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### MAMMALS ON MOUNTAINSIDES REVISITED: ANALYZING MULTIPLE DIMENSIONS OF DIVERSITY TO GAIN NEW INSIGHT ON COMMUNITY ASSEMBLY AND BIOGEOGRAPHY

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MAMMALS ON MOUNTAINSIDES REVISITED: ANALYZING MULTIPLE DIMENSIONS  
OF DIVERSITY TO GAIN NEW INSIGHT ON COMMUNITY ASSEMBLY AND  
BIOGEOGRAPHY

BY

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DISSERTATION

Submitted to the University of New Hampshire  
in Partial Fulfillment of  
the Requirements for the Degree of

Doctor of Philosophy  
in  
Earth and Environmental Sciences

September 2019

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On June 5, 2019

Original approval signatures are on file with the University of New Hampshire Graduate School.

To Quinn, Vaiea, Braelyn, and Madeline.

In hopes that their generation will be even more passionate and effective protectors of the planet's biodiversity than those that preceded them.

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## ABSTRACT

# MAMMALS ON MOUNTAINSIDES REVISITED: ANALYZING MULTIPLE DIMENSIONS OF DIVERSITY TO GAIN NEW INSIGHT ON COMMUNITY ASSEMBLY AND BIOGEOGRAPHY

by

Brooks A. Kohli

University of New Hampshire

Understanding how biodiversity is distributed, maintained, and altered is a fundamental goal of ecology and is especially important for predicting the effects of ongoing rapid environmental change. Traditionally, diversity has been described in taxonomic terms using the number and abundance of species (e.g., species richness). However, biodiversity is multi-faceted and includes functional (ecological traits) and phylogenetic (evolutionary relationships) dimensions that emphasize the similarities and differences among species. Functional diversity is particularly appealing because it quantifies the range and prevalence of traits in an assemblage and helps link patterns of diversity to the ecological processes that generate them. I used a multi-dimensional diversity approach to investigate elevation-diversity patterns, community assembly processes, and patterns and drivers of change in small mammal community structure over the last century in mountain ranges in the Great Basin of western North America.

In Chapter 1, I developed a novel trait-based approach for discriminating between environmental filtering and biotic interactions as possible drivers of species co-occurrence across environmentally heterogeneous sites. Expectations of environmental filtering were assessed using species similarity in the traits of habitat affinity and geographic range location whereas expectations of biotic interactions were based on similarity of diet and body size. When applying this hypothesis-testing framework to small mammal species pairs distributed among and within local sites distributed across three broad elevational gradients, most associations were consistent with environmental filtering. However, negative associations among four species pairs were consistent with expectations under biotic interactions, including two pairs for which competitive exclusion has previously been documented (two species of chipmunk of the genus *Tamias* and two species of pocket mice of the genus *Perognathus*). Discerning the mechanisms responsible for co-occurrence patterns was made possible by developing and testing explicit hypotheses based on trait similarity.

Although the appreciation and measurement of multiple dimensions of biodiversity has grown recently, refinement of trait data for mammals is much needed. Most studies rely on categorical rather than continuous traits. As a result, finer variation present among species is overlooked which may obscure patterns, particularly for studies on smaller species pools. In Chapter 2, I identified three continuous ecomorphological traits that have a demonstrable link to function and reflect traditionally used functional guilds. Specifically, I investigated the relative medullary thickness (RMT) of the kidney as a measure of habitat affinity (mesic-to-xeric spectrum), hair density as a measure of thermoregulatory ability, and an integrated suite of cranial and dental measurements as an indication of diet specialization. Each trait captured traditional functional group differences for 32 species of Great Basin small mammals while also

illuminating meaningful within-group variation. Although each trait had a strong phylogenetic signal, phylogeny alone obscures informative ecological differences (similar to the use of categories). The greater resolution of continuous trait data will facilitate more refined assessments of functional diversity and improve efforts to test ecological theories and track responses to environmental change.

With an improved functional trait matrix, including the ecomorphological traits from Chapter 2, I revisited the classic elevation-diversity relationship in Chapter 3 by investigating patterns of functional and phylogenetic diversity in addition to species richness along three elevational gradients. Elevation-species richness relationships are one of the most widely studied biogeographic patterns, but there have been few investigations using other dimensions of diversity. In contrast to the well-established mid-elevation peak in species richness, functional and phylogenetic diversity generally increased with elevation. Deviations among dimensions reveal that species richness is a poor surrogate for these other dimensions of diversity for small mammals. Decomposing functional diversity into subsets of traits that reflect specific niche axes can provide insight into the drivers of community assembly over elevation. Specifically, clustering of traits associated with abiotic conditions and habitat affinities provides evidence for environmental filtering where overdispersion among traits corresponding to resource acquisition and use suggests biotic interactions (namely competition) are structuring assembly among community members. I found strong evidence for environmental filtering in both low and high-elevation communities. Evidence for competition as a driver was not consistent with theoretical expectations under the stress dominance hypothesis, guild assembly rules, or competitor limitation of range margins.

In Chapter 4, I used resurveys of sites in Great Basin National Park and vicinity to track functional diversity responses to climate and habitat change. Over the 86-year interval between surveys, functional diversity decreased even though species richness and total community abundance were stable at sites. In general, communities become less functionally even; species with more generalized traits became more dominant and climate and habitat specialists constituted smaller components of most communities. Larger species with lower reproductive potential also tended to fare worse over time. Functional evenness decreased more due to climate responses whereas functional divergence and dispersion were reduced more among habitat traits. In sum, this analysis indicates how the individual and interactive effects of change in abiotic conditions, cover types, and resource base are translated to change in community structure through species' traits. My results emphasize the importance of using abundance-weighted functional diversity metrics to detect subtle or early-stage changes to community structure that may serve as an early warning of more dramatic diversity loss in the future.



## CHAPTER 1

# A TRAIT-BASED FRAMEWORK FOR DISCERNING DRIVERS OF SPECIES CO-OCCURRENCE ACROSS HETEROGENEOUS LANDSCAPES<sup>1</sup>

## INTRODUCTION

One of the central pursuits of ecology is to understand the factors that affect community assembly. Ecologists have long recognized the influence of deterministic processes, such as environmental filtering (Grinnell 1917, Whittaker 1967) and biotic interactions (Elton 1927, MacArthur and Levins 1967, Diamond 1975), as well as stochastic demographic and dispersal processes (MacArthur and Wilson 1967, Hubbell 2001) in contributing to species co-occurrence and community structure. However, it remains difficult to determine the relative roles mechanisms play because they may act concurrently rather than exclusively, may be scale dependent, and may fluctuate in dominance over time (Walther 2010, Boulangeat et al. 2012, Wisz et al. 2013, Araújo and Rozenfeld 2014). Despite this challenge, identifying the drivers of species co-occurrence is key to understanding community assembly processes and the potential effects of environmental change (Alexander et al. 2015, Lindenmayer et al. 2015).

Null model analysis of species co-occurrence is among the most commonly used approaches for identifying patterns of non-random community structure (Connor and Simberloff 1979, Brown et al. 2002, Gotelli and McCabe 2002). Null models allow for the detection of non-random species associations from presence-absence matrices (Gotelli and Ulrich 2012). Non-random associations can be positive (species tend to co-occur at sites; aggregated) or

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<sup>1</sup> Kohli, B.A., R.C. Terry and R.J. Rowe. 2018. *Ecography* 41: 1921-1933.

negative (species rarely or never co-occur at sites; segregated) and are inferred to result from an ecological process, most often biotic interactions or environmental filtering. When analyzing patterns from sites that are implicitly similar and internally homogeneous in their environmental characteristics, any deviations are inferred to result from biotic interactions (Diamond 1975). It is more difficult to discern the underlying mechanism when sites are heterogeneous (among and/or within sites) because biotic interactions and environmental filtering can produce similar patterns (López et al. 2013, Fowler et al. 2014). For example, species could be segregated either due to competitive exclusion or because they inhabit different sites according to individual environmental preferences.

Several null model approaches have been proposed to discriminate among multiple possible mechanisms of co-occurrence, including the use of constrained models to account for distributional or environmental differences (Peres-Neto et al. 2001, Sanderson 2004, Ovaskainen et al. 2010), and post hoc analyses incorporating the characteristics of sites (Sfenthourakis et al. 2006, Blois et al. 2014) or species (Sfenthourakis et al. 2006, Ulrich et al. 2010, Collins et al. 2011, Smith et al. 2016). Logical hypothesis-testing frameworks using site or species information are especially promising for distinguishing among causal mechanisms of co-occurrence (Sfenthourakis et al. 2006, Blois et al. 2014, D'Amen et al. 2018), but a repeatable and generalizable framework based on species traits has yet to be developed (but see Smith et al. 2016). Drivers of co-occurrence have been inferred using phylogenetic similarity, a proxy for ecological similarity based on the principle of niche conservatism (Sfenthourakis et al. 2006, Ulrich et al. 2010, Collins et al. 2011); however, trait-based approaches may be better suited for disentangling drivers because they more directly relate to mechanisms and facilitate more general hypotheses by isolating traits that relate to multiple mechanisms (Fox 1999, Spasojevic

and Suding 2012, Mouchet et al. 2013, Ovaskainen et al. 2017). Recent advances in pairwise co-occurrence analysis also afford more detailed insights by allowing one to determine drivers for individual species pairs, even for patterns that may differ from the assemblage as a whole (Gotelli and Ulrich 2010, Ulrich and Gotelli 2013, Veech 2014).

Our objective was to develop a trait-based framework that offers a general and versatile approach for inferring mechanisms from pairwise co-occurrence patterns of species across heterogeneous sites. Here we describe a novel hypothesis-testing framework that utilizes hierarchical spatial sampling and functional trait similarity to discriminate between the two most commonly invoked causes of non-random co-occurrence patterns: environmental filtering and biotic interactions. We demonstrate this framework using occurrence data and functional guild classifications of small mammals from mountain ranges in the Great Basin, USA. The basin and range topography of the region provides an opportunity to investigate drivers across broad environmental gradients that contain a high degree of local habitat heterogeneity (Brown 1971a, Rickart 2001, Rowe et al. 2010, 2011). Small mammals (rodents and shrews < 500g) are an excellent group for studying community assembly because they are taxonomically and functionally diverse, and sensitive to climate and habitat conditions (Hadly 1996, Moritz et al. 2008, Rowe et al. 2011). Decades of pioneering work on small mammals have demonstrated the role of competitive interactions (Brown 1971b, Bowers and Brown 1982, Fox and Kirkland 1992, Fox and Brown 1993, Dayan and Simberloff 1994), habitat heterogeneity (Rosenzweig and Winakur 1969, Stevens et al. 2012), stochastic processes (Brown 1971a, Lawlor 1998), and various combinations of these factors (Ernest et al. 2008) in structuring co-occurrence and community composition. Testing our framework in a well-studied system provides an excellent backdrop for generating trait-based hypotheses and for validating our findings.

## **MATERIALS AND METHODS**

### **Analytical Framework**

Our framework applies trait-based hypotheses to identify the ecological processes underlying non-random co-occurrence patterns among species pairs (Fig. 1-1). We achieve resolution through (i) hierarchical sampling and (ii) functional trait similarity. In our example, co-occurrence patterns are identified at two hierarchical spatial scales – landscape and local. We define landscape scale as the set of sites surveyed across the elevational gradient of a single mountain range. We define local scale as the set of microhabitats sampled at a site. At each scale, a species pair may exhibit a random association or a non-random association (segregated or aggregated). A multi-scale approach may reveal non-random patterns that would otherwise be missed if analyzed at only a single scale. For example, species that are aggregated at the landscape scale (found at the same sites along the gradient) may overlap in their abiotic requirements but segregate locally (found in different habitats within each site) due to competitive interactions.

Figure 1-1 depicts the three association types that yield nine possible combinations across the two spatial scales. The mechanism(s) that are strong enough to create a non-random pattern are then identified using tests of functional trait similarity. Of the nine combinations, eight are biologically meaningful while one, a pair that is segregated across the landscape yet aggregated locally (scenario 9 in Fig. 1-1), is not possible in a nested sampling design. If the conditions of a given trait-based test are met, the resulting mechanism is considered the parsimonious explanation for the observed co-occurrence pattern. The inference of a mechanism may require comparing similarity for one or both relevant trait types ('EF' or 'BI' traits in Fig. 1-1). In some cases, tests involving one trait type inform both mechanisms and the conditions represent

mutually exclusive couplets (scenario 3 and 6). Other cases involve separate tests of each trait type to support one mechanism over the other (scenario 2, 7, and 8). However, if the conditions of both tests are met, the simultaneous action of both mechanisms is implied.

For two of the eight possible pattern combinations (scenarios 1 and 4 in Fig. 1-1), there is no ambiguity in mechanism. For the other six, we determined whether environmental filtering or biotic interaction explain the observed patterns. Additional information may help to verify conclusions in these cases, such as whether the requirement of sympatry is met for biotic interactions. Lastly, in one case (scenario 5) similarity in both trait types is required to support a conclusion of biotic interaction to the exclusion of environmental filtering.

Although previous frameworks have also addressed dispersal limitation as a mechanism (e.g. Blois et al. 2014), we do not include it here because we assess co-occurrence at the landscape (along elevational gradients of each mountain independently) rather than the regional scale (e.g. among multiple mountain ranges). Regional scale questions would require a consideration of dispersal limitation, but within a mountain these species are not restricted by spatial distance because sites at the bottom and top of the mountain are no more than a few kilometers apart.

The choice of functional traits is crucial to drawing ecologically meaningful conclusions, especially when working at multiple spatial scales (Winemiller et al. 2015, Rosado et al. 2016). Several independent traits should be selected that are most appropriate for detecting environmental filtering (“EF traits”) and biotic interactions (“BI traits”) because different processes are often mediated through different traits, and more than one process may be acting simultaneously (Spasojevic and Suding 2012, Trisos et al. 2014). Furthermore, tests of one type of trait may be informative for discerning among both mechanisms (e.g. scenario 3 in Fig. 1-1).

Appropriate traits to test for environmental filtering often include those relating to climate or habitat requirements. Similarly, tests of biotic interaction should directly relate to resource acquisition and the ability of a pair to coexist, for example, based on their dietary preference or body size.

### **Study system**

The Great Basin of the western United States is characterized by a distinctive physiography containing numerous isolated mountain ranges (Grayson 2011). The cold desert ecosystem falls in the rain shadow of the Sierra Nevada and is generally arid. However, the basin and range topography creates strong temperature and moisture gradients which structure discrete vegetation zones, from desert shrublands in the valleys to alpine tundra on the highest peaks. Within these major zones, local moisture variation and edaphic factors create a mosaic of discrete, adjacent habitat types (Hall 1946, Trimble 1999). The diverse climate and habitat conditions of Great Basin mountain ranges harbor high small mammal species richness, including ecological specialists and generalists (Hall 1946, Badgley et al. 2014, Rowe and Terry 2014). For example, while some species are widespread and occur at nearly any elevation, others are restricted to particular zones, such as montane habitats or desert lowlands (Rickart 2001, Rowe et al. 2010).

### **Small mammal field surveys**

Occurrence data for small mammals were generated from comprehensive field surveys conducted during the summer months (May-September) in three independent Great Basin mountain ranges: the Ruby Mountains (2006-2008), Toiyabe Range (2009-2011), and Snake Range (2015-2016) (Fig. 1-2). These mountain ranges share a common biogeographic history and are all large – exceeding 3,450m in elevation and thus containing the full complement of the

region's habitat types along the elevation gradient (Mensing et al. 2013, Rowe et al. 2015b). The respective assemblages also share 52-69% of small mammal species captured during our surveys, with 15 of 34 species observed in all three mountain ranges (Appendix B, Table B1).

Survey sites ( $n > 20$ ) were distributed along the elevational extent of each mountain range. At each site, independent traplines were set within discrete habitats, encompassing the full range of local moisture availability and vegetative communities (e.g. open shrubland, woodland, meadow, riparian). The number of traplines per site (2-6) varied with the number of habitats present. All sampling was removal sampling and followed protocols detailed in Rowe et al. (2010), with sites trapped for a minimum of 480 trapnights (one trap, set for a 24-hour period) over at least three consecutive nights. Sherman box traps and snap traps (Museum Special and Victor rat traps) were baited with birdseed or peanut butter and rolled oats, and checked twice daily. Trapping was intended to sample terrestrial, non-volant mammals less than ~500g, and as such, species not reliably captured with these methods (e.g. lagomorphs, carnivores, gophers) were excluded from analyses.

In the Snake Range, a total of 16,127 trapnights at 26 sites spanning 1,823m (1,574-3,397m) in elevation yielded 1,805 individual captures of 24 rodent and shrew species. This effort and trap success is comparable to that in the Ruby Mountains (16,170 trapnights at 22 sites along a 1,424m gradient yielded 1,518 captures of 23 species) and Toiyabe Range (15,080 trapnights at 24 sites along a 1,055m gradient yielded 3,198 captures of 33 species) (Rowe and Terry 2014). Collecting procedures followed guidelines established by the American Society of Mammalogists (Sikes et al. 2016) and were certified by the Animal Care and Use Committee of the University of Utah (06-02001, 09-02004, 15-02001) and University of New Hampshire (111104A, 141103A; Appendix A). Specimens and field notes are archived at the Natural

History Museum of Utah (University of Utah), the Monte L. Bean Life Science Museum (Brigham Young University), and the Museum of Vertebrate Zoology (University of California, Berkeley).

### **Co-occurrence patterns**

Survey data were summarized into six presence-absence matrices: one at the landscape scale (species occupancy at sites) and one at the local scale (species occupancy in traplines placed in discrete habitats within each site) for each of the three mountain ranges. Species occurring at <5% of sites were considered rare and excluded from analyses (Peres-Neto 2004). This resulted in the removal of species found at only one site in a given mountain range ( $n = 3-4$  per data set). The resulting matrix dimensions were 15 species  $\times$  22 sites and 15 species  $\times$  62 traplines in the Ruby Mountains; 27 species  $\times$  24 sites and 27 species  $\times$  78 traplines in the Toiyabe Range; and 20 species  $\times$  26 sites and 20 species  $\times$  89 traplines in the Snake Range.

We tested for non-random pairwise species associations with the FORTRAN program Pairs (Ulrich 2008). Pairs calculates a C-score for all possible species pairs in a matrix and compares the scores to a null distribution generated by randomizing the matrix. C-scores indicate the nature of a species association (aggregated or segregated) and when standardized, a measure of association strength (Stone and Roberts 1990). To facilitate comparison across matrices, Pairs generates a standardized Z-score for each species pair. Due to the method of calculation, significant aggregations correspond to negative Z-scores and segregations have positive Z-scores. Pairs uses an empirical Bayesian approach to help control Type I error when determining the significance of individual species pairs, which is necessary due to the large number of non-independent pairwise comparisons (for details see Gotelli and Ulrich 2010, Blois et al. 2014). We report significant pairs according to the Bayes Mean criterion. We randomized matrices



10,000 times using the fixed row and column, sequential-swap algorithm (Ulrich 2008). Fixed-fixed algorithms are preferable when sampling units are not perfect replicates and species richness is variable among units, as is expected when sampling along gradients (Gotelli 2000). We ran Pairs three times for each matrix to verify reproducibility of results, which can contain minor variations, particularly for large, sparse matrices (von Gagern et al. 2015). Our matrices range in fill from 28-45% for sites and 16-27% for traplines. Only seven pairs from the Toiyabe Range (the largest assemblage) were inconsistently identified as significant by the Bayes Mean criterion (five from the sites matrix, two from the trapline matrix). We excluded these from analyses so that any conclusions were drawn only for the most certain associations.

In addition to pairwise analyses, we assessed whole-matrix structure based on the average C-score of all species pairs, using the R package ‘EcoSimR’ (Gotelli et al. 2015). Significant aggregated and segregated structure was determined by comparing the empirical C-score of each matrix to the 95% confidence interval of simulated scores generated using the fixed-fixed null model randomization algorithm. Random species  $\times$  site matrices were simulated 1000 times with a burn-in of 500 iterations. To ensure stationarity for the larger species  $\times$  trapline matrices, simulations were run for 10,000 iterations, with a burn-in of 5,000. We report standardized effect sizes (SES) that allow comparison among matrices of different dimensions (Gotelli et al. 2015). Positive SES values indicate segregated matrix structure, whereas negative values indicate an overall aggregated pattern.

### **Functional traits**

We categorized species into guilds for four functional traits (Table B1); two that reflect likely biotic interactions in the form of competition among small mammals (diet guild and body size class; Bowers and Brown 1982, Fox and Kirkland 1992, Fox and Brown 1993), and two

associated with environmental filtering (habitat affinity and geographic affinity; Brown 1971b, Terry et al. 2011, Stevens et al. 2012). In doing so, we build on a legacy of community assembly research on small mammals based on simple yet informative guilds (Fox 1999, Brown et al. 2002). For diet guilds, each species was categorized as an omnivore, herbivore, granivore, or insectivore (Rowe and Terry 2014). Body sizes were obtained from the PanTHERIA database (Jones et al. 2009) and then binned into four groups that reflect natural breaks (<12g, 12-30g, 31-100g, >100g). For habitat we used three guilds (xeric, mesic, or generalist) that reflect species' overall affinities for local conditions based on moisture as well as associated differences in cover and temperature (Rowe and Terry 2014). For example, xeric indicates drier habitats which often contain more sparse vegetation and can occur at higher elevations along exposed cliff faces and warmer south-facing slopes. Geographic affinity, or the placement of the majority of a species' distribution relative to the study sites, reflects broad-scale climate tolerance and was categorized as North, South, or no affinity. We used the combined median latitude of all sites surveyed (39.5°) as the benchmark for calculations and followed the methods in Terry et al (2011). Latitudinal range limits were obtained from PanTHERIA (Jones et al. 2009) except for three species for which occurrence records from VertNet ([www.vertnet.org](http://www.vertnet.org)) were used to incorporate substantial updates in taxonomy (*Perognathus mollipilosus*; Riddle et al. 2014a) or distribution (*Sorex tenellus* and *S. preblei*; (Rickart et al. 2004, 2011, Shohfi et al. 2006).

Functional trait designations were used to assess the causal mechanisms associated with pairwise associations (Fig. 1-1) and for the assemblage more generally (Table 1-1). For the latter, we pooled the significant pairwise results per mountain range and used an exact binomial test to compare the observed number of intra-guild and inter-guild pairs for each trait to the expected number given the distribution of species among guilds. Binomial tests were conducted separately

for each sampling scale and association type (aggregation or segregation). When a significant departure from expectation ( $p < 0.05$ ) arises between intra- or inter-guild pairs for a particular trait, the assembly mechanism can be inferred (Table 1-1). Results were compared among mountain ranges to assess the generality of patterns and underlying processes across the Great Basin.

## RESULTS

### Co-occurrence patterns

From across all six matrices, a total of 71 significant (non-random) pairs were detected out of the 1,292 analyzed (Table 1-2). The Toiyabe Range contained the greatest number of significant pairs (36), followed by the Snake Range (24), and the Ruby Mountains (11). Of these 71 species pairs, 19 (11 pairs in the Toiyabe Range, 7 in the Snake Range, 1 in the Ruby Mountains) were significant at both the local and landscape scale, and are thus represented twice (for a total of 38 pairs) in the data set, with the remaining 33 pairs significant at only one scale (Fig. 1-3 and B1, Table B2). Therefore, there are 52 unique species pairs that exhibited some combination of non-random associations. For species pairs significant at both scales, the nature of the association was the same at the local and landscape scale: either dual aggregated or dual segregated patterns (Fig. 1-3). Only three pairs repeated non-random associations in more than one mountain range (Table B2). Two pairs presented the same pattern in the Snake and Toiyabe Ranges: *Ammospermophilus leucurus* and *Dipodomys microps* (local aggregation), and *D. microps* and *Microtus longicaudus* (landscape segregation). A third pair, *Microtus montanus* and *Sorex vagrans*, was locally aggregated in all three study locations.

