hiko, 37.9230, -115.0083 (LVT-0915); Nye County: **73** – Cave Valley, 38.3673, -114.8243 (LVT-9957); **74** – Pahrump Valley, 36.1626, -115.8990 (LVT-6079); **75** – Ash Meadows, 36.4275, -116.3520 (LVT-10246-7); **76** – vacitity of Mercury Hwy and Hwy 95, 36.5971, -115.9536 (LVT-6317); **77** – Crater Flat, 36.8085, -116.6047 (LVT-470); **78** – vicinity of Beatty, 37.0970, -116.7958 (LVT-6316); **79** – vicinity of Hwy 376 and Hwy 6, 38.3896, -117.1595 (LVT-838-40, 843-5); **80** –Round Mtn dump site, 38.7049, -117.0742 (LVT-841-2); **81** – Railroad

Valley near Currant, 38.7243, -115.4783 (LVT-9464-6, 9481); Pershing County: **82** – Black Rock Desert, 40.7978, -119.0297 (LVT-920-2); Washoe County: **83** – Empire Range Rd, 40.6256, -119.4316 (LVT-6366-7); White Pine County: **84** – Hamlin Valley, 38.6599, -114.1502 (DGM-1104); **85** – Snake Valley, 38.9737, -114.0745 (CAS-223386, 3390, LVT-6362-3); **86** – Spring Valley, 39.1462, -114.5084 (LVT-9805); **104** – White River Valley, 38.99379, -115.07311 (LVT-10523); Oregon: Harney County: **87** – vicinity of Fields; 42.2527, -118.6606 (LVT-0936-40); Malheur County: **88** – Jordan Range Rd, 42.2149, -117.7841 (LVT-935); Utah: Box Elder County: **89** – West Desert, 41.4490, -113.6427 (DGM-1027-9); **90** – vicinity of Etna, 41.5426, -113.9629 (LVT-925-6); Iron County: **91** – Lund, 38.0245, -113.4044 (LVT-858-61); Millard County: **92** – Desert Experimental Range, 38.6623, -113.8493 (LVT-931-3); **93** – Sunstone Knoll, 39.1487, -112.7164 (CAS-228887); **94** – Tule Valley, 39.4333, -113.6333 (LVT-10462-3); Tooele County: **95** – vicinity of Callao, 40.1778, -113.8031 (LVT-930); **96** – Skull Valley Rd, 40.6641, -112.6739 (CAS-228889); **97** – vicinity of Wendover, 40.9936, -113.8401 (LVT-929); **98** – N of Wendover, 41.2356, -114.0244 (LVT-927-8); Washington County: **99** – Beaver Dam Slope, 37.0846, -113.9483 (CAS-228888, LVT-855-7); Mexico: Baja California North: **100** – El Moreno, 31.0267, -115.1010 (DGM-481); **101** – Valle Santa Clara, 31.2051, -115.3121, (DGM-477-8); Sonora: **102** – Puerto Penasco, 31.5536, -113.4735 (KVY-0013).

APPENDIX 3

GLOSSARY

Analogous climate: An association of climatic variables (either in combination or by correlation) used in model calibration that is the same as that used in the model projected either in time or across space.

Calibration: Development of species distribution models using a particular algorithm (e.g., General Linear Models, Bioclim, GARP, Maxent), records of species presence or presence-absence, and a set of environmental variables; establishing a baseline for model projection either in time or across space.

Calibration range: The range of values for a particular variable across a particular geographic extent used during the calibration of a species distribution model.

Clamping: The restriction of variable values during model projection to those encountered during calibration. In Maxent this is done by truncating the value to the minimum or maximum of the calibration range. The logistic probability (i.e. habitat suitability) of the truncated values in the projected model equals that of the minimum or maximum value used in calibrating the model.

Commission error: A geographic location identified by a model as suitable when no individuals of the focal species actually occur in the predicted area – over-prediction.

Extrapolation: Estimating new values beyond a discrete set of known values based on a hypothesized relationship. In species distribution modeling, this means estimating the response of a species to environmental values outside the range of known values.

Fundamental Niche: The full suite of environmental conditions under which populations of a particular species can potentially survive (sensu Hutchinson 1957). Organisms typically occupy a narrower range of conditions (i.e. realized niche) because of biotic interactions, barriers to dispersal, or non-existence of particular abiotic conditions during a certain time period.

Non-analogous climate: An association of climatic variables (either in combination or by correlation) used in model calibration that are NOT the same as those in the projected model (either in time or across space).

Omission error: A geographic location identified by a model as unsuitable when individuals of the focal species actually occur at the site – under-prediction.

Projection: Application of rules developed during the calibration of a species distribution model to a new set of environmental layers representing either a different time period or different area.

Projection range: Range of values for a particular variable across the geographic extent of a location on which a species distribution model will be projected.

Realized Niche: The suite of biotic and abiotic environmental conditions defining the actual occurrence of a species. Populations may be able to survive under a wider range of conditions (i.e. fundamental niche), but are limited to the realized niche because of factors such as biotic interactions, barriers to dispersal, or non-existence of particular abiotic conditions during certain time period.

Realized niche shift: A shift in the actual or potential occurrence of a species resulting from plasticity, changes in biotic interactions or the development of previously

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unavailable (non-existent) environmental conditions. Under such conditions, there is no

change in the fundamental niche, only a shift in the portion of the fundamental niche

occupied.

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