In all test data sets, more non-random pairs were identified at the local scale than the landscape scale, but segregations and aggregations were each detected at both (Table 1-2). The frequency of random association among species pairs was also similar at the landscape (94%-98%) and local scale (91%-95%). Aggregations were consistently more numerous than segregations, accounting for 50-79% of significant associations. This pairwise summary contrasts with the matrix-wide results, all of which indicated an overall segregated assemblage structure (observed matrix C-scores > 95% confidence interval).

The strength of association (Z-score) varied with the scale of analysis and association type but local aggregations exhibited the greatest average strength of any combination (Fig. 1-3, Table B2). At the landscape scale, aggregations (mean -2.61) were generally weaker than segregations (mean 3.26). Conversely, local aggregations (mean -3.78) were stronger on average than segregations (mean 2.93). Pairs that were significant at both scales tended to have the strongest associations, but not exclusively.

### **Trait-based tests of mechanisms**

Tests of functional trait similarity identified environmental filtering as the mechanism responsible for all but four of the 52 unique significant pairs (Fig. 1-3). Most aggregations (32 of 36) occurred between species from the same habitat affinity guild (intra-habitat) and nearly all segregations (15 of 16) were between species from different habitat affinity guilds (Fig. B1, Table B2). The second environmental trait investigated, geographic affinity, produced less conclusive results (Fig. B1, Table B2), underscoring the need to consider multiple traits for each category; our results thus focus on habitat affinity.

Biotic interactions were inferred to structure the co-occurrence patterns of two segregated pairs and two aggregated pairs (Fig. 1-3, Table B2). The two segregated or negative biotic

interactions (competition) were at the landscape scale (scenario 7) in the Snake Range (*Tamias dorsalis* and *T. umbrinus*) and Toiyabe Range (*Perognathus longimembris* and *P. mollipilosus*). These pairs consist of congeners with similar diets and overlapping habitat affinities (the *Perognathus* are both xeric granivores and the *Tamias* are xeric to generalist omnivores), and thus only meet the conditions required to infer negative biotic interaction (Fig. 1-1). Importantly, these species have overlapping or adjacent range margins, allowing the spatial contact required for competition to take place. The two aggregated pairs co-occur at both scales (scenario 6) in the Snake Range (*Callospermophilus lateralis* with *Lemmiscus curtatus* and *C. lateralis* with *Sorex tenellus*) and, on the surface, imply positive biotic interaction (facilitation) as the causal mechanism due to their differing environmental filter-related traits (Fig. 1-1 and 1-3). However, these species belong to nominally different, but functionally overlapping, habitat affinity categories: a generalist, *C. lateralis*, paired with a specialist, *L. curtatus* and *S. tenellus*, respectively. As a result, our use of overlapping habitat affinity categories (and not the test results) renders this equivocal, suggesting environmental filtering or positive biotic interactions may explain their coexistence. Our case studies did not include any instances in which both mechanisms were supported due to meeting the conditions of both trait tests.

Binomial tests on the pooled pairwise results provide strong support for environmental filtering and no support for biotic interactions (Table 1-3 and B3). Locally aggregated pairs belonged to the same habitat affinity guild significantly more than expected ( $p < 0.002$ ) in all three assemblages. In the Toiyabe Range, a significant deviation was also evident among intra-geographic affinity pairs ( $p = 0.025$ ). No significant deviation from expected proportions were observed for either of the two traits which would reflect competitive biotic interactions (diet

group and body size class). Additionally, no comparisons for segregated pairs differed from expected proportions.

## **DISCUSSION**

### **Evaluation of the framework**

Determining the mechanisms driving species co-occurrence patterns across heterogeneous landscapes is a persistent challenge in biogeography and community ecology (Peres-Neto 2004, Sanderson 2004, López et al. 2013, Blois et al. 2014). Here we have developed a novel hypothesis-testing framework that distinguishes between biotic interactions and environmental filtering for species pairs distributed across environmentally heterogeneous sites (Fig. 1-1). Our case study for small mammal assemblages along Great Basin elevational gradients demonstrates the effectiveness of this framework (Fig. 1-3). Using co-occurrence patterns alone, only five of the 52 significant pairwise associations could be attributed to a single mechanism (scenario #4; Fig. 1-1). For the remaining 47 pairs, parsimonious mechanistic explanations were reached following functional trait-based hypothesis testing, including cases of both mechanisms of interest (environmental filtering and biotic interactions).

While the hypotheses in the framework are generalizable, the functional traits used may differ from those presented here depending on the ecology of the taxa being studied. In addition, we recommend testing multiple traits for which there is strong theoretical and/or empirical support. For example, in our study, one of the two traits per mechanism was more consistent and conclusive than the other when taken singly; habitat affinity performed better than geographic affinity for environmental filtering and diet guild was more informative than body size for biotic interactions (Table B2).

## **Drivers of Great Basin small mammal co-occurrence**

Environmental filtering explained most of the significant landscape scale co-occurrence patterns for Great Basin small mammals (Fig. 1-3, Table 1-3). The consistency of this conclusion cannot be attributed to commonality in species pairs among mountain ranges as only three significant pairs were repeated (Table B2). Given the substantial heterogeneity in climatic and habitat conditions among and within our sites, a strong signal of environmental filtering is to be expected. Notably, however, even under this rather extreme scenario, our framework also identified associations influenced by biotic interactions, including pairs recognized as competitors in previous studies. Similarly, a recent study of grassland plant co-occurrence over elevation leveraged site location and environmental information (instead of traits) for follow-up testing of null model patterns and also identified instances of biotic interactions (D'Amen et al. 2018). Taken together, these findings corroborate the utility of null model approaches for detecting co-occurrence mechanisms along strong environmental gradients when combined with secondary analyses. Furthermore, the recognition of both aggregations and segregations in the same assemblage demonstrates the benefit of deconstructing co-occurrence patterns into pairwise associations rather than relying on the average C-score value for an assemblage (Sfenthourakis et al. 2006, Gotelli and Ulrich 2010, Soberón 2015).

Of all possible species pairs in our data set, over 90% exhibited random co-occurrence patterns (Table 1-2). Such high levels of randomness are common in pairwise co-occurrence studies across taxa and time periods (Pitta et al. 2012, Lyons et al. 2016, Li and Waller 2016), and are partly due to Pairs using an inherently conservative method to screen false positives (Gotelli and Ulrich 2010, Blois et al. 2014). Among non-random associations, the predominance of environmental filtering was observed at the local and landscape scales, as well as for each

mountain range when pooling pairwise results (Fig. 1-3, Table 1-3). Associations tended to be stronger and more frequent at the local scale than the landscape scale, particularly for aggregations (Fig. 1-3, Table 1-2), which reflects the importance of local habitat conditions for determining which species are found together in space (Price 1978, Kotler and Brown 1988, Stevens et al. 2012). Although sample sizes may contribute to a stronger signal at the finer, local scale (62-89 traplines compared to 22-26 sites), the effect size varies with association type (Fig. 1-3), suggesting that statistical power alone does not explain this trend in significant pairs across scales.

The dramatic environmental gradients present on Great Basin mountainsides and well-documented resource partitioning among small mammals should favor the dominance of segregated co-occurrence patterns in this system (Feldhamer 1979, Kelt and Brown 1999, Rickart 2001, Hamilton et al. 2015). Despite this, our pairwise results revealed equal or greater amounts of aggregations than segregations across all mountain ranges and scales (Table 1-2). Similarly, the only significant binomial tests were for aggregations, suggesting that for these assemblages, forces of exclusion (habitat exclusivity or competition) are not as influential (or at least not as consistent) as those that enable co-existence (Tables 1-1 and 1-3). This dominance of pairwise aggregations is atypical for modern assemblages (Sfenthourakis et al. 2006, Gotelli and Ulrich 2010, Lyons et al. 2016). Our findings also contrast with a previous study of North American mammals which found segregations to be nearly three times stronger than aggregations (Smith et al. 2016).

In contrast to our pairwise results, the whole-matrix approach (EcoSimR) found each assemblage to be segregated overall (Table 1-2). The mismatch between pairwise and whole-matrix patterns is not surprising because the pairwise approach reveals a relatively small number



of pairs that exhibit non-random associations and it is unlikely that these pairs would reflect the whole matrix pattern. However, several characteristics of our test data may possibly favor the detection of aggregations when using a conservative method like Pairs. For example, binary presence-absence data is likely to be sensitive to variations in habitat occupancy due to metacommunity dynamics within and among survey years (Brown and Kurzius 1987, Ernest et al. 2008, Stevens and Tello 2012). Therefore, our test data may be masking significant segregations that are generally present but appear to be less strict without abundance data. Segregations could also be obscured if species are partitioning at a finer scale than our coarse habitat definitions. Additionally, the assemblages of each mountain range may be non-randomly structured to begin with if competition and exclusion control species' geographic distributions (Bowers and Brown 1982). Such an effect would limit the co-occurrence of competitors within the same mountain range and thus favor aggregations over segregations within local assemblages, at least for segregations due to competition (Kelt and Brown 1999).

The greater frequency of aggregations in our data may also stem from the diversity of species analyzed together. Analyzing species from several guilds at once rather than only likely competitors within a single guild may create a dilution effect (Gilpin and Diamond 1982, Collins et al. 2011). Because there is little reason for a species to experience biotic interactions with many other very different species (i.e. no niche overlap), signatures of competition may be masked by the large number of random comparisons. This may contribute to the superficial contrast between our results and many previous small mammal co-occurrence studies, which have focused primarily on the rodent granivore guild restricted to low elevation desert habitats (M'Closkey 1978, Bowers and Brown 1982, Brown and Kurzius 1987). These and other studies have recognized the importance of competition in structuring rodent communities through

limiting similarity and niche partitioning (Heller 1971, Dayan and Simberloff 1994, Valone and Brown 1995, Brown et al. 2000).

Our findings are, however, generally consistent with Fox's guild assembly rule for desert small mammals (Fox 1987, Fox and Brown 1993, Brown et al. 2000), which also capitalizes on expectations between intra- and inter-guild associations. The rule is based on competition and functional complementarity driving community assembly and species coexistence, and states that as species richness increases, functional groups tend not to be repeated until all groups are represented (Fox 1987). Consistent with this rule, we had numerous aggregated pairs that share habitat affinity but differ in diet guild, including both aggregations repeated in more than one mountain range (Table B2). For example, *Dipodomys microps*, an herbivorous kangaroo rat, is frequently found with granivorous rodent species in desert habitats. However, binomial tests did not recover a significant deviation from expected proportions of intra-diet guild aggregations (Table 1-3), suggesting that resource partitioning and complementarity is instead manifest within a habitat type rather than along the gradient more broadly.

In sum, at the broader scale, the influence of environmental filters has primacy over biotic interactions for shaping Great Basin small mammal communities. The effects of competition may be less absolute, varying temporally and spatially, leading to fewer pairs exhibiting strong enough exclusion patterns to generate a significant segregation. As a result, our approach arguably identifies some of the strongest competitors ("super-competitors") in which two species limit each other's distributions, reinforced by local competition and partitioning. These pairs represent the best candidates for studying the implications of biotic interactions during range shifts and community restructuring in response to environmental change.

#### **Associations explained by biotic interactions**

Competition was consistent with the co-occurrence patterns of two species pairs, each with previous empirical support for negative interactions. Both pairs consist of closely related species that belong to the same diet guild: pocket mice (*Perognathus longimembris* and *P. mollipilosus*) and chipmunks (*Tamias dorsalis* and *T. umbrinus*). Thus, these pairs represent the classic theoretical expectation that congeners should compete more strongly for resources (Sfenthourakis et al. 2006, Collins et al. 2011). Both pairs exhibited landscape-scale segregation patterns (scenario 7; Fig. 1-1) and previous work has suggested that they compete and/or partition resources locally (Brown 1971b, Blaustein and Risser 1974). Additionally, their small body mass differentials (among the smallest of any significant pairs; Table B2), corroborate competition as the mechanism behind their segregated co-occurrence patterns.

In the case of the pocket mice, both are small, granivorous, quadrupedal heteromyids. Our survey data suggest the elevational distributions of these species narrowly overlap, with *P. mollipilosus* widespread and *P. longimembris* only at the lowest elevations, a pattern seen across the Great Basin for this species pair (Hall 1946, Bowers and Brown 1982). Experimental trials suggest direct aggressive interactions may reinforce competition where these species come into contact (Blaustein and Risser 1974). In the Toiyabe Range, *P. mollipilosus* and *P. longimembris* were detected at 19 sites and 4 sites, respectively, but only co-occurred at a single site. Similarly, two chipmunks in the Snake Range have abutting elevational distributions, with *T. dorsalis* found at mid-elevations and *T. umbrinus* found higher. A combination of fitness differences and direct competition is thought to reinforce this elevational zonation where their distributions meet in pinyon-juniper woodlands (Brown 1971a). Elevational zonation is well-documented among chipmunks, including for an ecologically analogous species pair in the southern Great Basin (*T. panamintinus* and *T. palmeri*; (Heller 1971, Lowrey and Longshore 2013).

In contrast, the two cases of potential positive biotic interactions (facilitation) identified in our example data (scenario 6; Fig. 1-1) have little empirical support. Each pair involves the co-occurrence of the golden-mantled ground squirrel (*Callospermophilus lateralis*), a habitat and diet generalist, with a specialist species, either the Inyo shrew (*Sorex tenellus*; mesic, insectivore) or the sagebrush vole (*Lemmyscus curtatus*; xeric, herbivore). These three species are generally considered montane, occurring at mid- to high-elevation, but differ greatly in size, diet, and autecology (Rickart 2001, Rickart et al. 2004). To date, there are no data to suggest these species would facilitate one another's presence. Instead, a more parsimonious explanation is that *C. lateralis* simply has broad tolerances which allow it to overlap with relative habitat specialists, implying environmental filtering. These cases illustrate how additional explanation may be required when using non-exclusive functional group categories because of their greater ambiguity.

### **Applications and Conclusions**

The framework we presented successfully identified species co-occurrence patterns driven by environmental filtering and biotic interactions, even in a system with extreme environmental heterogeneity. Conclusions can be drawn for individual pairwise associations and for the dominant pairwise patterns of an assemblage. We tested the approach on an elevational gradient, but it is applicable to occurrence data collected from heterogenous sites over a range of spatial scales and degrees of variability. Relying on functional traits rather than species identities facilitates scaling up to more species-rich assemblages as well as comparative work within and across systems. Our framework also does not require detailed information about sites or species distributions, which can often be difficult to obtain at an appropriate resolution. Other non-null model approaches, such as those based on species distribution modelling and site-specific

environmental data or interaction networks, are informative but relatively data-intensive and may not be practical for all datasets and questions (Ovaskainen et al. 2010, Pollock et al. 2014, Bar-Massada 2015, Harris 2016). Instead, our approach relies on observational occurrence data collected through systematic field sampling to address the heterogeneity among sites. If our framework is applied at very large spatial scales (e.g. continental), however, it may be necessary to include site characteristics and/or distances as dispersal limitation and the effects of historical biogeography become more influential (e.g. Blois et al. 2014). Overall, our results demonstrate that accounting for environmental heterogeneity among and within sites can dramatically improve the ability to identify non-random patterns and draw sound conclusions about mechanisms.

Our framework enables one to track drivers of community assembly across space but also through time, a topic that has received much recent attention (Blois et al. 2014, Lyons et al. 2016, Smith et al. 2016, Li and Waller 2016). Even if detailed environmental reconstructions are not available, basic knowledge of site conditions can be used with our approach to address the drivers of community structure through time. The rapid and global environmental changes we are currently experiencing are leading to shifts in species ranges and community composition, which are likely to have profound ecological implications (Williams and Jackson 2007, Alexander et al. 2015, Hope et al. 2015, Terry and Rowe 2015). Understanding the impact of these changes and predicting their future effects on species and communities relies in large part on identifying the underlying ecological mechanisms at work. While we acknowledge that our approach is correlative, it serves as an effective means for identifying pairs for which experimental tests or more detailed observations may be warranted. Applying this trait-based framework to temporal

data may help to better predict the community-level impacts of changes in climate, land cover, and species distributions.

Table 1-1. Summary of the possible mechanistic explanations for pooled pairwise co-occurrence patterns. Similar to the single pair assessment, functional trait similarity can distinguish among mechanisms based on the combination of exact binomial test results and association type (aggregation or segregation). Binomial tests compared the expected to observed proportion of intra-guild versus inter-guild pairs for segregations and aggregations separately. Conclusions hold across scales (landscape and local in our analyses).

Binomial test result	Association type	
	Aggregations	Segregations
<b>Intra &gt; Inter</b>	Environmental filtering	Biotic interaction (-)
<b>Intra &lt; Inter</b>	Biotic interaction (+/-)	Environmental filtering

Table 1-2. Summary of co-occurrence patterns for small mammal assemblages in the Ruby Mountains, Toiyabe Range, and Snake Range. Results from Pairs (pairwise) and EcoSimR (whole-matrix) are provided. For pairwise analyses, the total number of species pairs, proportion of pairs yielding random results, and number of pairs exhibiting non-random associations (segregated and aggregated), are provided for each scale as well as the combined totals. The EcoSimR standardized effect size (SES) of each matrix is reported. This was converted from the observed average C-score for each matrix with significance determined with respect to the 95% confidence interval (CI) of the simulated C-score distribution. Asterisks indicate significantly segregated assemblage structure (observed matrix score > CI).

Mountain Range	Scale	Total Pairs	Proportion Random	Number of Pairs			Matrix SES
				Non-random	Segregated	Aggregated	
Ruby	Landscape	105	0.981	2	1	1	6.214*
	Local	105	0.914	9	3	6	2.655*
	Combined	210	-	11	4	7	-
Toiyabe	Landscape	351	0.952	17	6	11	9.113*
	Local	351	0.946	19	4	15	8.414*
	Combined	702	-	36	10	26	-
Snake	Landscape	190	0.942	11	4	7	3.710*
	Local	190	0.932	13	3	10	4.408*
	Combined	380	-	24	7	17	-



Table 1-3. Results of exact binomial tests for observed to expected numbers of non-randomly associated pairs. Bolded p-values indicate significant deviations from expected proportions ( $p < 0.05$ ). Tests were conducted separately for each of four functional traits. Habitat affinity and geographic affinity relate to the role of environmental filtering whereas diet group and body size class relate to competition. Tests were conducted separately using the set of significant pairs identified by Pairs for each mountain range, scale, and type of association (aggregation or segregation). The observed number of non-randomly associated pairs (Obs. no. pairs) is reported for each association type-scale combination. The total number of possible species pairs ( $n$ ) is reported for each mountain range. Complete numbers and exact expected and observed values are reported in Appendix B, Table B3.

Functional Group	Ruby Mountains ( $n=105$ )				Toiyabe Range ( $n=351$ )				Snake Range ( $n=190$ )			
	Aggregations		Segregations		Aggregations		Segregations		Aggregations		Segregations	
	Landscape	Local	Landscape	Local	Landscape	Local	Landscape	Local	Landscape	Local	Landscape	Local
<i>Obs. no. pairs</i>	1	6	1	3	11	15	6	4	7	10	4	3
Habitat Affinity	1	<b>0.0019</b>	1	0.56	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.43	0.3	0.21	<b>0.0018</b>	0.32	0.56
Geographic Affinity	1	1	0.35	0.29	0.11	<b>0.025</b>	0.19	0.32	1	0.51	1	1
Diet Group	1	0.66	1	0.57	1	1	0.64	1	0.69	1	0.055	0.57
Body Size Class	1	0.66	1	1	0.31	0.38	0.65	0.053	1	0.47	0.23	0.55

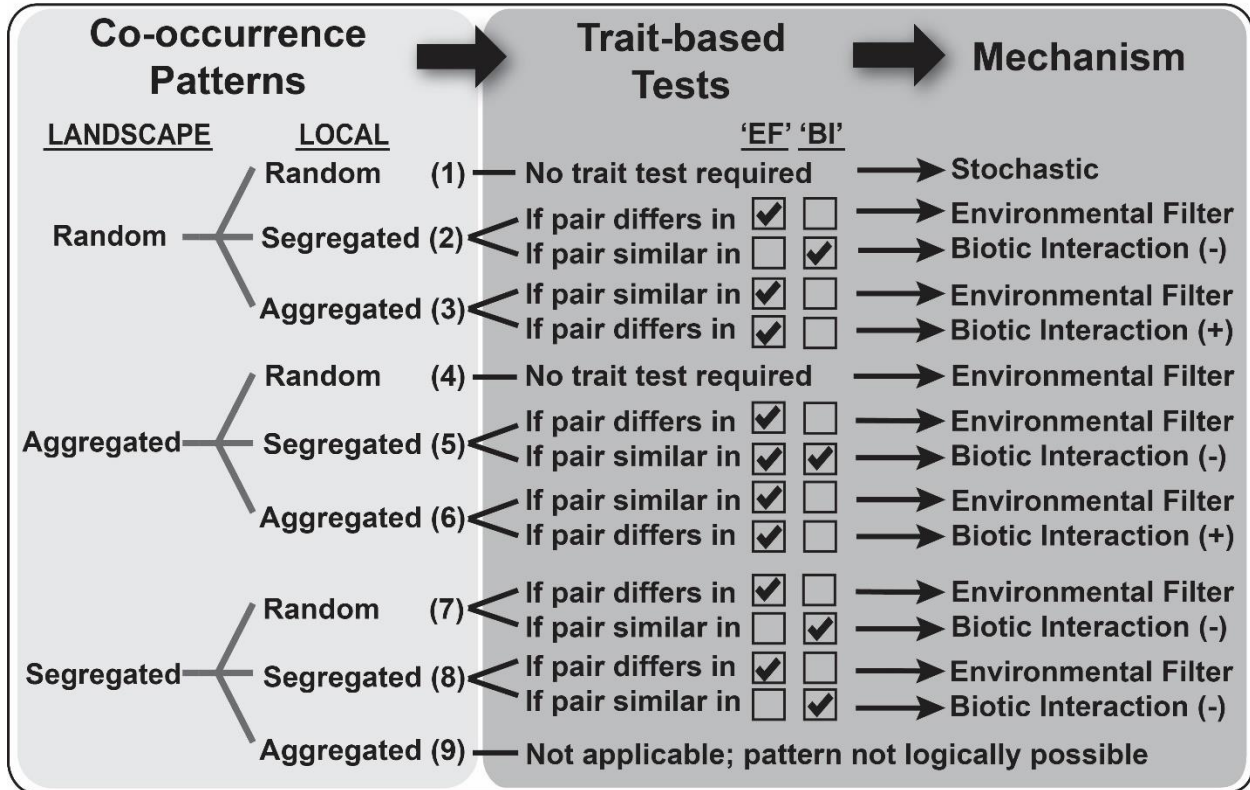


Figure 1-1. Analytical framework for incorporating functional trait similarity to identify the mechanisms structuring pairwise co-occurrence patterns. The logic tree summarizes the nine possible combinations of co-occurrence patterns at two sampling scales (landscape and local) and the tests of trait similarity used to determine the particular mechanism(s) responsible for generating them. A segregated pattern indicates two species that co-occur less often than random, and an aggregated pattern reflects species that co-occur more often than random. We propose trait-based hypothesis tests for distinguishing between environmental filtering (EF) and biotic interactions (BI), whether negative (competition) or positive (facilitation). The appropriate functional traits for testing each mechanism ('EF' and 'BI' traits) will vary based on the taxa studied. For small mammals, we selected habitat affinity and geographic affinity as "EF traits" and diet and body size categories as "BI traits". Checked boxes under a trait type indicate its application to a particular hypothesis test, and a condition that must be met for the subsequent mechanism to be invoked. If the conditions of both tests for a given pattern are met and are not mutually exclusive, both mechanisms are implied to be important.

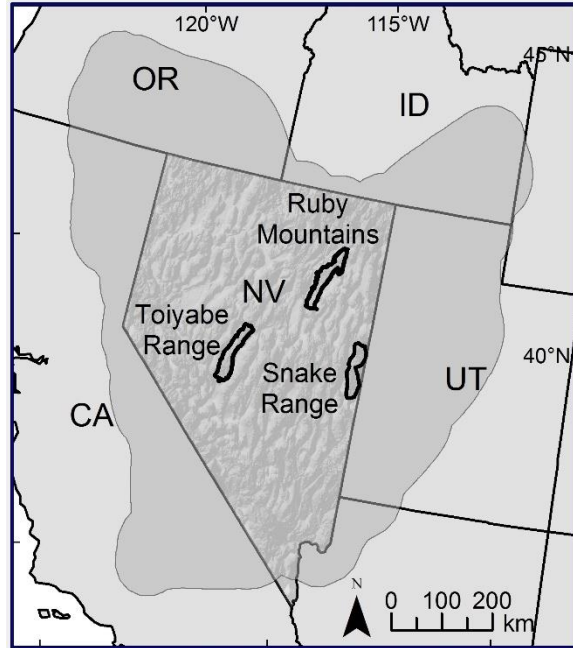


Figure 1-2. Location of the Ruby Mountains, Snake Range, and Toiyabe Range within the Great Basin (darkened outline), in the western United States. Small mammals were surveyed at sites spanning the elevational extent of each mountain range.

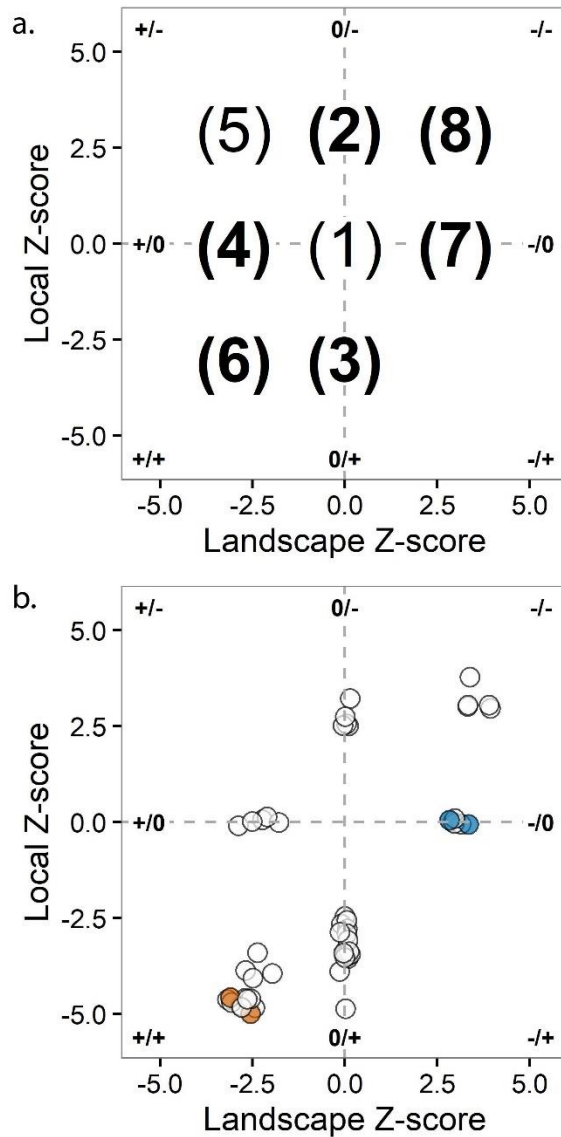


Figure 1-3. a.) Location of the eight possible co-occurrence pattern combinations, as numbered in Figure 1-1. Bold numbers are non-random patterns observed in our dataset. Scenario 1 represents random pairs, which are omitted in panel b. b.) Non-random pairwise co-occurrence patterns and their most parsimonious ecological mechanism for pairs of Great Basin small mammals. Signs (+/-) indicate the combination of association types each quadrant contains, for landscape and local scales, respectively. Due to the method of calculation, significant aggregations (+) correspond to negative Z-scores and segregations (-) have positive Z-scores. Zeros indicate a pair that showed a random pattern (Bayes Mean  $Z = 0$ ) at one scale. For the 19 species pairs significant at both scales, the nature of the association was the same at the local and landscape scale, thus occupying only two of the four quadrants. Color of points represents the inferred causative mechanism for the co-occurrence pattern, as determined by trait-based testing (white, environmental filtering; orange, possibly either facilitation or environmental filtering due to overlapping trait categories; blue, competition). Points are jittered for ease of visualization.

## CHAPTER 2

# BEYOND GUILDS: THE PROMISE OF CONTINUOUS TRAITS FOR MAMMALIAN FUNCTIONAL DIVERSITY<sup>2</sup>

### INTRODUCTION

Biodiversity is multifaceted and includes taxonomic, functional, and phylogenetic dimensions, among others (Magurran and McGill 2011, Pavoine and Bonsall 2011). Measures of taxonomic diversity are based only on the number and abundance of taxa (e.g., species richness) and represent the traditional method of quantifying diversity. In contrast, functional and phylogenetic dimensions of diversity consider species identities, or the similarities and differences among taxa in terms of their ecological or evolutionary characteristics, respectively (Kraft et al. 2007, Cadotte et al. 2011). These other dimensions of diversity may therefore offer a more nuanced framework for determining the mechanisms that underlie biodiversity patterns (Stevens et al. 2012, Whittaker et al. 2014, Willig and Presley 2016) and a more comprehensive approach to guiding conservation and management decisions (Flynn et al. 2009; Devictor et al. 2010; González-Maya et al. 2016).

In functional diversity, species are treated as assemblages of functional traits and the distribution of species in trait space is used to quantify ecological breadth, complementarity, and redundancy (Mason et al. 2005, Pavoine and Bonsall 2011). Broadly defined, functional traits are ecologically important characteristics that influence a species' niche requirements and the role it

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<sup>2</sup> Kohli, B.A. and R.J. Rowe. 2019. *Journal of Mammalogy* 100: 285-298.

plays in an ecosystem (Belmaker and Jetz 2013, Fountain-Jones et al. 2015). Functional traits can be derived from a species' ecomorphology, physiology, life history, or behavior, as well as the emergent properties of a species (e.g., geographic range size), and should be selected to directly address the ecological processes being studied (Rosado et al. 2016, Griffin-Nolan et al. 2018).

As long as traits are functionally relevant, nearly any type of data (e.g., binomial, categorical, continuous) can be used, but trade-offs often exist between data quantity and quality (Petchey and Gaston 2006, Maire et al. 2015). Categorical traits are typically easier to obtain (many can be scored using field guides or are available in collated databases), but underrepresent the true spectrum of interspecific variation present in an assemblage, rendering them insufficient for some applications (Fonseca and Ganade 2001, Wright et al. 2006). For example, categorical traits may provide an appropriate degree of resolution (quality) for global or continental studies because of the greater number of taxa included (e.g., Safi et al. 2011; Stevens et al. 2013), but higher-resolution trait data may be needed to adequately capture variation among species at finer spatial and taxonomic scales. Continuous traits offer fine-scale data that more fully express the range of variation, prevent subjective decisions that are often required when categorizing taxa, and can also provide increased statistical power for detecting associations between factors (Al-kahtani et al. 2004). To date, assessments of mammalian functional diversity have primarily relied on categorical traits related to resource use (e.g., diet guild, activity time, substrate use), continuous life history traits (e.g., litter size, age at first reproduction), and metrics of body size (but see Cisneros et al. 2014; Rodríguez and Ojeda 2014). More effort is needed to develop higher-resolution data, particularly to capture differences among species along axes of environmental tolerances and resource partitioning. Ultimately, developing a broader

complement of continuous functional traits will help generate stronger inferences about the drivers of community assembly, ecosystem function, and the effects of environmental change on mammalian communities.

Here, we seek to improve trait-based methods for mammals by identifying continuous measurements that can supersede the use of traditional functional categories for environmental tolerances and diet when higher-quality trait data are desired. Specifically, we assessed the relative medullary thickness (RMT) of the kidney as a metric of habitat moisture requirements; hair density as an indicator of temperature tolerance; and multivariate craniodental morphology as a measure of diet type and specificity. We chose these continuous traits because each has a demonstrated functional significance, is relatively easy to measure, and can be readily obtained from museum specimens. Our objectives were to determine whether RMT, hair density, and craniodental morphology reliably reflect traditional functional group categories and to assess the extent of within-group variation that can be used to generate more robust estimates of functional diversity. We also accounted for phylogeny and body size to isolate the influence of ecology on trait variation.

Relative medullary thickness (RMT) of the kidney is one of the oldest and most widely reported metrics of mammalian urine concentrating ability (Sperber 1944; Schmidt-Nielsen and O'Dell 1961; Al-kahtani et al. 2004), and has been linked to habitat aridity in rodents (Heller and Poulson 1972, Blake 1977, Deavers and Hudson 1979), shrews (Laakkonen 2002), and rabbits (Heisinger and Breitenbach 1969). The thickness of the medulla is correlated with maximum nephron length and thus the maximum length of the loops of Henle (the primary structure responsible for concentrating urine), which reflects concentrating ability. Although water metabolism relies on numerous other structures and genes (Beuchat 1996, Giorello et al. 2018),

RMT provides a simple and easily measured trait that explains a large amount of the variation in urine concentrating ability (Brownfield and Wunder 1975; Al-kahtani et al. 2004). In addition to water requirements, habitat affinities of small mammals are also strongly affected by temperature tolerance. Mammals employ many behavioral and physiological thermoregulatory strategies to regulate their body temperature relative to ambient temperatures, but hair is one of the primary means through which heat exchange is controlled (Scholander et al. 1950, Ling 1970). Hair density (hairs per unit area of skin) is a commonly used indicator of temperature tolerance and is preferable to other fur characteristics such as hair length and hair layer thickness that vary with piloerection and posture and are constrained by locomotor mode, particularly for small mammals (Steudel et al. 1994, Porter and Kearney 2009). Lastly, because the teeth, skull, and mandible of mammals represent the primary interface for processing food items, craniodental morphology can be used to capture the specificity of a species' diet (Martin et al. 2016). For example, incisors function primarily to gnaw, clip or pierce food items; cheek teeth (premolars and molars) grind and crush food; and the rostrum and mandible support muscle attachments that facilitate the gnawing and grinding actions of the teeth. The size and shape of these structures influences processing efficiency that varies with the physical properties of food items (e.g., seeds versus leaves). To comprehensively describe diet, it is important to capture potential variation in these interacting yet independent structures (Samuels 2009, McLean et al. 2018).

## **MATERIALS AND METHODS**

### **Specimens examined**

For each of the 3 traits (relative medullary thickness [RMT], hair density, and craniodental morphology), we sampled 32 of the most common and widespread species of small



mammals (28 rodents, 4 shrews) found in the Great Basin of western North America (Appendix C, Table C1). These species are ecologically diverse with respect to their habitat preferences, abiotic tolerances, and diet (Hall 1946, Zeweloff 1988, Rowe et al. 2011). We collected data from 3-6 individuals per species (mode = 5) using fluid-preserved (RMT and hair density) or skeletal (craniodental) museum specimens housed at the Natural History Museum of Utah and the Museum of Southwestern Biology (Appendix C, Table C2). Total sample sizes varied slightly due to availability of specimen types but were similar across the 3 traits (RMT,  $n = 156$ ; hair density,  $n = 155$ ; craniodental,  $n = 159$ ). For all 32 species, we sampled adults of both sexes and, where possible, used individuals collected from localities within the Great Basin to limit the effect of age, sex, and geographical variation within species. Only six fluid specimens (4%) were from sites outside the Great Basin, in adjacent ecoregions: four of five *Dipodomys deserti* (MSB 105322-105325) and one of five *Onychomys torridus* (MSB 37135) from southern California, and one of three *Otospermophilus variegatus* (UMNH 31016) collected from the Aquarius Plateau in central Utah. Most specimens examined came from recent field work conducted by ourselves or our colleagues as part of the Great Basin Resurvey Project (Rickart et al. 2011, Rowe and Terry 2014, Kohli et al. 2018, Chapter 1). Collecting procedures followed guidelines established by the American Society of Mammalogists (Sikes et al. 2016) and were certified by the Animal Care and Use Committee of the University of Utah (06-02001, 09-02004, 15-02001) and University of New Hampshire (111104A, 141103A; Appendix A). Standard information about the preparation of each voucher specimen examined and its associated collecting event can be accessed in the Arctos database (<http://arctos.database.museum>).

To determine whether each continuous trait recovered traditional categorical assignments, each species was classified *a priori* according to diet guild (granivore, herbivore, insectivore,

omnivore), habitat guild (mesic, xeric, or generalist), and geographic affinity group (northern, southern, or no affinity; Kohli et al. 2018, Chapter 1; Appendix C, Table C1). Geographic affinity refers to the placement of a species' range relative to a study location and reflects broad-scale climate tolerances (Terry et al. 2011). Importantly, these categories are not meant to represent obligatory diet or environmental requirements, but rather the tendency for species to be more specialized or restricted along a given niche axis.

### **Kidney data collection**

Following Sperber (1944), relative medullary thickness (RMT) is calculated as:

$$RMT = \frac{10(\text{absolute medullary thickness})}{\sqrt[3]{\text{kidney volume}}},$$

where kidney volume is the product of kidney length by width by thickness. To measure RMT, we extracted kidneys from adult fluid-preserved specimens fixed with either formalin or alcohol (ethanol or isopropanol) and stored in alcohol. We used digital calipers (iGaging, San Clemente, California) to measure the external width, length, and depth (0.01 mm precision) of the kidney. We then used a razor blade to make a mid-sagittal section that bisected the papillae and measured the thickness of the cortex and medulla using a digital microscope (INSIZE USA Co., Loganville, Georgia) calibrated with a stage ruler. Medullary thickness was measured transverse to the longest axis of the kidney from the tip of the papillae to the furthest edge of the cortico-medullary junction, as determined visually (Schmidt-Nielsen and O'Dell 1961; Brownfield and Wunder 1975; Al-kahtani et al. 2004). Following the method of Geluso (1978), we measured the curvature of the papillae along the midline into the body of the kidney, when appropriate. Sectioned kidneys were kept moist with ethanol while under the microscope to prevent shrinkage from desiccation.

Other common indices of urine concentration ability include the ratio of cortex to medulla thickness and percent medullary thickness (medullary thickness divided by the sum of the cortical and medullary thicknesses). For all species examined, we have provided values for these metrics to facilitate comparative work, as they are often reported together with RMT (Appendix C, Table C3). However, we focus on RMT because it is the most commonly reported of the three and deformation of kidney shape during fixation likely affects cortex thickness more than medullary thickness. Preservation method of the specimens did not appear to influence RMT measurements.

### **Hair data collection**

To measure hair density, we removed skin punches from fluid-preserved specimens rather than study skins to avoid error from stretching that occurs when preparing and drying study skins. To limit the effect of molt stage on hair density, we sampled individuals that were not molting and, where available, used specimens collected in the wild from May-September to primarily capture summer pelage density. Only 10 of the 155 hair-density specimens (6%) were collected outside of this time frame (Appendix C, Table C3). We dried the fur of each fluid specimen with paper towels and compressed air and used an electric razor to shave a small area (roughly 1 x 2 cm) on the dorsal surface within and posterior to the interscapular region. We then used a 4-mm diameter biopsy punch to remove three skin punches from the shaved area (Huestis 1925) and placed the punches between two microscope slides for transport and storage. Prior to conducting hair-density counts, excess hair and debris were removed by washing the skin punches with ethanol. In some cases, individual hair stubs could not be counted clearly due to remaining layers of tissue that prevented enough light from passing through the punch under the

microscope. To remedy this problem, we soaked a skin punch in hydrogen peroxide (3% solution) for 24-48 hrs in a 1.5-ml centrifuge tube.

We counted the number of hair stubs rooted in 16 random ocular grid cells (0.065 mm<sup>2</sup> each) per punch on a compound microscope equipped with an eyepiece grid reticle at 40X magnification (McClure and Porter 1983, Reynolds 1993). We included all hair types (e.g., guard hairs, underfur) in our counts. Hair stub counts (per mm<sup>2</sup>) were averaged across punches per individual and then per species. The total area counted per individual was 3.12 mm<sup>2</sup>. Previous studies of small mammal hair density have varied widely in the area of skin surveyed (Sealander 1951, Viro and Koskela 1978, McClure and Porter 1983), so the effect of unmeasured patchiness within individuals was unclear. To assess this, we calculated the correlations among total counts from each of the 3 punches taken per individual. Additionally, we examined the potential effect of area sampled by comparing average total hair counts (from 48 cells across 3 skin punches) to values calculated from 5 random subsamples (a total of 42, 36, 30, 24, and 18 grid cells counted).

### **Craniodental data collection**

To assess craniodental morphology, we selected eight linear measurements of the skull and teeth based on previous evidence of their relationship to diet among rodents (Ben-Moshe et al. 2001, Samuels 2009, Martin et al. 2016). Using only adult specimens (i.e., all teeth erupted, skull sutures closed), we measured upper incisor width (transverse) and depth (anterio-posterior), lower incisor width (transverse across 1 tooth), upper cheek teeth row length and width (the greatest distances on the occlusal surface), rostrum length (from anterior tip to nasal-frontal suture) and width (transverse, at the location of the maxilla-premaxilla suture), and jaw lever length (distance from the tip of the condyloid process to the point of maximal bite force; Martin et al. 2016). Jaw lever length is a measure of mandible robustness and in rodents the point of

maximal bite force is the anterior-most point of the second molar (Martin et al. 2016), whereas for shrews it is the highest cusp of the first molar (Young et al. 2007). For all specimens, we measured the right side of the animal unless damage required the left side to be used. For shrews, incisor depth was limited to the enlarged first cusp of I1, and only molariform teeth were considered for tooth row dimensions to make the measurements more functionally comparable to rodent teeth. For a single individual (*O. variegatus*, UMNH 7666), the first cheek tooth was missing, and the edge of the alveolus was used instead. We measured rodent skulls with digital calipers and shrew skulls with a digital microscope calibrated with a stage ruler (0.01 mm precision). All measurements were repeated three times per individual. The average of these was calculated and used to generate an average value per species for each of the eight morphological characters.

### **Statistical analyses**

We conducted all statistical analyses in R v. 3.5.1 (R Core Team 2016). Prior to analysis, continuous trait data including body size (species average mass in g; Jones et al. 2009) were  $\log_{10}$ -transformed. When assessing trait variation among species, it is critical to assess the influence of shared ancestry of species as well as their ecology (Felsenstein 1985, Garland Jr. et al. 1993, 2005, Rezende and Diniz-Filho 2012). To estimate phylogenetic relationships, we used the branch lengths in the “best dates” tree from a recent mammalian supertree (Fritz et al. 2009), which is an updated version of the tree published by Bininda-Emonds and colleagues (2007). We pruned the phylogeny to retain only our 32 species and forced a fully dichotomous tree without altering existing branch lengths using the ‘multi2di’ function in the package *ape* (Paradis et al. 2004). Two polytomies were resolved (one among *Peromyscus* species, and the other among *Sorex* species), causing only minor changes to the topology (Appendix C, Fig. C1).

To quantify the phylogenetic signal of each trait, we used the  $K$  metric (Blomberg et al. 2003) for body size, RMT, and hair density and its multivariate counterpart,  $K_{\text{mult}}$  (Adams 2014a), for craniodental morphology. A  $K$ -value of 1 indicates that a trait varies across the tree according to Brownian motion,  $K < 1$  indicates that closely related species are less similar in a trait than expected, and  $K > 1$  indicates that closely related species are more similar than expected. We tested the null hypothesis of no phylogenetic covariance by permuting trait data on the phylogeny tips 1,000 times using the package *geomorph* (Adams et al. 2018).

To determine the relationship of RMT, hair density, and craniodental morphology to traditional categorical traits while simultaneously accounting for relatedness, we performed phylogenetic analysis of covariance (ANCOVA) using a phylogenetic generalized least squares (PGLS) regression framework with the appropriate category (habitat guild, geographic affinity group, or diet guild) as the predictor variable and body size as a covariate. PGLS regression uses phylogenetic distances to account for the non-independence of species due to shared ancestry and can accommodate a variety of model structures (Grafen 1989, Adams 2014b). We also conducted non-phylogenetic analyses to make general comparisons to phylogenetic analyses, but because they ignore the variance due to phylogeny they should be interpreted with caution (Freckleton 2009). With PGLS models, significant associations between our categorical traits and continuous traits can be attributed to ecology. Additionally, by including body size as a covariate, we avoid the pitfalls of using residuals from linear regression of trait values on body size to correct for allometric trait relationships (García-Berthou 2001, Freckleton 2009). For RMT, we tested for differences among habitat guilds. For hair density, we tested for differences among habitat guilds as well as geographic affinity categories because both temperature and moisture sensitivity influence local habitat selection (mesic to xeric habitat preference), and

temperature tolerance should be manifest in the geographic distribution of a species (north, south, or neither) relative to the region. We tested for differences in overall craniodental morphology among diet guilds using phylogenetic multivariate ANCOVA (MANCOVA) due to the non-independence of the individual skull and tooth characters. Univariate phylogenetic ANCOVA models were fit using packages *nlme* (Pinheiro et al. 2018) and *ape* (Paradis et al. 2004) assuming a Brownian correlation structure. We used Procrustes distance PGLS (`procD.pgls` function in the package *geomorph*; Adams et al. 2018) for the craniodental phylogenetic MANCOVA, with significance assessed via 999 permutations of the data across the tips of the phylogeny. This method has greater statistical power to detect associations than parametric methods when analyzing multivariate data (Adams 2014b).

We followed the craniodental MANCOVA with phylogenetic discriminant function analysis (DFA) to further examine the relationships between morphology and diet group. We performed a phylogenetic DFA by adapting code made available by Arregoitia et al. (2017) and the core functions associated with the `phylo.fda.R` script published by Schmitz and Motani (2011). DFA was used to assess how well the morphology predicted diet group membership and to visualize the variation within and among groups. However, because larger rodents tend to have proportionately larger teeth than expected for their size (Samuels 2009), body size would greatly affect the distribution of species in craniodental morphospace. Because our primary interest was in identifying the ability of craniodental features to classify diet groups and not in the effect of body size, we used the residuals from the regression of log-transformed species means against  $\log_{10}$ -body size for the DFA (Appendix C, Table C6).

## RESULTS

## Phylogenetic signal

All continuous traits exhibited non-random phylogenetic signal (body size:  $P < 0.001$ ,  $K = 0.705$ ; RMT:  $P < 0.001$ ,  $K = 0.836$ ; hair density:  $P < 0.001$ ,  $K = 0.428$ ; craniodental morphology:  $P < 0.001$ ,  $K_{\text{mult}} = 0.853$ ). As such, phylogenetic correction in statistical tests was warranted to appropriately interpret all results.

## Relative medullary thickness

Mean uncorrected RMT per species ranged from a low of 5.07 (western water shrew, *Sorex navigator*; formerly *S. palustris*, Hope et al. 2014) to a high of 13.61 (little pocket mouse, *Perognathus longimembris*), with a mean of 8.4 (Appendix C, Table C3). Mean RMT was significantly associated with habitat guilds (phylogenetic ANCOVA:  $F_2 = 5.48$ ,  $P = 0.0098$ ) and body size ( $F_1 = 9.636$ ,  $P = 0.004$ ). Smaller species had proportionally greater RMT in our data set, as has been reported previously (Lawler and Geluso 1986, Beuchat 1990). The interaction between body size and habitat guild was not significant ( $P = 0.42$ ) and thus the interaction term was not included in the final model. Pairwise comparisons among habitat guilds indicated no significant differences; however, there was a directional trend in RMT with mesic-habitat species showing the lowest values, followed by habitat generalists with intermediate values, and xeric-habitat species with the highest RMT values (Fig. 2-1, Table 2-1; mesic-xeric pairwise  $P = 0.055$ ). When phylogeny was not incorporated, significant differences were detected between all groups following the same trend ( $P \leq 0.001$ ).

## Hair density

Average hair density ranged from 50-167 hairs/mm<sup>2</sup> among the 32 species sampled (mean = 111 hairs/mm<sup>2</sup>; Appendix C, Table C3). Hair density and habitat guild were significantly associated (phylogenetic ANCOVA:  $F_2 = 7.64$ ,  $P = 0.002$ ) with a trend toward



denser hair for mesic specialists compared to xeric specialists, but no significant pairwise comparisons (Fig. 2-1, Table 2-1). Our results ( $F_1 = 49.62$ ,  $P = 0.001$ ) also corroborate the significant effect of body size on hair density (Sandel 2013), even among small mammals; the smallest species in our data set, *Sorex tenellus* (Inyo shrew; 3.8 g), had the greatest hair density and the largest species, *O. variegatus* (rock squirrel; 715 g) had the least dense hair. In the absence of phylogenetic information, xeric-habitat species were found to have sparser hair than both mesic specialists and habitat generalists (both  $P < 0.03$ ). In a separate test, hair density was also significantly associated with geographic affinity (phylogenetic ANCOVA:  $F_2 = 5.13$ ,  $P = 0.013$ ) and body size ( $F_1 = 43.85$ ,  $P < 0.0001$ ) and southern species had sparser fur than northern and no affinity species (both  $P < 0.005$ ); only a trend was detected by the non-phylogenetic ANCOVA (Fig. 2-1, Table 2-1). The interaction between body size and ecological categories were not significant for habitat guild ( $P = 0.57$ ) or geographic affinity ( $P = 0.46$ ), and thus interaction terms were not included in the final models.

We investigated the potential effects of hair patchiness and sampling area on hair density estimates by comparing counts among individual skin punches as well as random subsamples of ocular grid cell counts. Hair counts among the three punches per individual were highly correlated ( $r \geq 0.91$ ,  $P < 0.0001$ ), indicating minimal patchiness of hair. Additionally, counts generated from all five subsampling regimes were highly correlated ( $r > 0.996$ ,  $P < 0.0001$ ) and differed by only 1-7% of mean hair density per species (1-6 hairs/mm<sup>2</sup>) compared to the full 48-cell count totals (Appendix C, Fig. C3). These results suggest that a robust measure of hair density can be estimated from a total counted area as low as 1 mm<sup>2</sup> per individual (obtainable from a single skin punch), which would enable less destructive sampling of voucher specimens in future studies.

## Craniodental morphology

Significant morphological differences were detected among diet guilds (phylogenetic MANCOVA:  $F_3 = 2.992$ ,  $P = 0.001$ ) and were also associated with body size ( $F_1 = 172.81$ ,  $P = 0.001$ ). The interaction between body size and diet guild was significant ( $F_3 = 1.04$ ,  $P = 0.001$ ), indicating that our diet guilds differed in their craniodental allometries. Variation in size-corrected craniodental morphology was described by three discriminant functions that distinguish diet groups in morphospace and reveal interspecific differences within each group (Fig. 2-2). The first function explained 75.41% of variation and was most influenced by rostrum length, cheek teeth row length, rostrum width, lower incisor width, and upper incisor depth (Table 2-2). The second function accounted for 18.35% of variation and was correlated with cheek teeth and incisor dimensions. The third function made up the remaining 6.2% of variation and was dominated by jaw lever length, cheek teeth width, and upper incisor depth.

For their body size, herbivores in this Great Basin small mammal assemblage had short and narrow rostra, long cheek tooth rows, thin blade-like upper incisors, and wide lower incisors (Appendix C, Table C6). Granivores had the shortest size-corrected toothrows, long and wide rostra, deep and wide (square-shaped) upper incisors, and slender mandibles. Insectivores (predominantly shrews of the genus *Sorex*) had relatively long and wide cheek teeth, narrow rostra, and deep but narrow upper incisors. Omnivores had intermediate values for most characteristics, except for rostra and mandibles, which were relatively wide and robust, respectively. Overall, omnivores were morphologically most similar to specialist granivores and differed most from specialist herbivores.

The phylogenetic discriminant functions correctly classified 75% of species (24 of 32) to their *a priori* diet group assignments using the eight morphological features we measured (Table

2-3). Among diet groups, 89% of granivores (8 of 9), 83% of herbivores (5 of 6), 67% of insectivores (4 of 6), and 64% of omnivores (7 of 11), were correctly predicted based on morphology. Misclassifications (*a priori* category did not match the category predicted by morphology) in the DFA may represent species whose morphology is truly atypical for their diet or are simply examples of the limitations of *a priori* diet categorization.

Phylogenetic and non-phylogenetic DFA results were qualitatively and quantitatively similar in identifying distinct morphospaces among diet groups, including strong correlations ( $r > 0.94$ ) among non-phylogenetic and phylogenetic discriminant scores (Fig. 2-2, Appendix C, Table C4 and Fig. C2). Correspondence of craniodental morphology to the *a priori* diet guild classifications was less successful in the phylogenetic DFA (75% correct) than the non-phylogenetic analysis (84% correct; Appendix C, Table C5). Specifically, the two methods shared five misclassified species, but the phylogenetic DFA resulted in three additional misclassified omnivores (*O. variegatus* as a granivore, *Urocitellus beldingi* and *Ammospermophilus leucurus* as insectivores).

## **DISCUSSION**

A multi-dimensional perspective of biodiversity can shed new light on ecological patterns and processes. Functional diversity analyses of mammals would benefit from the use of a broader array of functional traits, especially continuous traits that better capture interspecific variation and correspond to species' environmental tolerances and resource use. Our results suggest that the continuous ecomorphological traits of relative medullary thickness (RMT), hair density, and craniodental morphology capture meaningful differences within and among ecological guilds and thus have strong potential for improving the quality and precision of interpretations of functional

diversity. Furthermore, these traits are simple to measure and readily obtainable from museum specimens, which provides an opportunity for studying many other species, even those whose ecology is poorly known or unable to be observed (Van Valkenburgh 1987, Laakkonen 2002, Samuels 2009). However, current use of traits like RMT that require soft tissues may be constrained, as fluid-preserved specimens are less prevalent in natural history collections than traditional study skin and skeleton preparations. To facilitate diverse future research in trait-based ecology it is essential for specimen collection to continue and for collectors to use a variety of preparation techniques (McLean et al. 2016, Malaney and Cook 2018).

### **The role of phylogeny**

Each of the continuous traits we measured was significantly influenced by phylogenetic relatedness. While detecting phylogenetic influence on functional trait variation is not surprising for a small assemblage dominated by a few divergent lineages (Cricetidae, Heteromyidae, Sciuridae, and Soricidae), the relatively strong phylogenetic signal ( $K$  or  $K_{\text{multi}}$ ) we observed was consistent with previous studies on these and similar morphological traits across rodents and mammals more broadly (RMT— Al-kahtani et al. 2004; Diaz et al. 2006; hair density— Sandel 2013; craniodental characters— Arregoitia et al. 2017; Alhajeri and Steppan 2018; McLean et al. 2018). Although not identical, results of phylogenetic and non-phylogenetic tests recovered the same general trends among guilds and traits, supporting the overriding influence of ecology in shaping RMT, hair density, and craniodental morphology. Ultimately, our results emphasize that strong phylogenetic signal (which is critical to estimate and account for) does not necessarily diminish the utility of traits for discerning ecological patterns of diversity.

Notably, our study identified several instances in which RMT, hair density, and craniodental morphology were not strictly constrained by phylogeny, presumably as a result of

ecological differences. For example, RMT differs among the three chipmunks studied (*Tamias umbrinus*, *T. dorsalis*, and *T. minimus*; but see Patterson and Norris 2016 for proposed use of *Neotamias*), corresponding with their different habitat affinities (Fig. 2-3). *Tamias umbrinus*, a montane forest inhabitant, had the lowest size-corrected and uncorrected RMT; *T. dorsalis*, often found in mid-elevation pinyon-juniper woodland, had intermediate values; and *T. minimus*, a species associated with lowland open sagebrush shrublands, had the highest RMT values (rivaling some kangaroo rats and other desert-adapted species). This result echoes findings from previous studies on other chipmunk species that inferred the importance of physiological limitations and RMT in determining habitat and elevational distributions (Heller and Poulson 1972, Blake 1977). In another case, *Dipodomys microps*, an herbivore within a genus of granivores, possessed teeth and skull features more similar to herbivores than to other *Dipodomys* (Fig. 2-2). These and other examples caution against the use of relatedness as a proxy for ecological similarity, because doing so may overlook differing ecologies that can be detected by measuring continuous ecomorphological traits.

### **Relationship to categorical traits**

The interspecific variation in RMT, hair density, and craniodental morphology aligned well with the *a priori* placement of species among ecological guilds (Fig. 2-1, Fig. 2-2). This agreement validates the previous use of these categorical traits as appropriate but simplistic proxies. Differences among habitat and diet guilds are relatively distinct based on RMT and craniodental morphology, respectively. Guilds appear to overlap more in hair density, but this greater variation likely reflects the complexity of thermoregulation and the inability of a single trait to summarize environmental tolerances. Hair density, like all traits, will be most informative when used in combination with other relevant traits (e.g., body size, use of burrows, daily and

seasonal activity patterns) to comprehensively characterize the function of interest and thus the functional diversity of an assemblage (Lefcheck et al. 2015, Griffin-Nolan et al. 2018). Indeed, the significant phylogenetic signal and body size relationships found in all our traits reiterate the dynamic ecological and evolutionary processes that can affect trait evolution.

### **Advantages of continuous functional traits**

Measuring functional diversity requires selecting functionally relevant traits that maximize information content and quality (Petchey and Gaston 2006, Rosado et al. 2016). Our results demonstrate that RMT, hair density, and craniodental morphology provide more detailed and accurate information about environmental affinities and diet differences than their respective categorical traits. The extensive variation in these continuous traits is otherwise hidden using traditional categories and should improve comparisons of species within and among guilds. Importantly, each continuous trait varied according to ecological expectations (e.g., *Sorex navigator* is the most strictly water-restricted species in our assemblage and had the lowest RMT value; Fig. 2-1, Fig. 2-3), and even capture some more complex interactions among ecological factors. For example, herbivores that are xeric habitat specialists (e.g., *Neotoma lepida* and *Lemmiscus curtatus*) obtain more water from food compared to xeric-habitat specialist granivores and omnivores that rely less on green vegetation, and therefore should have reduced demand for high urine concentration and lower RMT values, which we observed (Appendix C, Table C3). Furthermore, categories are most useful when they are discrete (i.e., they are not functionally overlapping), but most small mammals are relatively opportunistic and fall along a continuum of generality. When categories are broad and overlap with others (e.g., omnivore, habitat generalist), some amount of arbitrary or subjective decisions are required when assigning species to these categories. Our DFA misclassifications best demonstrate this pitfall of

categories; seven of the eight diet guild misclassifications in the phylogenetic DFA involved the use of omnivory as a diet category (either as the *a priori* or the predicted classification of the species), whereas species with more specialized diets, either on seeds (most heteromyids), green vegetation (voles), or invertebrates (shrews) were more reliably classified by diet morphology (Fig. 2-2, Table 2-3). Thus, analyses of functional diversity can convey more realism when they include continuous ecomorphological traits that better represent the true functional spectrum utilized by species and effectively avoid subjectivity.

Greater realism in trait data may be most beneficial in community ecology. Compared to continuous data, categorical classification inflates the perception of functional redundancy among species and does not allow the relative position or functional role of a species to vary with assemblage composition (Petchey and Gaston 2006). The misclassification of *Neotoma lepida* (desert woodrat) in the craniodental DFA exemplifies this concept. This species of woodrat was categorized *a priori* as a specialist herbivore, but clustered more closely with insectivores in the size-corrected morphospace (Fig. 2-2). There is little empirical evidence to suggest that the diet of *N. lepida* relies heavily on invertebrates, although they may exploit a wider variety of foods than the other herbivores included in our study (*Neotoma cinerea*, *D. microps*, and several voles; Zeveloff 1988; Verts and Carraway 2002). Therefore, the location of this species in morphospace likely results from its inclination toward omnivory relative to the core group of specialist herbivores. Indeed, when only rodents were analyzed, *N. lepida* was classified correctly as an herbivore (data not shown). For all of our traits, the variation among species will help to better capture the functional implications of local community composition, which can vary greatly over space and time (Brown and Kurzius 1987, Ernest et al. 2008).

### **Intraspecific trait variation**

In this study, we have focused on interspecific variation in ecomorphological traits. We attempted to minimize any potential intraspecific variation by measuring adults of both sexes and limiting the selection of specimens to those collected from within the study region during the summer months. Intraspecific variation is rarely considered in the current literature on functional traits, and especially for studies of terrestrial vertebrates, but may be warranted (Violle et al. 2012). Additionally, because the relative contribution of genetic differences and phenotypic plasticity to variation in these traits is an outstanding question, it is possible that some of the variation we observed is due to sampling of wild-caught individuals from uncontrolled environmental conditions (Garland Jr. and Adolph 1991, Oswald 1998). With respect to the taxa and traits we investigated, a limited number of studies have reported geographic variation in kidney morphology metrics for chipmunks (Blake 1977), ground squirrels (Rickart 1989), and two *Peromyscus* species (Heisinger et al. 1973), as well as fur characteristics (Wasserman and Nash 1979) and skull shape (Grieco and Rizk 2010) of *P. maniculatus*. Similarly, of our focal traits, morphological change over time has only been investigated for craniodental morphology and results are mixed, suggesting complex drivers including environment, diet, and genetic drift (Eastman et al. 2012, Holmes et al. 2016, Walsh et al. 2016). Although current evidence for intraspecific variation in these traits is sparse, future studies would be strengthened by examining the extent and causes of geographic or temporal variation in more depth.

## **Conclusions**

As the impacts of environmental change continue to increase, it will be imperative to consider fine-scale variation in species requirements and capabilities to better interpret and predict the responses of mammalian species, populations, and communities. General conclusions about which traits are the best predictors of response to environmental change or indicators of



which species are most at risk remain elusive (McCain and King 2014, MacLean and Beissinger 2017), but investigating traits more explicitly tied to underlying physiological limitations offers a path forward. Similarly, more-detailed measures of resource use and partitioning will refine our understanding of the complex effects of shifting resource bases (Ernest et al. 2008, Rowe et al. 2011, Terry and Rowe 2015). RMT, hair density, and craniodental morphology are traits that show great promise in meeting these goals, but remarkably little of the mammalian tree of life has been surveyed for these and other ecomorphological traits. And yet, if the difficult endeavor to consolidate demographic parameters and life history traits has been so successful and widely utilized (Ernest 2003, Jones et al. 2009, Wilman et al. 2014), surely identifying and gathering a core suite of essential ecomorphological traits for mammals should not be seen as an untenable challenge.

Table 2-1. Group means and standard deviations (in parentheses) of relative medullary thickness (RMT) and hair density for habitat guild and geographic affinity categories of 32 Great Basin small mammal species. See Appendix C, Table C1 for species assignments. Raw and log-transformed values (not accounting for covariation in body size or phylogeny) are summarized. RMT was not compared among geographic affinity groups.

Category	Relative medullary thickness (RMT)		Hair density (hairs/mm <sup>2</sup> )	
	Raw	Log-transformed	Raw	Log-transformed
Habitat guild				
Mesic ( <i>n</i> = 8)	6.09 (0.58)	0.78 (0.042)	135.49 (29.35)	2.12 (0.11)
Generalist ( <i>n</i> = 7)	7.76 (1.44)	0.88 (0.079)	108.32 (44.11)	2.00 (0.20)
Xeric ( <i>n</i> = 17)	9.74 (1.94)	0.98 (0.083)	101.28 (24.62)	1.99 (0.11)
Geographic affinity				
Northern ( <i>n</i> = 8)	--	--	121.44 (33.41)	2.07 (0.13)
No affinity ( <i>n</i> = 9)	--	--	116.41 (30.82)	2.05 (0.13)
Southern ( <i>n</i> = 15)	--	--	102.98 (34.16)	1.99 (0.15)

Table 2-2. Phylogenetic discriminant function (DF) analysis loadings for the eight craniodental measurements used in this study.

Measurement	DF1	DF2	DF3
Rostrum length	-0.53	-0.22	-0.46
Rostrum width	-0.44	-0.24	0.39
Upper incisor width	0.17	-0.51	0.18
Upper incisor depth	-0.42	-0.57	0.44
Cheek teeth row length	0.47	0.64	0.10
Cheek teeth row width	0.01	0.63	-0.64
Jaw lever length	-0.06	0.22	0.84
Lower incisor width	0.44	-0.47	0.33

Table 2-3. Phylogenetic discriminant function analysis classification table based on eight craniodental measurements for 32 Great Basin small mammal species. The number of species correctly classified per group is along the diagonal. Overall, 75% of species were correctly classified.

<i>A priori</i> group	Predicted group				% correct
	Granivore	Herbivore	Insectivore	Omnivore	
Granivore ( $n = 9$ )	8	0	0	1	89
Herbivore ( $n = 6$ )	0	5	1	0	83
Insectivore ( $n = 6$ )	0	0	4	2	67
Omnivore ( $n = 11$ )	2	0	2	7	64

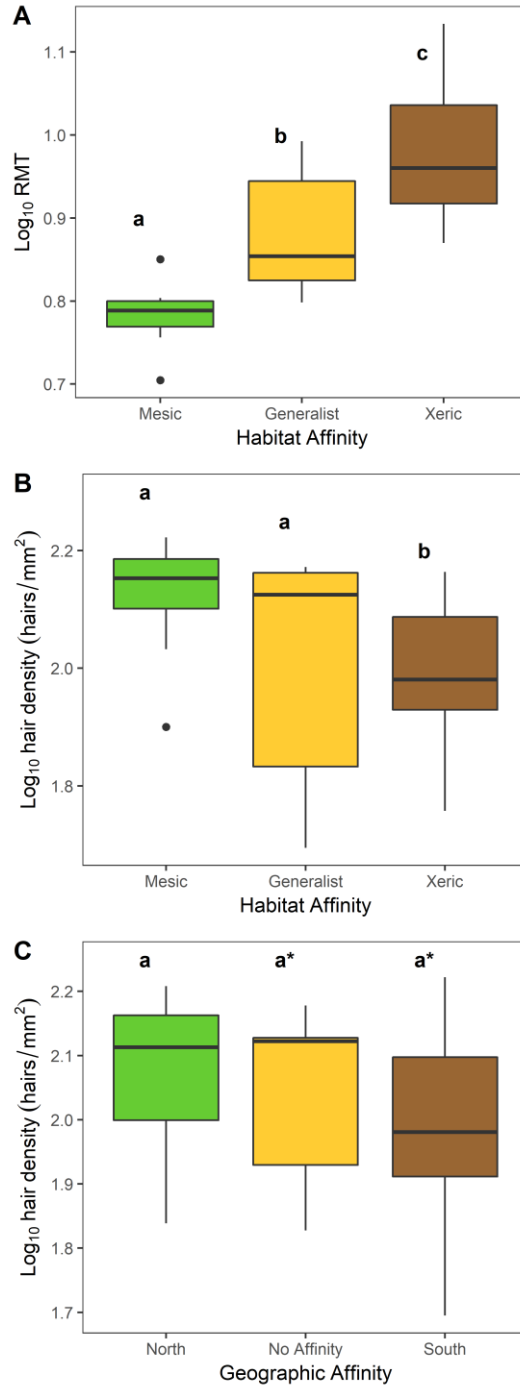


Figure 2-1. Boxplots showing variation within and among habitat guilds for the relative medullary thickness (RMT) of the kidney (A) and hair density (B) as well as hair density among geographic affinity groups (C). Plotted values are the log-transformed values for 32 species of small mammals. Asterisks indicate significantly different means among groups from tests accounting for phylogenetic relatedness and covariation in body size. Letters identify groups that differed in non-phylogenetic tests. The RMT mesic-habitat guild contains 2 outliers, *Neotoma cinerea* (bushy-tailed woodrat) above the group average and *Sorex navigator* (western water shrew) below the group average. For hair density, the mesic-habitat outlier is *N. cinerea*.

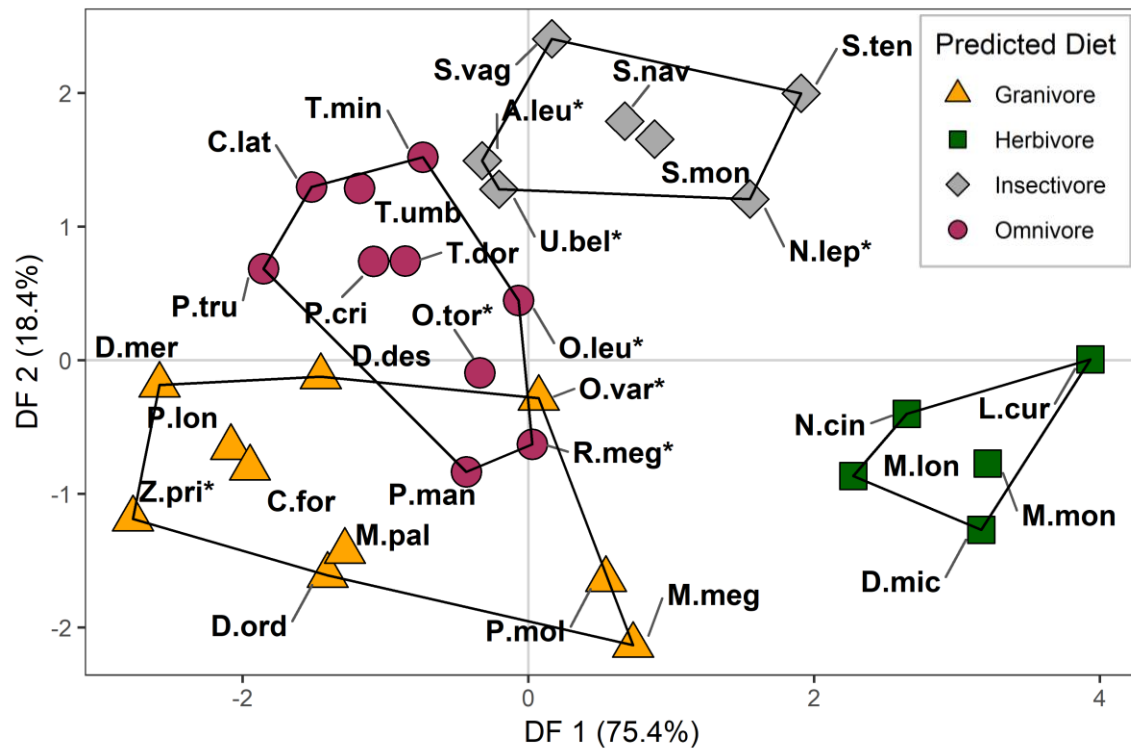


Figure 2-2. Morphospace derived from phylogenetic discriminant function analysis (DFA) based on eight craniodental measurements for 32 small mammal species. The first two discriminant functions (DF) account for 93.8% of the morphological variation. The percentage explained by each DF is included in the axis labels. Points are labeled with species abbreviations corresponding to Appendix C, Table C1. Shape and color of points correspond to the diet group predicted for each species based on size-corrected morphology (see key in upper right-hand corner). Polygons are convex hulls showing the distribution of the predicted diet groups in morphospace. Species whose diets were misclassified (predicted diet group did not match *a priori* diet category;  $n = 8$ ) are indicated with an asterisk.

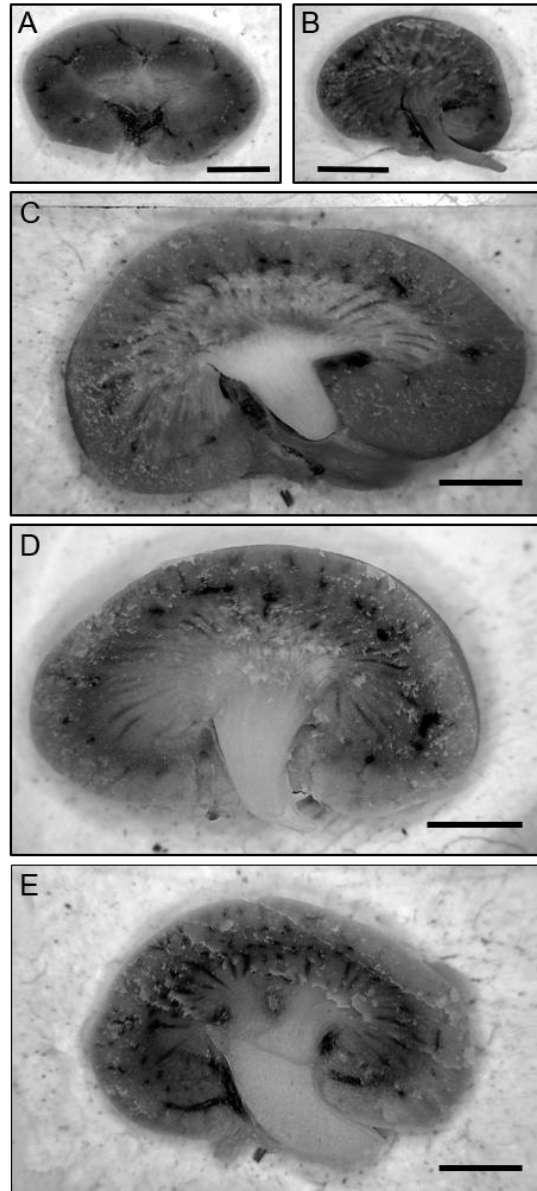


Figure 2-3. Digital microscope photographs of mid-sagittal sections of kidneys used to measure relative medullary thickness (RMT). For each panel, the black scale bar denotes 2 mm. Panels A and B represent the extremes of kidney morphology among the 32 small mammal species in this Great Basin assemblage: A) *Sorex navigator*, a mesic habitat specialist with the lowest RMT (mean = 5.1), B) *Perognathus longimembris*, a xeric habitat specialist with the highest RMT (mean = 13.6). Note the difference in the length of the renal papillae, which extend far outside the body of the kidney in the xeric species, enabling greater urine concentration. Panels C-E show this same trend in morphology and mean RMT among congeners (three chipmunk species, *Tamias*) that differ in habitat guild: C) *T. umbrinus* (mean RMT = 7.0) is found in high-elevation montane and subalpine forests, D) *T. dorsalis* (mean RMT = 8.3) is found predominantly at mid-elevations among dryer, warmer pinyon-juniper woodlands, and E) *T. minimus* (mean RMT = 9.8) inhabits sagebrush shrublands and other open, dry habitats at various elevations.

## CHAPTER 3

### MAMMALS ON MOUNTAINSIDES REVISITED: FUNCTIONAL AND PHYLOGENETIC DIVERSITY REVEAL COMPLEX ASSEMBLY PROCESSES

#### INTRODUCTION

Understanding the distribution of biodiversity is fundamental to community ecology, biogeography, and conservation. For over a century, efforts to describe and explain biogeographic gradients of diversity have primarily focused on patterns of species richness across latitude and elevation (Rahbek 1995, Hillebrand 2004). Recently, there is growing recognition that investigating multiple facets of diversity may improve our ability to infer the ecological and evolutionary mechanisms that underlie observed patterns (Weiher et al. 2011, Violle et al. 2014). In contrast to species richness, phylogenetic (PD) and functional diversity (FD) describe an assemblage in terms of the evolutionary or ecological properties of the species that comprise it, and because PD and FD quantify the degree of similarity among species, they are promising approaches for linking pattern to process (Diaz et al. 1999, Cavender-Bares et al. 2009, Pavoine and Bonsall 2011). PD quantifies the evolutionary differences among species, an approach that can be traced back to early investigations of species/genus ratios (Elton 1946, Webb 2000). FD views species through the traits they possess and describes the distribution of species in niche space by quantifying functional traits (Mason et al. 2005, Petchey and Gaston 2006). Functional traits are measurable properties of organisms, including morphological, physiological, and behavioral features, that potentially affect an individual's growth,



reproduction, and survival and/or contribute to ecosystem function (Cadotte et al. 2011).

Niche-based assembly mechanisms, namely biotic interactions and environmental filtering, are often inferred by analyzing the dispersion of communities in trait- or phylogenetic-space (Weiher et al. 1998, Webb et al. 2002, Kluge and Kessler 2011). FD and PD provide a strong link between diversity patterns and community assembly processes because distances in functional trait space reflect both the filters that delimited the species pool and the subsequent degree of niche partitioning, and distances in a phylogeny convey the degree of ecological similarity through the assumption of phylogenetic niche conservatism (Weiher and Keddy 1995, Webb 2000, Pavoine and Bonsall 2011). If competition for limited resources determines assemblage structure, niche separation among coexisting species should be evidenced by overdispersion in niche-space, especially in traits related to resource acquisition (MacArthur and Levins 1967, M'Closkey 1978, Cavender-Bares et al. 2004). Conversely, if environmental filters are influential, high redundancy in the habitat affinities and abiotic tolerances among community members causes species to be clustered, or underdispersed (Weiher and Keddy 1995). If more closely related species are assumed to be more similar ecologically, phylogenetic distances can also be used to infer whether one of these assembly mechanisms is acting (Webb et al. 2002, Losos 2008). Although a multi-dimensional perspective of diversity is becoming more common, formal evaluations of community assembly along geographic gradients are relatively uncommon (Bryant et al. 2008, Kluge and Kessler 2011, Lamanna et al. 2014).

Mountains have long provided an excellent system for testing mechanisms that structure diversity patterns because they encompass broad environmental gradients over short spatial distances and typically harbor high diversity. Nearly a quarter of the Earth's surface is mountainous, thus providing ample replicates with which to test for commonality in pattern and

process (Lomolino 2001, Körner 2007). Indeed, elevational gradients of diversity have been studied extensively to address questions that bridge the fields of community ecology, biogeography, global change, and evolution (Rahbek 1995, Moritz et al. 2008, Kozak and Wiens 2010, Rowe et al. 2011). Elevation-richness relationships from a variety of taxa and geographic locations have revealed common patterns, but general conclusions about the underlying causes remain elusive (McCain and Grytnes 2010, Sanders and Rahbek 2012). The most commonly observed elevation-richness patterns are a monotonic decline toward higher elevations and a mid-elevational peak, or hump-shaped relationship (Rahbek 1995, McCain 2005). Strong support has been found for multiple causative factors including area, geometric constraints, evolutionary processes, climate, and productivity, but their importance varies across taxa and mountains (Rahbek 1995, Lomolino 2001, Graham et al. 2014). For example, the same elevation-richness pattern, even for the same species group and region, can be structured by different drivers (Rowe 2009). Elevational gradients offer an excellent opportunity to understand what drives community assembly as well, and studies of elevation-diversity relationships have begun to use elevational patterns of phylogenetic and functional diversity in addition to species richness (Bryant et al. 2008, Kluge and Kessler 2011, Jiang et al. 2018).

Here we sought to describe multi-dimensional diversity patterns and the processes that drive assembly of small mammal communities along elevational gradients in the Great Basin of western North America. We compared three gradients in the same ecoregion to test for commonality in pattern and process. Our first objective was to compare elevational patterns of species richness, PD, and FD to assess surrogacy among dimensions. If all dimensions of biodiversity share similar patterns over elevation, species richness may be justified as a surrogate for the other dimensions. However, explicit investigations of the relationships among multiple

dimensions are rare and the findings variable (Devictor et al. 2010, Safi et al. 2011, Stevens and Gavilanez 2015). Given the theoretical expectation of a positive, saturating relationship of PD and FD with species richness (Kluge and Kessler 2011, Safi et al. 2011) and the typical hump-shaped pattern of species richness over elevation for temperate small mammals (Rickart 2001, McCain 2005, Rowe 2009), our null expectation is that all dimensions share a similar mid-elevational peak.

Our second objective was to leverage functional trait information to determine the elevations at which environmental filtering and competition influence assembly, and whether the importance of these mechanisms varies along mountainsides. The power of trait data to test mechanisms is greatest when hypotheses are explicitly articulated and traits are identified that are directly tied to those mechanisms (Spasojevic and Suding 2012, Lopez et al. 2016). The importance of community assembly processes likely varies across elevation and processes may act simultaneously at the same elevations through separate traits (Jiang et al. 2018). By decomposing FD into separate niche axes or traits, the unique expectations of each assembly process can be tested. Randomness of trait-based patterns with respect to elevation suggests neutral processes play a predominate role (Colwell et al. 2004, Laiolo et al. 2018).

We test several alternative hypotheses for assembly mechanisms across elevation; one for environmental filtering and three for competition. We expect the signal of environmental filtering to be strongest at both the lowest and highest elevations because environmental conditions along Great Basin mountainsides vary from hot and dry lowlands to cool and wet highlands. These extremes are physiologically stressful for small mammals and are thought to act as strong environmental filters (Brown 2001) that would result in significant clustering in trait-space relative to null models, while communities found in more moderate conditions at mid-

elevations should be more dispersed in trait-space (Weiher and Keddy 1995). Communities in which competition is important should show overdispersion in traits related to resource acquisition and use. The stress-dominance hypothesis (Coyle *et al.*, 2014) asserts that competition will be most influential where environmental conditions are least stressful, presumably around mid-elevations (Weiher and Keddy 1995, Kluge and Kessler 2011). Alternatively, according to the Species Interactions-Abiotic Stress Hypothesis, species range limits should be determined by competition at the warmer edge (i.e., southern geographical or lower elevational margin) which is assumed to be a more benign environment than the colder edge of a species' range (i.e., northerly or upper elevational margin) which is controlled instead by abiotic stress (Alexander *et al.* 2015, Louthan *et al.* 2015). Under this model, overdispersion relative to null models would be expected in low- to mid-elevation communities, where the majority of lower range margins occur for our study species (Rickart *et al.* 2008, Rowe *et al.* 2010). Previous work has demonstrated a role for competition in setting range limits of Great Basin small mammals and in structuring their lowland desert communities (Brown 1971b, Bowers and Brown 1982, Dayan and Simberloff 1994). This pattern is not mutually exclusive with environmental filtering at low elevations because these mechanisms are tested with different traits. Lastly, the signal of competition may be strongest at low and high elevations according to the expectations of Fox's guild assembly rule (Fox 1987) which states that as species richness increases, each functional guild is added until all are represented, then species are sequentially added within guilds. The effect is that competition tends to maintain maximal niche differences among species to a saturation point, after which species are then packed into the occupied functional space relative to the amount of resources available (Fox 1999). Support for this assembly rule has been found among desert rodents across the Great Basin lowlands and other

southwestern US deserts, but it has not been tested among higher-elevation communities (Fox and Brown 1993, Brown et al. 2000). Extending this concept to the typical mid-elevation peak in small mammal richness generates a testable pattern of trait dispersion: traits associated with resource acquisition and use should be overdispersed at low and high elevations (the few species present should be highly differentiated) and become less dispersed toward mid-elevations as functionally redundant species are added (Pigot et al. 2016).

## **MATERIALS AND METHODS**

### **Study area and taxa**

We studied assemblages of non-volant small mammals (rodents and shrews) within the Great Basin of western North America (Fig. 3-1). The Great Basin is characterized by basin and range physiography, containing numerous mountain ranges that reach elevations exceeding 3,000 m and span broad precipitation and temperature gradients – from relatively wet, cool alpine conditions near mountaintops to dry, hot deserts in the intervening valleys (Grayson 2011). Although the region falls within the rain shadow of the Sierra Nevada and is thus a cold temperate semi-desert, the relatively discrete vegetation zones that are stratified along these steep mountainsides show great variability in conditions; major zonation includes low-elevation desert shrublands, mid-elevation mixed woodland and shrubland, mid-to-high-elevation subalpine forests and montane meadows, and alpine forest and tundra at the highest of elevations (Hall 1946, Trimble 1999). The region’s mountain ranges share a common biogeographic history and a common species pool, including a diverse assemblage of more than 40 species of small mammals (Badgley et al. 2014, Riddle et al. 2014b), providing an excellent opportunity for

comparative analyses on the patterns and drivers of diversity (Brown 1971a, Rickart 2001, Fleishman et al. 2001).

Small mammal occurrence data were derived from comprehensive, multi-year field surveys conducted during the summer months (May-September) in three Nevada mountain ranges located over 150km apart: the Ruby Mountains (2006-2008, Rowe et al. 2010; 2013, Rowe unpublished data), Snake Range (200-2003, Rickart *et al.* 2008; 2015-2016, Kohli *et al.*, 2018, Chapter 1), and Toiyabe Range (2009-2011, Massey et al. 2017). In each mountain range, we trapped small mammals at >20 sites distributed across elevation. Sampled extents ranged from 1550-3050 m in the Ruby Mountains, 1500-3400 m in the Snake Range, and 1600-2700 m in the Toiyabe Range (Table 3-1). Our sampling of the Toiyabe Range gradient was proportionally less because the highest elevations were not as accessible; however, it is important to note that vegetation only extends upwards another ca. 350 m (Linsdale 1938), and that the area above our highest traplines accounts for only 8% of the area of the mountain range even though the elevational gradient continues for nearly 900m reaching a maximum of 3593m at Arc Dome. In the Ruby Mountains and Snake Range sampling reached the upper limits of vegetation, above which lies talus slopes and rocky outcrops that are generally inhospitable to small mammals and difficult to access. For each mountain range the lowest elevations sampled approximate the true local minimum elevations in adjacent valleys, which sit far above sea level in the central Great Basin (Grayson 2011).

We used removal sampling methods with a variety of trap types (Sherman and Tomahawk live traps, Museum Specials, Victor rat-traps, and pitfall traps) to ensure that the entire community of non-volant rodents and shrews under 500 g was sampled (see Rowe et al. 2010 for additional details). At each site, discrete traplines were established in all available

habitat types (spanning the local moisture gradient) and were typically located within a <1 km radius and differed in elevation by <100 m. Although sighting and salvaged specimens were opportunistically recorded, they were not included in these analyses. We also excluded species that require targeted trapping or survey methods (e.g., gophers, lagomorphs, small carnivorans). Collecting procedures followed guidelines established by the American Society of Mammalogists (Sikes et al. 2016) and were certified by the Animal Care and Use Committee of the University of Utah (06-02001, 09-02004, 15-02001) and University of New Hampshire (111104A, 141103A; Appendix A). Specimens and field notes from all surveys are archived at the Natural History Museum of Utah (University of Utah, USA), Field Museum of Natural History (Chicago, Illinois, USA), Monte L. Bean Life Science Museum (Brigham Young University, USA), and Museum of Vertebrate Zoology (University of California, Berkeley, USA).

Our analyses included 34 species of small mammals (28 rodents, 6 shrews), 15 of which occurred in all three of the mountain ranges (52-69% of species were shared between mountains). In total, 1915 individuals of 19 species were captured at 22 sites from 1590-3014 m elevation in the Ruby Mountains, 2384 individuals of 24 species across 36 sites from 1547-3397 m elevation in the Snake Range, and 3183 individuals of 31 species were captured at 24 sites from 1627-2698 m elevation in the Toiyabe Range. For each mountain range we grouped occurrences into 100-m elevational bins (e.g., 1500-1599 m; Table 3-1) and applied the range-through assumption, where each species is presumed present at all elevational bins between its highest and lowest recorded occurrence. Only two bins were unsampled (1650-1749 m in the Ruby Mountains and 2700-2799 m in the Snake Range) and only 7.6-13.3% of occurrences were interpolated per mountain. Binning by elevation intervals and interpolating within species range

margins are common approaches in elevational gradient studies because suitable habitat likely exists at intervening elevations but individuals go undetected due to the practical limitations of field surveys (Rowe and Lidgard 2009, McCain and Grytnes 2010).

To characterize and compare the climatic gradients along each mountainside, we calculated mean annual total precipitation (MAP) and mean annual temperature (MAT) during the years of each survey and the three years prior (e.g., 2003-2008 for the Ruby Mountains). For mountain ranges surveyed multiple times, we used the survey period over which the bulk of the samples were collected. To derive mean values per elevation bin, we extracted climate values in ArcGIS v.10.4.1 from at least 100 random points placed >100 m apart on 100-m contour lines corresponding to each sampling bin, overlaid on high-resolution (30 arcsec, 800 m) climate data (LT81 model; PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, Daly *et al.*, 2002). The PRISM model is known to have high accuracy in topographically complex regions (Parra and Monahan 2008).

### **Phylogenetic and functional trait data**

Following the methods and updated taxonomy used by Kohli and Rowe (2019, Chapter 2), we quantified phylogenetic diversity (PD) metrics using the “best dates” supertree of Fritz *et al.* (2009) pruned to the 34 rodents and shrews in our dataset, which included representatives of five mammalian families (Cricetidae, Heteromyidae, Sciuridae, Soricidae, Zapodidae). From this regional species tree, which contained branch lengths in millions of years, we created a separate phylogeny for the assemblage of each mountain range from which to calculate PD. We used R package *ape* (Paradis *et al.* 2004) for all phylogenetic tree manipulation and preparation. All analyses were conducted in R v. 3.5.1 (R Core Team 2016) unless otherwise noted.



To quantify functional diversity (FD), we compiled data for 23 traits and organized them under four niche components: environmental tolerances (n = 8), resource acquisition (n = 12), life history (n = 2), and body size (Table 3-2). These niche components or axes broadly encompass how a species interacts with its environment, including other species, and therefore can reveal the processes structuring community assembly (Weiher 2011, Winemiller et al. 2015). The environmental tolerance component corresponds to the Grinnellian niche (or  $\beta$ -niche *sensu* Pickett and Bazzaz 1978), consisting of traits related to inhabiting abiotic conditions and physical space along environmental gradients, and thus is most useful for identifying environmental filtering processes (Ackerly et al. 2006, Silvertown et al. 2006). The resource acquisition component is reflective of the Eltonian niche ( $\alpha$ -niche of Pickett and Bazzaz 1978), and includes traits most strongly tied to diet and foraging ecology which can reveal the role of competitive interactions and limiting similarity in assembly (Ackerly et al. 2006, Silvertown et al. 2006). Life history traits are those related to the allocation of resources to reproduction and survival. Body size is treated as its own component because we view it as a synthetic trait related to nearly all aspects of an organism's ecology (West et al. 1997), and has direct influence on environmental tolerances, resource acquisition, and life history.

For each niche component, we compiled data on a suite of appropriate traits in order to investigate the potential contribution of both assembly mechanisms that may operate simultaneously, whether through different traits or at different spatial scales (Weiher et al. 1998, Trisos et al. 2014). We used a combination of categorical and continuous traits obtained by measuring morphological features (Kohli and Rowe 2019, Chapter 2), reviewing available literature (especially Mammalian Species Accounts and other compiled sources), or from existing trait databases (Ernest 2003, Jones et al. 2009, Wilman et al. 2014). Across all species,

22 of 1190 trait values (2%) were unavailable after initial data compilation; all attributed to rarely captured shrews, *Sorex tenellus*, *S. merriami*, and *S. preblei*. No reproductive information has been published for *S. tenellus*, so we obtained litter size and litters per year values by examining placental scar and embryo counts from *S. tenellus* specimens we collected (Kohli et al. unpublished data). Ten traits were estimated for both *S. merriami* and *S. preblei*. We estimated eight craniodental measurements using regression with the other *Sorex* species studied here ( $n = 4$ ). For hair density and kidney RMT we substituted the mean value of other arid-habitat *Sorex*, excluding values for *S. navigator*, which is an outlier for these traits due to its semi-aquatic lifestyle (Kohli and Rowe 2019, Chapter 2). Estimation of missing values via regression was inappropriate for shrew hair density and kidney RMT because neither trait strongly correlates with body size among shrews, and their strong phylogenetic signals prohibit estimation from rodent trait values (Laakkonen 2002, Kohli and Rowe 2019, Chapter 2).

We calculated functional distance matrices with the R package *FD* (Laliberté et al. 2014) using Gower's dissimilarity to accommodate traits of various types (continuous, nominal, binomial) and weighted multichoice nominal traits equally by the reciprocal of the number of exclusive categories within each trait (Podani and Schmera 2007, Pavoine et al. 2009). We log<sub>10</sub> transformed body mass and craniodental measurements prior to distance calculations.

### **Patterns of diversity**

As a metric of taxonomic diversity we used species richness, the most common form of diversity used to investigate elevation-diversity gradients (Rahbek 1995, McCain 2005). To quantify patterns of PD and FD over elevation, we used mean pairwise distance metrics (Webb et al. 2002, Weiher 2011). Mean pairwise distances provide a general assessment of overall PD and FD by calculating the average distance among species pairs in terms of phylogeny branch lengths

(mean phylogenetic distance, MPD) or in functional traitspace (mean functional distance, MFD). Greater mean distance values reflect greater diversity. MPD and MFD summarize the range and variety of types present in each elevational bin and provide for pattern comparison to species richness over elevation. We calculated MPD and MFD using the R package *picante* (Kembel et al. 2010). To compare the shape of the elevation-diversity relationships, we determined the best fit model (linear, quadratic, or cubic) for each dimension using regression. We fit species richness with a generalized linear model with a quasi-Poisson distribution and log-link function. For FD and PD, we fit general linear models of observed mean pairwise distances. For each dimension and mountain, we compared model goodness of fit with *F*-tests. We also calculated Pearson's correlation coefficients between all metrics to assess the degree of covariation.

### **Inferring community assembly processes**

To test the role of environmental filtering and competition in community assembly across elevation, we calculated the mean nearest neighbor distance (MNND) for FD (Weiher et al. 2011). MNND is a more informative metric used to reveal the structure of assemblages and community assembly processes. By only considering the average distance to the nearest neighbor in functional space, MNND quantifies how clustered or dispersed members are on average. If an assemblage is highly clustered, it is generally assumed that a strong environmental filter greatly limits the variety of species that can survive there (Weiher 2011). On the other hand, a highly dispersed assemblage is typically taken as a sign of strong competition and limiting similarity preventing species that are too similar from coexisting (Weiher 2011). To isolate the effect of these two processes, we calculated MNND separately for traits associated with either the  $\beta$ -niche (abiotic conditions and habitat) or the  $\alpha$ -niche (resource acquisition and use) components (Ingram and Shurin 2009, Cisneros et al. 2014, Dreiss et al. 2015). We used null models to

calculate standardized effect sizes (SES-MNND) for each elevational bin, which provides a comparable measure for significance tests of nonrandom structure among our assemblages. For our null models, we randomized the species occurrence matrix using the independent swap algorithm (Gotelli 2000) which maintains species richness and species occurrence frequency across elevational bins. The significance (non-randomness) of the empirical MNND values were assessed by comparing to 999 randomizations computed with the *picante* package (Kembel et al. 2010). Positive SES-MNND values indicate overdispersion and negative values indicate clustering. Significance tests were one-sided because the separate niche components each address only a single directional hypothesis ( $p > .95$  for significantly overdispersion of  $\alpha$ -niche traits and  $p < .05$  for significantly clustering of  $\beta$ -niche traits).

We compared the goodness of fit of linear, quadratic, and cubic models for each dimension and mountain in order to evaluate our alternative hypotheses about where along elevational gradients each assembly process may be most influential (see Introduction). We also plotted  $SES-MNND_{\alpha}$  against a simple yet informative aridity index ( $MAP / [MAT + 10]$ ; Baltas, 2007) to more directly investigate the effect of the underlying abiotic gradient on assembly processes, rather than the proxy of elevation, and to capture variation in that gradient among mountain ranges. Lower index values indicate more arid conditions. Although the three study mountains are found in the same ecoregion, the extent of their respective climate gradients is partially determined by their relative locations within the Great Basin. The Ruby Mountains are located furthest north while the Toiyabe Range is the furthest west, placing it closer to the rain shadow of the Sierra Nevada (Grayson 2011).

## RESULTS

## **Elevation-diversity relationships**

Small mammal species richness, MPD, and MFD exhibited different relationships to elevation within and among mountains in the Great Basin (Fig. 3-2). Species richness peaked at mid-elevation in all three mountains (Fig. 3-2a-c). In contrast, MPD and MFD generally increased with increasing elevation. Although the shape of the relationship differed among mountains and diversity dimensions, there was a consistent departure of FD and PD patterns from the mid-elevation hump-shaped species richness pattern. Observed MPD peaked at a higher elevation and then remained high in the Toiyabe Range, increased linearly with elevation in the Snake Range, and showed a positive but statistically nonsignificant trend in the Ruby Mountains (Fig. 3-2d-f). Observed MFD showed more complex patterns; the best supported model in all three mountains was a cubic relationship increasing with elevation, but with variation in the exact pattern among mountains (Fig. 3-2g-i). Thus, while species richness was comparably low on the ends of each elevation gradient, high elevations contained more disparate assemblages of species in terms of their relatedness and functional traits.

In addition to differences in the shape of their relationships, correlations between species richness and the other diversity dimensions were generally low and did not match the null expectation of a positive relationship among dimensions (Fig. 3-3). Two of the six correlations with species richness were significant; a positive relationship with MFD in the Ruby Mountains ( $r = 0.65$ ,  $p = 0.009$ ; Fig. 3-3f) and a negative relationship with MPD in the Snake Range ( $r = -0.58$ ,  $p = 0.009$ ; Fig. 3-3b). The relationship between MPD and MFD adhered more to theoretical expectations with significant correlations detected in the Toiyabe Range ( $r = 0.958$ ,  $p < 0.001$ ) and the Snake Range ( $r = 0.57$ ,  $p = 0.01$ ), but not in the Ruby Mountains ( $r = -0.13$ ,  $p = 0.64$ ).

## **Assemblage structure**

Patterns of assemblage structure across elevation were complex and varied among mountains for both  $\alpha$ -niche traits and  $\beta$ -niche traits (Fig. 3-4). Negative SES-MNND $_{\beta}$  values indicated clustering in environmental tolerance traits, with the greatest departure from null models observed near the ends of the elevational gradients, but with variation in which gradient extreme(s) among mountains. Environmental filtering is inferred to be a primary driver of assembly in the small mammal communities at the lowest elevations in the Toiyabe Range, low and high elevations in the Snake Range, and high elevations in the Ruby Mountains (Fig. 3-4a-c). The best supported model for SES-MNND $_{\beta}$  also differed among the mountains, with a quadratic relationship with elevation in the Toiyabe Range, a cubic relationship in the Snake Range, and a linear relationship in the Ruby Mountains. Relatively weaker relationships were observed for SES-MNND $_{\alpha}$  and elevation per mountain which also varied in the shape of relationships: cubic in the Toiyabe Range, negative linear in the Snake Range, and a nonsignificant but negative trend with elevation in the Ruby Mountains (Fig. 3-4d-f). Positive SES-MNND values indicate overdispersion of resource acquisition traits and were found for some communities in each mountain range, although their placement along the elevation gradients varied. Our findings suggest limiting similarity is an important mechanism in some high-elevation assemblages in the Toiyabe Range, various (but especially the lowest) elevations in the Snake Range, and low-mid elevations in the Ruby Mountains. Thus, there was evidence of both mechanisms in the lowlands of the Snake Range.

When SES-MNND $_{\beta}$  values for each mountain are superimposed and plotted against aridity, instead of elevation, the patterns align (Fig. 3-5). Assemblages in the Snake Range spanned much of the central portion of the sampled aridity gradient. In contrast, the Toiyabe Range and Ruby Mountains only cover the more arid and less arid portions of the gradient,

respectively, converging where SES-MNND<sub>β</sub> values were highest. This result reflects the differences in climate among these mountains; the Toiyabe Range is the warmest and driest of the three mountains, the Ruby Mountains are the coolest and wettest, and the Snake Range is intermediate in both temperature and precipitation (Fig. 3-5a-b). Elevational bins encompassing the ends of the aridity gradient (aridity index values <15 and >25) were the most clustered in β-niche space (Fig. 3-5c). Therefore, environmental filtering is inferred to be acting at both ends of the sampled climate gradient, where conditions are most extreme.

## **DISCUSSION**

Recent analytical and conceptual advances in the study of multi-dimensional biodiversity provide a great opportunity to reveal ecological pattern and process (McGill et al. 2006, Cavender-Bares et al. 2009, Lopez et al. 2016). Here, we assessed relationships among multiple dimensions, identified traits to test separate mechanisms, and articulated explicit hypotheses to inform on the generality of diversity patterns and community assembly processes along gradients. We observed decoupled patterns of species richness, PD, and FD over elevation, which suggests that these dimensions are not adequate surrogates of one another. Furthermore, we found that different mechanisms contribute to assembly at different elevations, structured in part by aridity in our desert montane system.

### **Multi-dimensional diversity patterns**

The contrasting elevation-diversity patterns we observed among dimensions for Great Basin small mammals add to a growing body of evidence suggesting that different factors may be structuring different dimensions along elevational gradients (Roth et al. 2015, Willig and Presley 2016, Bässler et al. 2016, Laiolo et al. 2018). We recovered the typical hump-shaped elevation-richness pattern for small mammals in all three mountain ranges PD and FD differed

from this pattern. Differences among mountains and diversity dimensions are greatest at mid- and high-elevations where species richness sharply declines but PD and FD do not (Fig. 3-2). Conversely, patterns are generally congruent at low elevations, with relatively low values across all metrics (Fig. 3-2). Thus, low and high elevations have comparably low species richness but species in low-elevation communities tend to be phylogenetically and functionally similar whereas high-elevation communities are comprised of more distantly related species that differ more in their traits.

Hanz et al. (2019) recently suggested that a decreasing elevational relationship may be emerging as a general pattern for PD and FD regardless of species richness; however, relatively few analyses have explicitly compared patterns among dimensions and tropical and wet temperate gradients have received more attention (Bryant et al. 2008, Kluge and Kessler 2011, Dehling et al. 2014, Dreiss et al. 2015, Bässler et al. 2016). Even for a comparatively well-studied group such as small mammals, ours is only the second explicit comparison of multiple dimensions of diversity on an elevation gradient. In contrast to the decoupled patterns for Great Basin small mammals, Dreiss and colleagues (2015) found congruent elevational patterns of decreasing species richness, PD, and FD on a tropical gradient in the Peruvian Andes, suggesting adequate surrogacy of dimensions in that system. Although Dreiss and colleagues (2015) used different diversity metrics, specific traits, and taxonomic boundaries than our study (only rodents versus rodents and shrews), it seems unlikely that these methodological differences account for the starkly different conclusions. In the temperate Cantabrian Mountains of Spain, FD was found to increase with elevation for bees and showed more complex patterns among grasshoppers and birds (Laiolo et al. 2018). These and other examples emphasize the need for more comparative



work in order to assess general patterns of FD and PD within and among taxa, ecosystems, and regions of the world.

Several evolutionary or historical factors may contribute to the contrast between low and high-elevation community patterns. The predominance of a few desert-adapted lineages whose diversification is strongly tied to the development of the Great Basin and other North American deserts (Hafner et al. 2007, Badgley et al. 2014, Riddle et al. 2014b) may drive much of the low diversity patterns in lowlands. Numerous rodents from the families Heteromyidae (kangaroo rats, pocket mice, etc.) and Cricetidae (mice, rats) dominate low elevations across the region and the remaining families in our regional species pool – Sciuridae (squirrels), Dipodidae (jumping mice), and Soricidae (shrews, the most highly divergent lineage in our data set phylogenetically) – are poorly represented at low elevations. The imbalanced representation of distinct lineages translates to high phylogenetic redundancy in desert communities, causing consistently low PD (Fig. 3-2). FD is also low because the dominant lowland species share many traits such as adaptations to hot, dry conditions and diets largely consisting of seeds (Morton 1979, Kelt et al. 1996, Kohli and Rowe 2019, Chapter 2).

Increases in PD and FD from the lowland valleys toward montane habitats may result from faunal turnover, greater habitat diversity, and the consequences of dynamic historical dispersal, colonization, and extinction events. Diversity patterns tended not to correspond to distinct boundaries between major life zones (ecotones), but as elevation increases and desert shrublands transition to woodlands, forests, and montane meadows, the addition of more disparate species, including shrews, causes increases in PD and FD throughout broad transitional zones around mid-elevations (Fig. 3-2). Great Basin mountains harbor a diverse mosaic of habitats at mid- and high-elevations as a consequence of edaphic, exposure, and aspect variation

along mountain slopes (Trimble 1999, Rickart 2001). Thus, while there is a general turnover from desert-adapted to montane species, montane communities include representatives from all five of the families studied, including one heteromyid, *Perognathus mollipilosus*, where sagebrush steppe occurs broadly across the gradient. Although montane species have been more prone to local extinction events during Late Pleistocene climate fluctuations (Brown 1971a), the maintenance of high PD in modern high-elevation communities underscores that representatives of numerous lineages either persisted through time or were able to re-colonize these mountains through a combination of deterministic and stochastic dispersal events (Grayson 1987, Lawlor 1998, Rickart 2001). For FD, this confers greater diversity because co-occurring species from these separate lineages are morphologically, physiologically, and behaviorally quite different due to a combination of adaptive and stochastic evolutionary processes. Therefore, the evolutionary and biogeographic history of the lineages represented along Great Basin elevational gradients may influence the distribution of PD and FD beyond the factors controlling species richness.

### **Surrogacy of dimensions**

Deviations in elevational patterns among dimensions emphasize that species richness may be a poor surrogate and underscores the need to describe diversity gradients with more than the taxonomic dimension alone (Cisneros et al. 2014, Oliveira et al. 2016). We found limited support for the null expectation of a positive, saturating relationship between species richness and other diversity dimensions (only supported for richness-FD in the Ruby Mountains; Fig. 3-3). Thus, the various dimensions of biodiversity are either governed by different factors or reflect the effect of different ecological or evolutionary processes. The instance of a significant inverse relationship (Snake Range richness-PD) reiterates the need to reconcile empirical and theoretical relationships among dimensions (Devictor et al. 2010, Stevens and Gavilanez 2015).

A positive relationship between PD and FD is expected given the assumption of phylogenetic niche conservatism and the concept of PD as a synthetic proxy of all trait information, measured and unmeasured (Losos 2008, Cadotte et al. 2011). This relationship was supported in our data by the correlations between PD and FD and the known conservatism of many of the traits we measured (Kohli and Rowe 2019, Chapter 2). While generally correlated, there were deviations between PD and FD patterns within each mountain that emphasize the information provided by these dimensions is complementary rather than purely redundant (Ingram and Shurin 2009, Pavoine and Bonsall 2011). The most dramatic example of incongruence between PD and FD is in the Ruby Mountains, where PD shows no significant trend with elevation but FD increases (Fig. 3-2). Because FD is measured with specific traits of known functional significance, it may provide a more sensitive metric than PD, which may not fully reflect ecological differences among species (Kohli and Rowe 2019, Chapter 2). In sum, our work highlights the risks of using one dimension as a surrogate for others and shows that a multi-dimensional description of diversity will often better describe diversity gradients and inform conservation goals (Devictor et al. 2010, Roth et al. 2015, González-Maya et al. 2016).

### **Assembly mechanisms**

Although PD and FD patterns alone may be indicative of assembly mechanisms (Kluge and Kessler 2011), we chose to directly test for environmental filtering and competition with functional MNND metrics. Decomposing FD into  $\alpha$  and  $\beta$  niche components allowed us to test separate hypotheses about where along these elevational gradients environmental filtering and competition are structuring communities. Environmental filtering was a consistent driver of assembly across elevational bands in each mountain (Fig. 3-4, Fig. 3-5). Support for environmental filtering is not surprising given the dramatic changes in abiotic conditions that

occur along Great Basin mountainsides and the dominant role of environment in driving pairwise species co-occurrence patterns in the region (Kohli et al. 2018, Chapter 1). Although our comparison of patterns of clustering in  $\beta$ -niche traits along elevation among mountains appears to lack congruency (Fig. 3-4), assessing that pattern along an aridity gradient provided unified support for environmental filtering in the hot, dry habitats and cool, wet habitats (Fig. 3-5c). Only the Snake Range contained a wide enough range of climate conditions for the effects of environmental filtering to be detected in the small mammal assemblage structure at both high and low elevations. Low elevations in Toiyabe Range are the most arid and contain communities that are significantly clustered in  $\beta$ -niche traits, but aridity is relatively high across the elevational extent of the Toiyabe Range. In contrast, the Ruby Mountains in northeastern Nevada are cooler and wetter, even at lower elevations and do not contain the high aridity conditions seen in the Toiyabe Range. As a result, the desert-adapted communities that characterize low elevations in the Snake and Toiyabe Ranges are not replicated in the Ruby Mountains and the environment-induced functional redundancy is not seen. Furthermore, the most arid end of the gradient contained the most non-randomly clustered communities with a sharp decline below aridity index values of  $\sim 10$  (Fig. 3-5), suggesting that very dry and hot conditions may represent the strictest environmental filter for small mammals. Thus, as climate change continues to push desert regions toward even more extreme aridity – beyond the physiological and behavioral limits of more species (Rymer et al. 2016) – functional diversity may be an especially powerful complement to taxonomic indicators for tracking and understanding the collapse or restructuring of desert assemblages (Iknayan and Beissinger 2018).

Competition and niche partitioning have long been considered an important community assembly mechanism for small mammals (Rosenzweig and Winakur 1969, Fox and Brown 1993,

Stevens et al. 2012), but elevational patterns of  $\alpha$ -niche trait overdispersion did not consistently conform to the three alternative hypotheses we tested. If the guild assembly rule governed assembly at all elevations, low and high elevations should be overdispersed and mid-elevations less so as communities increase in richness through the addition of more functionally similar species (species packing), resulting in lower MNND in trait-space. The shape of the relationship of SES-MNND $_{\alpha}$  and elevation in the Toiyabe Range approaches the expected curve of this hypothesis, but the low-elevation, low-richness communities are not overdispersed in  $\alpha$ -niche space (Fig. 3-4d). Neither of the other two mountains support an overarching elevational pattern of functional overdispersion related to community species richness that Fox's guild rule and pervasive competition predict. The strongest signal of competition is in the Snake Range where  $\alpha$ -niche traits dispersion is negatively related to elevation, with the most non-random overdispersion in the lowest elevational band (Fig. 3-4e). This pattern is in agreement with the assertion that desert small mammal coexistence is driven largely by competition through trophic and habitat niche partitioning (Bowers and Brown 1982, Fox and Brown 1993, Dayan and Simberloff 1994, Kelt and Brown 1999). However,  $\beta$ -niche trait clustering on this same part of the elevational gradient indicates that environmental filtering and biotic filters are acting simultaneously at low elevations in the Snake Range. Thus, while traits corresponding to the use of particular food items and microhabitat use may be restricting which species can coexist, all species that occur there also must have adaptations to cope with the extremely hot, dry climate, such as kidneys that can produce highly-concentrated urine to conserve water (Lawler and Geluso 1986, Kohli and Rowe 2019, Chapter 2). A few other communities were overdispersed in  $\alpha$ -niche space, but their locations do not conform to any theoretical predictions we tested, such as the control of lower range margins via competition (Alexander et al. 2015, Louthan et al. 2015).

Overall, in the context of community assembly along these elevational gradients, competition plays a limited role compared to the broader effects of environmental filters. These community-level results mirror the conclusions derived from analyzing the drivers of pairwise species co-occurrence among Great Basin small mammals (Kohli et al. 2018, Chapter 1).

Based on their shared elevation-species richness patterns, diversity in these relatively similar mountains that share a biogeographic history might appear to be controlled by the same factors at equivalent parts of each gradient. However, the differences revealed by analysis of FD components show that such a conclusion misses the complexity of community assembly processes over elevation and among mountains. A trait-based approach provides clarity about which class of mechanisms (e.g. abiotic or biotic filters) are acting and where along gradients, yet comparative analyses of PD and FD patterns among multiple mountains have been limited (Machac et al. 2011, Hanz et al. 2019). Across a variety of taxa, ecosystems, and phylogenetic or trait-based metrics used, the most common explanation based on dispersion patterns invokes environmental filtering at high elevations and competition at low elevations (e.g., Machac *et al.*, 2011; Brehm *et al.*, 2013; Dehling *et al.*, 2014; Jiang *et al.*, 2018). Relatively few studies have found environmental filters to be acting at both low and high elevations, as in our system (Graham et al. 2009, Kluge and Kessler 2011). Graham et al. (2009) reported clustering at high elevations and both clustered and overdispersed communities of hummingbirds in low elevations in the Andes, corresponding to dry and wet habitats, respectively. Their study and our results using aridity emphasize the importance of investigating patterns and processes of diversity using underlying environmental gradients rather than elevation per se.

## **Conclusion**

Determining the underlying causes of elevational diversity gradients is a persistent challenge but examining multiple dimensions of diversity offers a promising way forward that bridges community ecology and biogeography (Weiher et al. 2011, Violle et al. 2014, Lopez et al. 2016). With a more comprehensive description of diversity we can also better address conservation and management issues and track how and why diversity is affected by environmental change. Here we have shown that small mammal communities in the Great Basin are most affected by environmental conditions, which suggests that ongoing climate change and land uses that affect water availability are likely to significantly impact these communities (Rickart et al. 2013, Hamilton et al. 2015, Kohli et al. 2019). Furthermore, high-elevation communities are more acutely subject to climate change (Beever et al. 2003), harbor less evolutionary and ecologically redundant species, and are more difficult to recolonize, putting them at greater risk of suffering rapid or dramatic declines in function if species are lost (Flynn et al. 2009). On the other hand, species at low elevations are more ecologically redundant but represent a unique subset of the PD and FD of the species pools of each mountain and should therefore also be considered conservation priorities, especially given the more extensive human land use in valleys across the Great Basin (Morris and Rowe 2014).

Table 3-1. Sampling data for each mountain range, including the total elevational extent of the local gradient (m), extent of sampled gradient (with the percentage of the total extent sampled in parentheses), the number of 100-m bins, and the range of species richness observed within elevational bins.

Mountain	Gradient extent (m)	Sampled extent (m)	Number of bins	Richness per bin
Ruby	1590-3470	1590-3014 (76%)	15	3-14
Snake	1510-3982	1547-3397 (75%)	19	5-14
Toiyabe	1627-3593	1627-2698 (54%)	11	8-18



Table 3-2. Functional trait information. The 23 traits used to quantify functional diversity were assigned to one of four niche axes and consisted of continuous and categorical (Cat.) data types. For details about specific measurements or categorical determinations, see the primary data sources listed.

Niche Axis	Trait description (with categories where appropriate)	Type of data	Source(s)
Body Size	Mean body mass (g.)	Continuous	Jones et al. 2009
Life history	Mean litter size per year	Continuous	Ernest 2003, Jones et al. 2009, Carraway and Verts 1999, this study
	Mean number of litters per year	Continuous	Ernest 2003, Jones et al. 2009, this study, literature
Environmental tolerance ( $\beta$ -niche)	Hair density (hairs per mm <sup>2</sup> )	Continuous	Kohli and Rowe 2019, Chapter 2
	Relative medullary thickness (RMT) of the kidney (metric of urine concentrating ability)	Continuous	Kohli and Rowe 2019, Chapter 2
	Annual dormancy pattern (long-term) - obligate, facultative, none	Cat., nominal	this study; literature
	Geographic affinity (the location of a species' geographic range relative to the study area) - north, south, equivalent	Cat., nominal	Kohli et al. 2018, Chapter 1
	Habitat affinity (abiotic) - mesic, xeric, generalist	Cat., nominal	Rowe and Terry 2014, literature
	Daily activity time - nocturnal, diurnal, crepuscular	Cat., binary	Wilman et al. 2014
	Nest location - underground, ground level (<2m above ground), aboveground (>2m), rock crevices/cliffs	Cat., binary	this study; literature
	Habitat Use (primary habitat types) - shrubland, woodland, forest, rock features, riparian/water features, sand dunes	Cat., binary	this study; literature
Resource acquisition ( $\alpha$ -niche)	Locomotion style - quadrupedal, bipedal	Cat., nominal	literature
	Foraging location - aquatic, ground level, above ground level	Cat., binary	this study; literature
	Diet guild - omnivore, herbivore, granivore, insectivore	Cat., nominal	Rowe and Terry 2014, literature
	Possess cheek pouches - yes or no	Cat., binary	literature
	Rostrum length	Continuous	Kohli and Rowe 2019, Chapter 2
	Rostrum width	Continuous	Kohli and Rowe 2019, Chapter 2
	Upper incisor width	Continuous	Kohli and Rowe 2019, Chapter 2
	Upper incisor depth (anterio-posterior)	Continuous	Kohli and Rowe 2019, Chapter 2
	Molar (all cheekteeth) toothrow length	Continuous	Kohli and Rowe 2019, Chapter 2
	Molar toothrow width	Continuous	Kohli and Rowe 2019, Chapter 2
	Jaw fulcrum length (index of mandible robustness)	Continuous	Kohli and Rowe 2019, Chapter 2
Lower incisor width	Continuous	Kohli and Rowe 2019, Chapter 2	

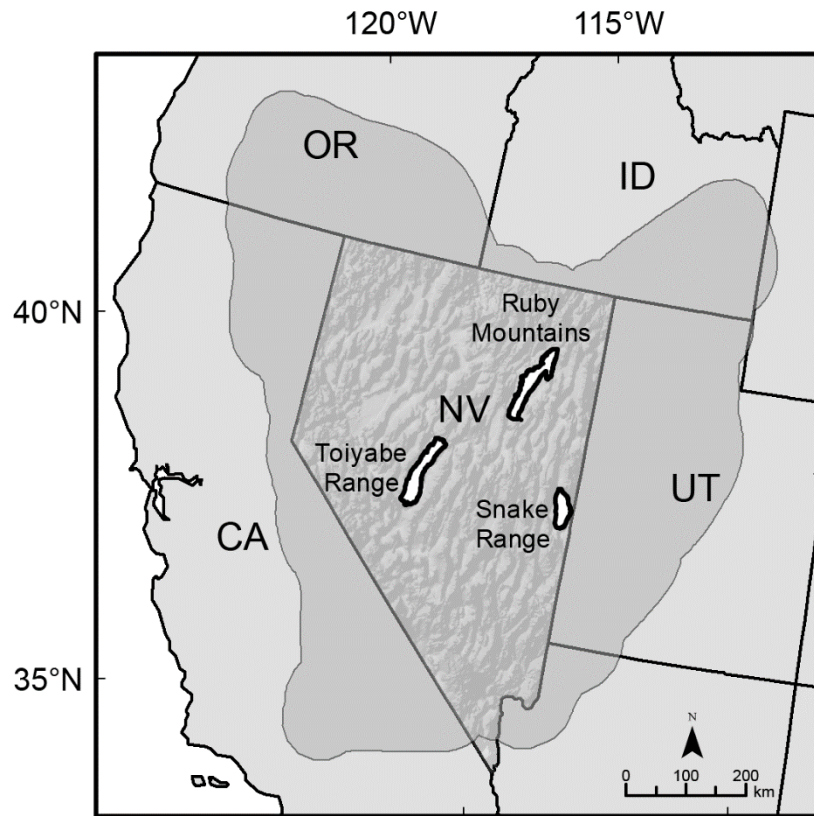


Figure 3-1. Map of the three mountain ranges surveyed for small mammals, showing their placement within the Great Basin ecoregion (dark overlay).

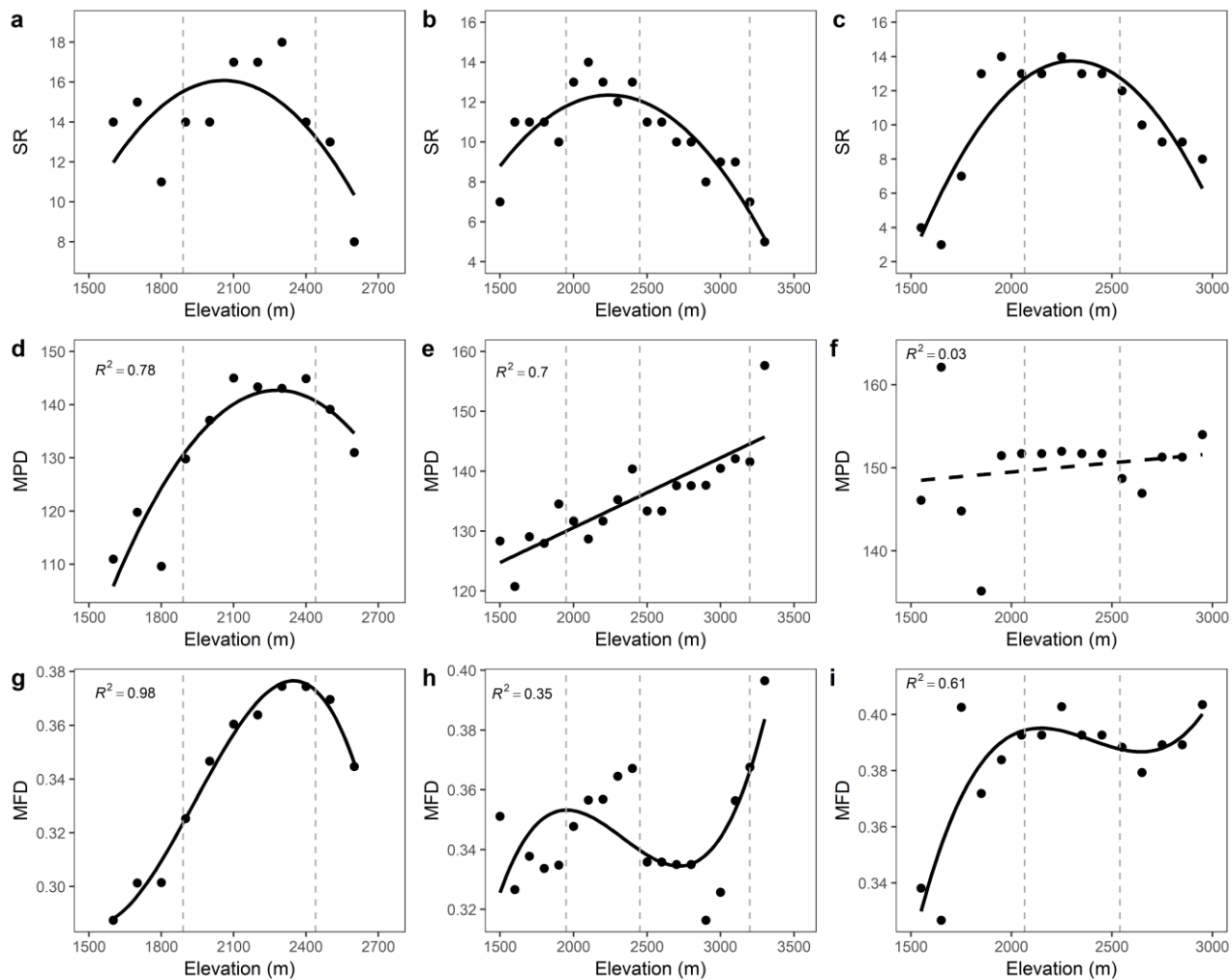


Figure 3-2. Diversity patterns over elevation for small mammals in three Great Basin mountain ranges. Columns are mountains (left to right: Toiyabe Range, Snake Range, and Ruby Mountains) and rows are metrics corresponding to different dimensions of diversity: species richness (SR), observed mean phylogenetic distance (MPD), and observed mean functional distance (MFD) based on all 23 traits. Solid lines are the best fit of either a linear, quadratic, or cubic relationship with elevation. A dashed line represents a nonsignificant trend. The horizontal dotted lines are ecotone boundaries among major life zones and have been added for reference.

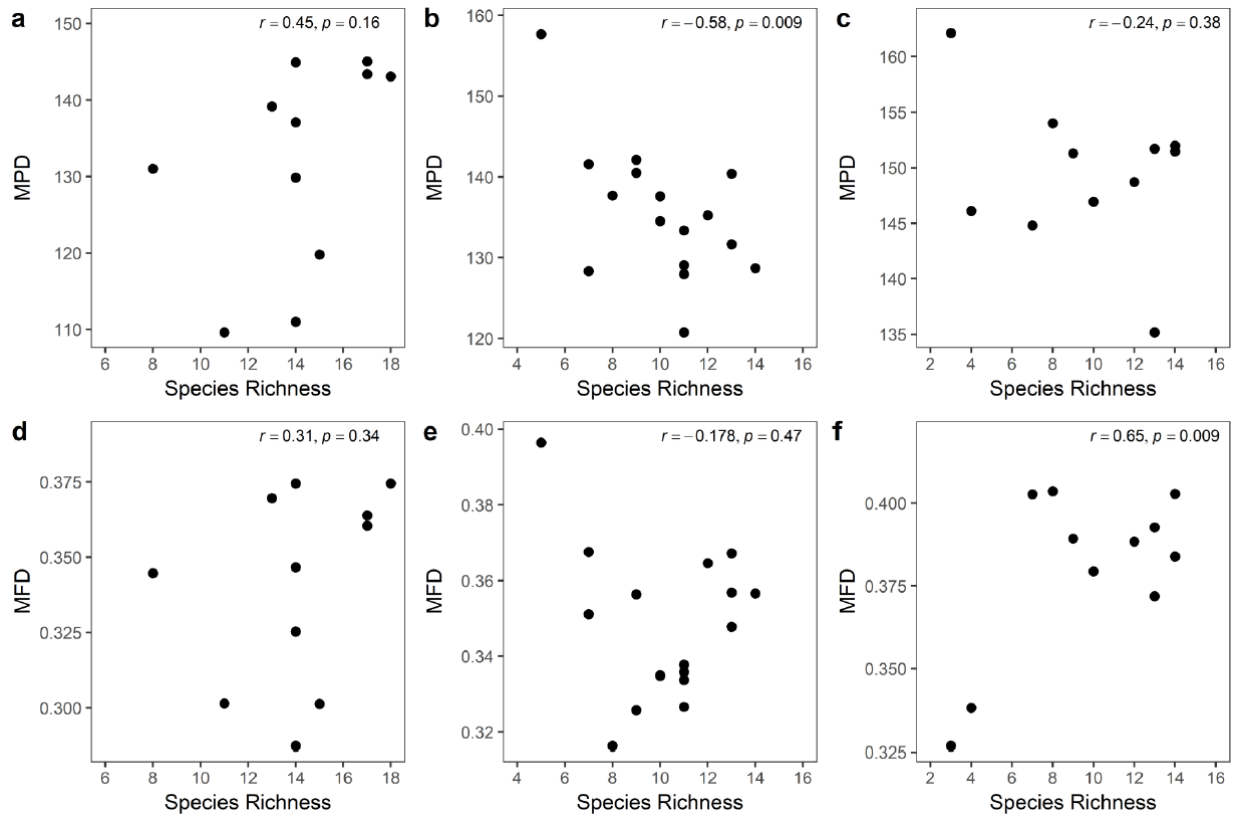


Figure 3-3. Correlation among species richness and observed mean phylogenetic distance (MPD) and mean functional distance (MFD) based on all traits for small mammal assemblages in 100-m elevational bins in three Great Basin mountain ranges (columns, left to right: Toiyabe Range, Snake Range, and Ruby Mountains).

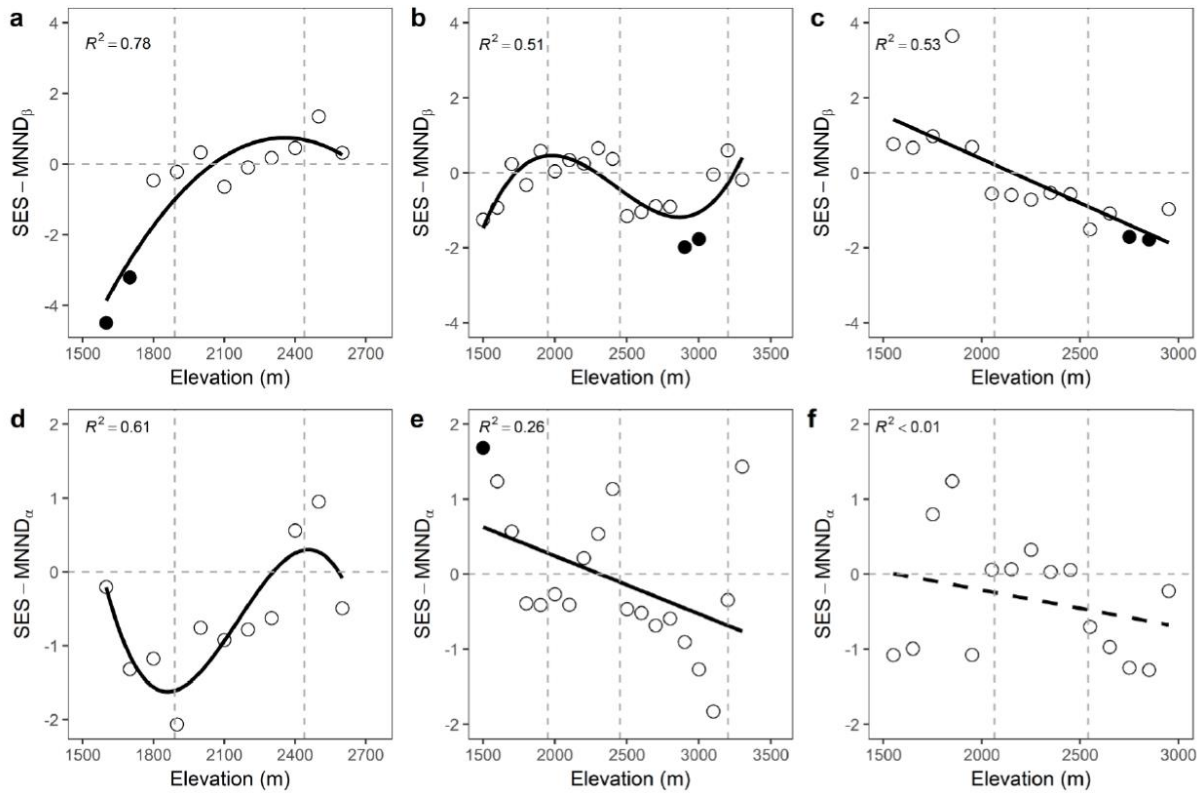


Figure 3-4. Functional dispersion of small mammal assemblages in elevational bins in the three mountain ranges (columns, left to right: Toiyabe Range, Snake Range, and Ruby Mountains). The top row (panel a-c) shows standardized mean nearest neighbor distances (SES-MNND) calculated from  $\beta$ -niche traits only and the bottom row (d-f) shows SES-MNND values based on  $\alpha$ -niche traits only. Negative values indicate assemblages that are clustered in traitspace whereas positive values represent overdispersed assemblages. The filled dots are elevations bins that are significantly structured compared to null model randomizations ( $p = 0.05$ ) and lines are the best fit relationships with elevation. A dashed line represents nonsignificant trends. Vertical dotted lines are ecotone boundaries among major life zones and have been added for reference.

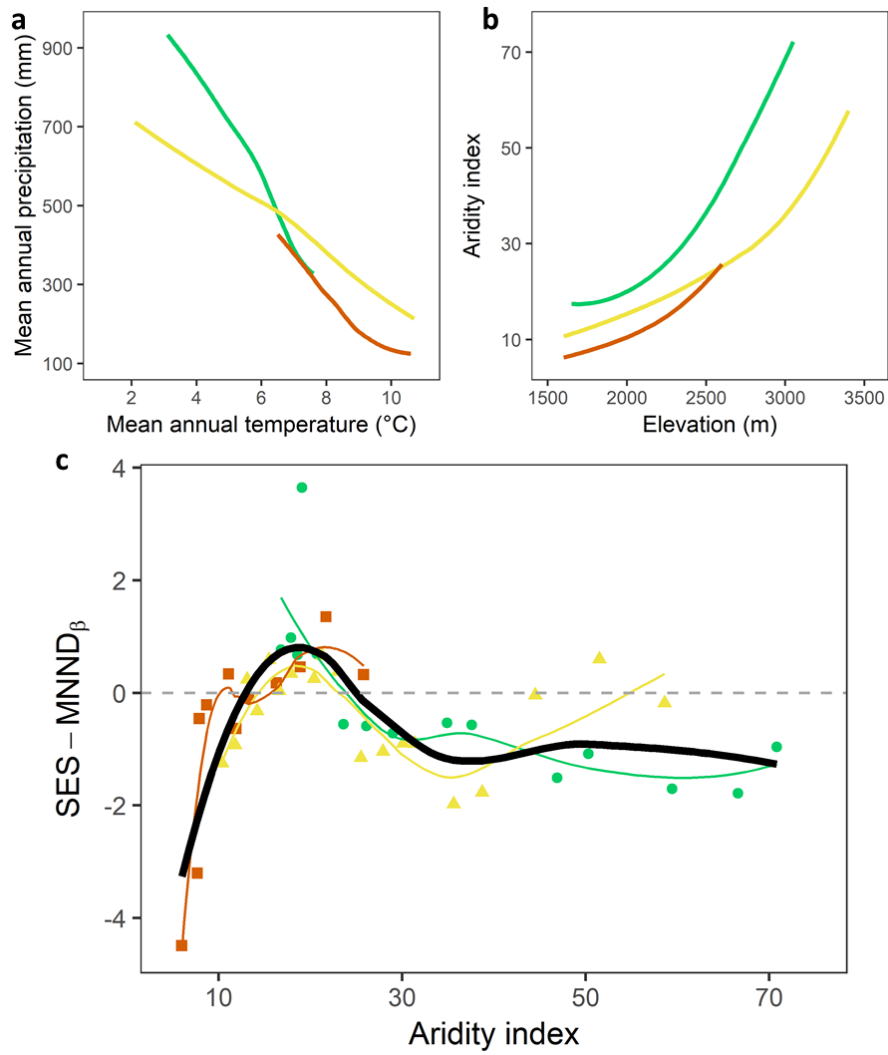


Figure 3-5. Clustering of  $\beta$ -niche traits ( $SES-MNND_{\beta}$ ) relative to aridity. A) Annual mean temperature and total precipitation in each elevational bin of the three mountain ranges (Ruby Mountains, green circles; Snake Range, yellow triangles; Toiyabe Range, brown squares). B) Relationship of mean aridity index with elevation; lower values represent hotter and drier conditions. C) Relationship of  $SES-MNND_{\beta}$  against aridity. Negative  $SES-MNND_{\beta}$  values indicate clustering, suggestive of an environmental filtering assembly process. Lines are Loess regression curves for each mountain and overall (thick black line), revealing a unified pattern across the region.

## CHAPTER 4

### LOSS OF FUNCTIONAL DIVERSITY AMONG SMALL MAMMAL COMMUNITIES IN GREAT BASIN NATIONAL PARK AND VICINITY

#### **INTRODUCTION**

The unprecedented pace of human-induced environmental change is causing dramatic declines in biodiversity worldwide (Cardinale et al. 2012, Ceballos et al. 2017). The drivers of diversity change are complex and include climate change, habitat alteration, and invasive species, among others, that vary with scale, ecosystem, and taxon. While much has been learned about the responses of individual species, more work is needed to describe and understand the impact on the composition and structure of communities. Recent work has shown that a trait-based community-level approach is powerful for identifying patterns and potential drivers of change (Flynn et al. 2009, Mouillot et al. 2013, Terry and Rowe 2015). Functional diversity (FD) summarizes the value, range, and prevalence of functional traits (e.g. physiological tolerances, diet, life history) within communities, and can be used to detect changes in the ecological complementarity and redundancy of co-occurring species (Flynn et al. 2009, Mouillot et al. 2013). As a result, changing environmental conditions may cause changes in FD even if species richness remains constant, suggesting that FD provides a more sensitive indicator of disturbance and more complete information for conservation and management actions (Clavel et al. 2010, Devictor et al. 2010, Cadotte 2011).

The functional trait composition of communities can be used to test alternative

hypotheses about biotic response to environmental change (Mouillot et al. 2013, Boersma et al. 2016). Functional responses include no change (the null expectation), equal impacts among all trait states (species), shifts in trait composition and dominance, reduction or expansion of occupied traitspace, or complete functional turnover (Boersma et al. 2016). To test these hypotheses, a variety of FD metrics can be used to quantify the abundance, range, or central tendency of trait states in multivariate trait space, which indicates whether and how certain trait combinations allow species to cope with changing conditions. FD metrics that incorporate abundance information may be especially useful for detecting subtle or gradual changes to communities, in which abrupt species losses or gains (and associated trait turnover) have not yet occurred, and therefore may serve as an early warning of change (Säterberg et al. 2013, Aspin et al. 2019).

Here, we tracked change in the functional diversity of small mammal communities in response to changing climate and habitat conditions over the past century in the Snake Range of Nevada, which includes Great Basin National Park. Resurveys – modern field surveys of sites trapped historically – provide a unique opportunity to compare animal communities over time and detect how complex drivers of change interact across a landscape (Moritz et al. 2008, Tingley et al. 2009, Rowe et al. 2011). Over the last century, climate change has coincided with intense human land use and widespread habitat conversion across the Great Basin (Wisdom and Chambers 2009, Morris and Rowe 2014). Responses to these multiple stressors by small mammals have been variable, but the increase of diet and habitat generalists and decline of specialists indicate that a closer investigation of species traits may help better understand community dynamics over time and space (Rowe et al. 2011, Rowe and Terry 2014, Terry and Rowe 2015). Our main objective was to quantify change in taxonomic and functional diversity of



small mammal to determine the effects of altered climate and habitat on community structure and composition. We assessed these two dimensions of diversity in order to more fully describe community responses across elevation but also to compare their ability to detect composition changes and infer the underlying drivers.

## **MATERIALS AND METHODS**

### **Study system**

The Snake Range is located in east-central Nevada between Spring Valley to the west and Snake Valley to the east, which straddles the Nevada-Utah border (Fig. 4-1). The elevational gradient from the floor of Snake Valley (near 1,500 m) to the summit of Wheeler Peak (3,982 m) represents the greatest relief of any mountain range in the central Great Basin (Grayson 2011). The Snake Range is also home to Great Basin National Park, which was established in 1986 and is the only national park located entirely within the physiographic Great Basin. The region is generally arid, but conditions vary dramatically with elevation from hot, dry desert valleys to cool, wet alpine peaks. Major plant associations transition relatively abruptly with elevation and include desert shrublands (below ca. 1950 m), pinyon-juniper woodlands (ca. 1951-2450 m), montane mixed-conifer forests (ca. 2451-3200 m) and alpine forest and tundra (above ca. 3200 m; Trimble 1999; Grayson 2011). Riparian zones and rocky outcrops or talus slopes occur at nearly any elevation. At ecotones and within each vegetation zone there is a spatial mosaic of habitat types due to slope, aspect, edaphic factors, and water availability. The mountain range is inhabited by a diverse assemblage of small mammals (rodents and shrews < 500 g), with 28 documented species that vary widely in their ecologies and elevational distributions (Rickart et al. 2008).

The Great Basin has experienced substantial environmental change since the mid-1800s that affect mammals through physiological effects of climate as well as habitat modification (Grayson 2011, Morris and Rowe 2014). Over the past century, temperatures across the Great Basin have increased by an average of 0.5°C, but some mountain ranges have experienced increases greater than 1°C (Chambers and Wisdom 2009, Rowe et al. 2010). Annual precipitation has also increased over this period in most areas, although interannual variation has increased as well (Chambers and Wisdom 2009; Rowe and Terry 2014). A variety of land use practices and habitat shifts have impacted the region, including livestock grazing, mining, groundwater extraction, pinyon-juniper woodland expansion, and the spread of invasive grasses, in particular cheatgrass (*Bromus tectorum*; Miller and Wigand 1994, Patten et al. 2008, Morris and Rowe 2014). These drivers of change have altered the habitat structure and resource base available for use by wildlife species across elevations.

### **Small mammal surveys**

Occurrence and abundance data for small mammals were generated from two comprehensive field surveys conducted over 80 years apart. Comparable trapping methods were used during historical (1929-1930, 1939) and modern (2015-2016) surveys to sample terrestrial, non-volant small mammals (rodents and shrews <500 g). Survey sites in each era spanned >1,500m elevation and all vegetation zones (Fig. 4-1). Trapping at each survey site covered the full range of habitat types present.

During the early 20<sup>th</sup> century a systematic effort to document vertebrate distributions across the Great Basin was carried out by researchers at the Museum of Vertebrate Zoology (MVZ), University of California, Berkeley (Hall 1946). Our historical data come from a survey of the Snake Range conducted by E. R. Hall, W. C. Russell, and R. D. Moore between May and

August of 1929. During this period, they surveyed 16 sites, and later revisited one for more extensive trapping in July 1930. To improve historical high-elevation sampling, we also included data from an additional site (elevation 3,058 m) trapped in 1939 by J. R. Alcorn and W. M. Longhurst. Detailed collector field notes associated with each survey were obtained from the MVZ Archives (Appendix D, Table D1) and used to reconstruct historical survey site locations, survey effort (the number of trapnights, one trap set for one 24-hour period), collection method, trapline habitat, and the identity and abundance of each species captured each day. These records detail the total number of individuals captured per species, including those not preserved as museum specimens. Data on effort and abundance cannot be obtained from catalogs of specimen records alone, but may be critical for interpreting trends over time (Tingley et al. 2009, Rowe et al. 2010, Rowe 2017). Occasionally, field notes provided approximate numbers which were compared to specimen records to estimate conservative minimum values.

Modern surveys were conducted at 28 sites between May and August of 2015 and 2016, including 12 resurveys of historical sites. Sherman live traps and snap traps (Museum Special and Victor rat traps) were baited with birdseed or peanut butter and rolled oats and checked twice daily. Daily field notes detailing modern survey trapline effort and capture totals were recorded by collectors and deposited with specimens at the Natural History Museum of Utah (University of Utah), the Monte L. Bean Life Science Museum (Brigham Young University), the Field Museum of Natural History (Chicago, Illinois), and the MVZ. Collecting procedures followed guidelines established by the American Society of Mammalogists (Sikes et al. 2016) and were certified by the Animal Care and Use Committee of the University of Utah (15-02001) and University of New Hampshire (111104A, 141103A; Appendix A).

We limited our temporal comparison to records of species reliably obtained using comparable methods, and thus removed all captures that resulted from targeted trapping techniques in both the historical (e.g., steel leg-hold traps, firearms, gopher traps) and modern (e.g. pitfall traps, gopher traps) time periods. In addition, due to requirements of the analytical methods and diversity metrics used (see below), we only retained historical data from sites trapped a minimum of two consecutive nights and with at least four species captured. Suitable survey data for our analysis were available from 10 historical sites and 24 modern sites, including nine paired resurveys distributed across nearly the entire elevational gradient (1,633-3,174 m; Fig. 4-1). Our analysis focuses on the nine paired resurveys, but data from the unpaired sites were used to ensure that the resurvey sites were representative of the general conditions across the landscape during both survey periods. The historical sampling at the paired resurvey sites totaled 3,112 trapnights (110-743 per site, mean = 346) over 39 nights (2-9 per site, mean = 4) and resulted in 427 individual captures of 20 species (Appendix D, Table D2). Modern effort at the same nine sites totaled 7,135 trapnights (480-1507 per site, mean = 793) over 40 nights (4-8 per site, mean = 4) and yielded 721 captures of 20 species (Appendix D, Table D2). Survey data were effort-standardized to make comparisons over time (see *Diversity metrics* below).

### **Climate data**

To provide context for the interpretation of changes in small mammal taxonomic and functional diversity, we quantified changes in total annual precipitation (mm) and mean annual temperature (°C) over the 86-year sampling interval. We averaged across the years accounting for the bulk of the capture data during each survey period and the three years prior (1926-1929 and 2012-2016). We used ArcGIS v.10.4.1 to extract annual means for each site from high-resolution (800 m) gridded climate data (LT81 model; PRISM Climate Group, Oregon State

University, <http://prism.oregonstate.edu>, Daly *et al.*, 2002); values were interpolated based on the distances to the neighboring grid cells. The PRISM model is known to have high accuracy in topographically complex regions (Parra and Monahan 2008).

### **Trait data**

Functional diversity can be calculated from virtually any type of trait data, but trait choice should be strongly related to the process(es) being investigated (Griffin-Nolan *et al.* 2018, Aspin *et al.* 2019). Our process of interest was the response of small mammals to environmental change. To quantify functional diversity, we compiled data for 23 traits and organized them under the following three niche components: traits mediating response to climate change (hereafter climate traits), traits mediating response to structural habitat change and associated shifts in the resource base (habitat traits), and life history traits (Table 4-1). Climate response traits ( $n = 8$ ) included body size ( $\log_{10}$ ), hair density, relative medullary thickness of the kidney, hibernation strategy, geographic affinity, abiotic affinity, daily activity time, and nest location. These traits summarize thermoregulatory and water conservation strategies and species' physiological tolerances and many have been shown to relate to species distributions along abiotic gradients or responses to climate change (McCain and King 2014, Terry and Rowe 2015, Kohli and Rowe 2019, Chapter 2). We selected 13 habitat response traits: habitat type, locomotor mode, presence of cheek pouches, foraging location, diet guild, and eight craniodental measurements ( $\log_{10}$ ) that summarize diet specificity. This suite of traits characterizes how small mammals use and move through a landscape as well as acquire food resources, and thus help to infer responses to alterations in habitat or the resource base (Rosenzweig and Winakur 1969, Kotler and Brown 1988, Stevens *et al.* 2012, Kohli and Rowe 2019, Chapter 2). Life history traits relate to the allocation of resources to reproduction and survival and can thus influence

recovery potential from changes in conditions, be that climate, habitat, or the resource base (Lightfoot et al. 2012). We included two life history traits, average litter size and number of litters per year. We evaluated functional diversity for all 23 traits combined and separately for both climate and habitat traits to better identify which aspects of environmental change may be most influencing community diversity over time (Mouillot et al. 2013, Cisneros et al. 2015).

Trait data come from multiple sources. Thirteen continuous trait measurements were obtained from Kohli and Rowe (2019, Chapter 2) or existing trait databases (body size and life history data), and 10 categorical traits were assigned based on available literature (especially Mammalian Species Accounts and other compiled sources) and existing databases (Ernest 2003, Jones et al. 2009, Wilman et al. 2014). Only the two life history parameters of *Sorex tenellus* (Inyo shrew) were unavailable from these sources, because no reproductive information has been published for this rarely captured species. To estimate values, we examined 17 specimens of female *Sorex tenellus* collected during recent surveys in Great Basin mountain ranges (Rickart et al. 2004, 2011, 2018, Matocq et al. 2017). Placental scar and embryo counts were used to estimate litter size and litters per year (Kohli et al. unpublished data).

### **Diversity metrics**

For each site in each time period, we calculated taxonomic and functional diversity metrics. For taxonomic diversity, we measured species richness and total abundance (the sum of effort-standardized abundances for all species at a given site). Effort-standardized abundance accounts for differences in trap effort over time and was calculated by resampling individuals, with replacement, for 1000 iterations using the minimum number of trapnights and then taking the mean of these estimates (Rowe et al. 2011). We performed 9 separate rarefactions, one for each pair of samples at each resurvey site.

For functional diversity, we calculated four complementary metrics: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv; Villéger et al. 2008), and functional dispersion (FDis; Laliberté and Legendre 2010). Of these, FEve, FDiv, and FDis incorporate abundance data and for which we used the effort-standardized abundances described above. FRic measures the volume of traitspace a community occupies and was standardized from 0-1 relative to the global FRic (entire species pool). FEve measures the regularity of species distributions and abundance in traitspace; more evenly distributed assemblages have larger values. FDiv quantifies how distant the most abundant species are from the functional centroid of an assemblage; larger values indicate that the most abundant species have more extreme trait values. FDis measures the mean distance of species to the abundance-weighted assemblage centroid; larger values indicate greater dispersion of species in traitspace or more pronounced trait differences among species.

We conducted all statistical analyses in R v. 3.5.1 (R Core Team 2016). We calculated functional distance matrices with the R package *FD* (Laliberté et al. 2014) using Gower's dissimilarity to accommodate traits of various types (continuous, nominal, binomial) and weighted multichoice nominal traits equally by the reciprocal of the number of exclusive categories within each trait to avoid a numerical bias toward certain traits (Podani and Schmera 2007, Pavoine et al. 2009). Principal coordinates analysis (PCoA) was then performed to reduce the dimensionality of the data in traitspace, with the resulting PCoA axes used to calculate functional metrics. Calculation of FRic and FDiv rely on finding the minimum convex hull which requires more species than traits (Villéger et al. 2008). Therefore, including sites with very low species richness means only a limited number of PCoA axes can be used in computations, resulting in a quantifiable loss of information across the entire dataset. Preliminary

analyses found that including resurvey sites with three species (two PCoA axes retained) resulted in FRic and FDiv traitspace qualities around 40%, whereas representation quality improved to roughly 60% when using sites with more than three species. For this reason, we limited our paired resurvey sites to the nine which had four or more species observed in both time periods. All PCoA axes were always used to estimate FEve and FDis, which are not limited by low species richness.

### **Data analysis**

We used our taxonomic and functional diversity metrics to assess change in small mammal diversity over time and to test the alternative hypotheses of Boersma et al. (2016) – no change, Equal Impact Hypothesis, Trait Abundance Shift Hypothesis, Functional Turnover Hypothesis, and the Convergence/Divergence Hypothesis. We assessed change in each metric at the nine paired resurvey sites using paired *t*-tests. With our low sample size, these tests likely have limited power when  $p = 0.05$ , and an adjusted *p*-value may be warranted to interpret significance. We determined power using the R package *pwr* (Champely et al. 2018) to evaluate an appropriate  $\alpha$  threshold. We assessed overall change in functional diversity as well as for climate traits alone and habitat traits alone. Life history traits were not used in isolation because they potentially relate to response under both habitat and climate change and therefore cannot be used to infer specific mechanisms. To identify any elevation-specific changes, we evaluated whether the magnitude of change in a metric was correlated with elevation. To alleviate additional methodological concerns about the influence of our effort-standardization resampling procedure on the results, we also determined if change in abundance-weighted metrics was correlated with historical trap effort (the minimum number of trapnights used to rarefy abundances at each site) or disparity in trap effort between time periods. The resampling



procedure has been applied to aggregate community properties (Rowe et al. 2011, Rowe and Terry 2014), but we use this additional conservative test for this first application to evenness metrics, which may be more sensitive.

To identify links between changes in FD metrics and community composition, we analyzed individual species outcomes over time using the FSECchange function in R (Mouillot et al. 2013). Using output from this function, we tallied the number of local site introductions and extirpations for each species as well as the number of sites at which a species experienced marked change in relative abundance (defined as an increase or decrease of >50% compared to its relative abundance during the historical period) to identify “winners” and “losers” over time. We use these species-specific changes in occurrence and abundance to illustrate the effect of individual drivers on FD more broadly.

## **RESULTS**

### **Climate change**

Temperature and precipitation increased in the Snake Range over the 86-year interval between the two survey periods (Fig. 4-2). Across all sites surveyed during the historical and/or modern period, mean annual temperature increased by a mean of 0.52°C (-0.1-1.1°C) and total precipitation increased by a mean of 66.6 mm (29.8-89.4 mm). The direction and magnitude of these local climate changes are consistent with the linear increases documented elsewhere in the region over the last century (Chambers and Wisdom 2009, Rowe et al. 2010).

### **Community diversity over time**

Taxonomic diversity, as measured by species richness and total effort-standardized abundance, changed over time at individual sites, but on average did not differ between time periods (Fig. 4-3a-b, Table 4-2). In contrast, changes in small mammal functional diversity at

paired resurvey sites were detected. Diversity primarily decreased over time among abundance-weighted functional diversity metrics (Fig. 4-3c-f, Table 4-2). Given the low power of our tests (Table 4-2), we interpret  $p$ -values  $\leq 0.10$  as significant. When all sites were used (including non-paired resurvey sites) the range of values for each diversity metric was similar between time periods, and the nine resurvey sites were representative of broader landscape-scale patterns and changes (not shown). There was no significant correlation between the degree of change in any diversity metric and elevation (Pearson's  $r$ , -0.4-0.56;  $p$ , 0.12-0.97). Additionally, abundance-weighted metrics were not correlated with the magnitude of the difference in trap effort between survey periods ( $r$ , -0.54-0.56;  $p$ , 0.11-0.44) or the number of historical trapnights ( $r$ , -0.24-0.45;  $p$ , 0.22-0.88).

When all traits were considered, FEve significantly declined over time ( $t_8 = 2.52$ ,  $p = 0.036$ ) and FDis showed a decreasing trend ( $t_8 = 1.54$ ,  $p = 0.16$ ). FEve measures the evenness of abundance distribution in traitspace and FDis summarizes how distant species are on average from the most generalized functional state of an assemblage. Thus, these results suggest that under modern conditions the functional composition of communities is not as equitable as in the past and that less-specialized functional types are more favorable relative to others. The overall decline in FEve appears to be largely driven by shifts in climate trait space ( $t_8 = 3.0225$ ,  $p = 0.017$ ; Fig. 4-3). Although climate-trait FEve has decreased, FRic increased ( $t_8 = -1.9$ ,  $p = 0.09$ ). This results from the addition of species with relatively extreme climate traits that increase the convex hull volume. For habitat response traits the data suggest a decrease over time in mean FDiv ( $t_8 = 1.97$ ,  $p = 0.084$ ) and FDis ( $t_8 = 1.79$ ,  $p = 0.11$ ). Declines in FDiv and FDis reflect a shift in relative abundance toward species with more generalized habitat and diet preferences (closer to community centroids) that are less distinct from each other on average.

## Species outcomes

Dynamic changes in species distributions and abundances over time across the resurvey sites contributed to functional community restructuring. Although 22 species were captured across all nine paired resurvey sites, only 18 of them were shared between time periods (Appendix D, Table D2). *Dipodomys ordii* (Ord's kangaroo rat) and *Sorex tenellus* (Inyo shrew) were only captured during the modern surveys at these nine sites, although *D. ordii* was taken at an unpaired historical site. *Onychomys leucogaster* (northern grasshopper mouse) and *Peromyscus crinitus* (canyon mouse) were only captured during the historical surveys, but both species have been detected during recent surveys at other sites in the Snake Range, and thus have not been lost from the system entirely (Chapter 3; Rickart et al. 2008). Eight of the nine resurvey sites experienced some compositional change over time, involving 16 species that show at least one site-level species introduction or extirpation. Abundance changes were also common and were consistent in direction across sites (increase or decrease) for 18 species. Substantial (>50%) decreases in relative abundance in at least one site were detected for 11 species and increases for seven species. The remaining three species responding in different directions at different sites (*Peromyscus maniculatus*, deer mouse; *Perognathus longimembris*, little pocket mouse; *Tamias umbrinus*, Uinta chipmunk). Taken together, we identified the greatest directional changes (abundance and occurrence frequency) for individual species over time, including three big “winners” (*Microtus longicaudus*, long-tailed vole; *Peromyscus truei*, pinyon mouse; and *Sorex vagrans*, vagrant shrew) and three big “losers” (*Callospermophilus lateralis*, golden-mantled ground squirrel; *Neotoma cinerea*, bushy-tailed woodrat; and *Tamias minimus*, least chipmunk; Fig. 4-4).

## DISCUSSION

The functional diversity of biotic communities is threatened by anthropogenic factors including habitat alteration (Flynn et al. 2009, Rader et al. 2014, Cisneros et al. 2015) and climate change (Albouy et al. 2015, Mason-Romo et al. 2017). The impacts on diversity can be abrupt (Aspin et al. 2019) or gradual (Törnroos et al. 2019), and detecting and understanding them often requires a multi-faceted approach (Mayfield et al. 2010, Jarzyna and Jetz 2017). By examining trends in functional diversity using paired resurvey data, we revealed niche-based responses of small mammal communities to nearly a century of environmental change in and around Great Basin National Park. Communities showed complex, but largely negative, responses to climate and land cover change across habitat types and elevations, emphasizing the need to consider multiple independent and interactive drivers. These community-level changes resulted from variable individual species responses in distribution and abundance. The sum of individual changes led to shifts in functional diversity but no change in common metrics of taxonomic diversity. Thus, our results highlight how functional trait and abundance data can be used to detect subtle or early-stage changes to community structure.

### **Declines in functional diversity**

Changes in the functional diversity of small mammal communities in the Snake Range were most consistent with the Trait Abundance Shift Hypothesis (Boersma et al. 2016). This hypothesis states that in response to disturbance differences in the relative abundance of traits will change but not the range or volume of traitspace occupied. Over the 86-year interval of our study, the relative abundance or dominance of trait combinations shifted, resulting predominately in decreasing FEve, FDiv, and FDis over time across all trait subsets (Fig. 4-3c,e,f), but stability in overall and habitat-related FRic. Climate-related FRic did increase (Fig. 4-3d), but the consistent response of abundance-weighted metrics indicates that the addition of novel types to

communities did not prevent overall declines in FD, leading to greater homogenization and redundancy.

Climate and habitat changes each contributed to the declines in FEve, FDiv and FDis. The decline in functional evenness over time indicates that abundance within communities is now more concentrated among fewer functional types, meaning the most dominant species in the modern period tend to have similar traits whereas the historical distribution of abundance in traitspace was less redundant. Among trait types, decreases in evenness was greater for climate response traits than habitat response traits (Table 4-2). Concurrent declines in functional divergence (FDiv) and in dispersion (FDis) support movement toward functional homogenization, a phenomenon seen across a variety of systems and scales (Clavel et al. 2010, Savage and Vellend 2015, Jarzyna and Jetz 2017). Abundance in modern communities is less dispersed through the available traitspace than in historical communities, meaning favored trait combinations are less diverse in the modern. This is particularly true for habitat response traits that most closely track the structure and resource base made available by different habitat types. The decline in habitat-trait FDiv signals that the abundance of species with trait combinations near the periphery of multivariate traitspace have declined over time in favor of species with more generalized diet and habitat requirements. This corroborates findings from other resurveys across the Great Basin showing that diet and habitat generalists have increased in biomass, energy use, and total abundance relative to specialists over the last century (Rowe et al. 2011, Rowe and Terry 2014). Differences in life history likely contribute to the reduction of overall FD as species with higher reproductive potential are better positioned to respond to environmental disturbances of all kinds (Lightfoot et al. 2012).

### **Individual species responses**

The FD results suggest that community structure is influenced by the complex effects of climate and land-use driven changes in habitat among resurvey sites. The species-specific responses of our biggest winners and losers help to illustrate how changes in species occurrence and abundance have translated to community FD change. Here we refer to species-specific changes in occupancy and abundance at the nine resurvey sites, but patterns hold when considering unpaired site data as well. Although warming was greatest at high elevations where most cold-adapted species occur, the absence of a correlation between elevation and the degree of change in any diversity metric emphasizes that community responses are influenced by more than warming alone. Recent increases in temperature (Fig. 4-2) simply may not yet be substantial enough to translate to wholesale functional turnover in the Snake Range, and instead we are observing early-stage disruptions to community composition via abundance shifts. Two of the three species showing the greatest overall decline, *Neotoma cinerea* and *Callospermophilus lateralis* support this hypothesis. These species are among the largest in our dataset and both have montane distributions (Brown 1971a, Rickart 2001), potentially making them physiologically susceptible to warming (Brown 1968, Eastman et al. 2012). In accordance with a response to warming, the lower range margin of *C. lateralis* (an obligate hibernator with a northerly distribution) appears to have contracted upslope by as much as 1,000 m and this species has decreased in abundance where it still occurs, at the highest resurvey site (Fig. 4-4). Historically, the lower elevational limit for *C. lateralis* was at about 2,000 m and the species was detected on both slopes of the mountain range (Hall 1946, Rickart et al. 2008), but today it is only found above ca. 3,100 m on the wetter eastern slope. *Neotoma cinerea* (a mesic- and cold-adapted species with a northerly distribution) still occurs in the lower portion of its historical range, but is dramatically decreased in relative abundance there (Rickart et al. 2008; Fig. 4-4).

This species primarily inhabits caves and deep rock crevices on north-facing slopes that provide the cooler, moister microclimatic conditions it requires to escape high temperatures (Smith 1997). The loss of *N. cinerea* from the highest resurvey also suggests that the suitability of high elevation habitat may be declining as temperatures rise. Although the cause is unclear, loss of this species at high elevations has also been documented from resurveys in the Sierra Nevada (Moritz et al. 2008, Rowe et al. 2015a).

The stress of increased temperature on montane species may be dampened by periods of higher precipitation, especially when combined with a reduction in grazing intensity over time. Field notes (Appendix D, Table D1) indicate that livestock grazing was prevalent across the Snake Range during the historical period, including at and near our resurvey sites. Efforts to regulate grazing began in earnest shortly after the historical surveys with the passage of the Taylor Grazing Act in 1934. Today, grazing is restricted to the foothills and lowland valleys, below the boundary of Great Basin National Park (Fig. 4-1). This interaction of land use change and climate change likely facilitated the recovery of riparian habitat and contributed to the shifts in occurrence and abundance of mesic-adapted species (Rowe 2007, Rickart et al. 2013). Increases in occurrence and relative abundance of two of the three biggest winners over time, the long-tailed vole (*Microtus longicaudus*) and vagrant shrew (*Sorex vagrans*), exemplify this pattern. These two species might be expected to fare better during periods of greater precipitation than most species in our dataset because they have among the lowest values for a morphological index of water conservation ability (kidney RMT, Kohli and Rowe 2019, Chapter 2), and voles and shrews tend to be heavily reliant on the cover and food sources afforded by riparian habitats (Hamilton et al. 2015). Both *M. longicaudus* and *S. vagrans* had greater occupancy and abundance at mid-elevation resurvey sites in the modern than historically (Fig. 4-4). The site-

level introductions of these and other mesic-adapted specialist species contributed to the increase in functional richness (FRic) of climate traits observed over time within communities, and their abundance gains likely contributed to the decreased FEve (Fig. 4-3). However, these gains did not extend to low elevations. Lowlands have experienced the most diverse stressors that have likely prevented recovery of mesic-adapted species at the lowest elevations. For example, intensive water use during the first part of the 20<sup>th</sup> century has reduced groundwater aquifer levels and exacerbated the effects of land use and warming, leading to the severe reduction in mesic habitats among valleys (Patten et al. 2008).

The interactive effects of changes in climate and land use practices has also facilitated the expansion of pinyon-juniper woodland across the Great Basin (Tausch et al. 1981, Miller and Wigand 1994, Romme et al. 2009), including on the slopes of the Snake Range (Hamilton et al. 2019). Expansion has been both up and downslope encroaching predominately into native sagebrush shrublands. Woodland expansion has triggered widespread habitat conversion that has translated to changes in species distribution and abundance across the region (Rickart et al. 2008, Rowe et al. 2010, Massey et al. 2017) as well as reduced local rodent diversity and biomass where encroachment has occurred (Hamilton et al. 2019). One commonly observed pattern is the contrasting response between the pinyon mouse (*Peromyscus truei*, a species typically associated with pinyon-juniper woodlands; Hoffmeister 1981) and the least chipmunk (*Tamias minimus*, a species with an affinity to sagebrush steppe; Verts and Carraway 2001), and our comparison of resurvey sites in the Snake Range reveals it as well. *Peromyscus truei*, predictably tracked the expansion of woodland both upslope and downslope to occupy five resurvey sites in the modern, up from just one historically (Fig. 4-4). Conversely, *T. minimus*, was extirpated at three of five historical sites, and greatly decreased in abundance at a fourth. The expansion of *P. truei* and



persistence of *T. minimus* only at range margins is consistent with the coinciding expansion and infilling of the pinyon-juniper zone. Decline in sagebrush habitat extent and quality may also be related to the spread of cheatgrass, an invasive annual grass, which has been found to negatively impact rodent diversity and populations through changes in habitat structure and forage quality and availability (Ostoja and Schupp 2009, Freeman et al. 2014, Lucero et al. 2015).

## **Conclusion**

Functional diversity and abundance data are an effective tool for documenting diversity declines in small mammals on decadal-to-centennial time scales. These animals are excellent indicators of environmental change because they have diverse ecologies and life histories and are highly sensitive to habitat and climate perturbation (Hadly 1996, Moritz et al. 2008, Rowe et al. 2011). Small mammals also contribute crucial ecological functions as seed dispersers and consumers, food sources for predators, and ecosystem engineers (e.g. burrow excavation; Brown and Heske 1990, Whitford and Kay 1999, Hollander and Vander Wall 2004). Therefore, if the observed trend toward greater functional redundancy and homogenization continues, these communities may reach a threshold beyond which more dramatic reductions in diversity and ecosystem function are triggered (Säterberg et al. 2013, Barbet-Massin and Jetz 2015). Although protected areas such as national parks represent potential reservoirs of biodiversity in an increasingly human-modified landscape, our work reiterates that protected lands are not exempt from the broader patterns of biodiversity decline (Newmark 1995, Mason-Romo et al. 2017). Deserts in particular already represent extreme conditions in which species may be near critical physiological thresholds, and thus may represent sensitive ecosystems for detecting change (Chillo and Ojeda 2012, Iknayan and Beissinger 2018). Our temporal comparison of nine paired sites along the Snake Range gradient based on high-quality historical records offers a strong

signal of change in functional diversity and underscores the need for continued conservation efforts as well as more long-term monitoring of communities to provide a more-detailed assessment of the effect of environmental change on biodiversity.

Table 4-1. Description of the 23 continuous and categorical (Cat.) traits used to quantify small mammal functional diversity, each assigned to one of three niche axes. For details about specific measurements or categorical determinations, see the original data sources listed.

Niche Axis	Trait description (with categories where appropriate)	Type of data	Source(s)
Life history	Mean litter size per year	Continuous	Ernest 2003, Jones et al. 2009, Carraway and Verts 1999, Chapter 3
	Mean number of litters per year	Continuous	Ernest 2003, Jones et al. 2009, Chapter 3, literature
Climate response	Mean body mass (g.)	Continuous	Jones et al. 2009
	Hair density (hairs per mm <sup>2</sup> )	Continuous	Kohli and Rowe 2019, Chapter 2
	Relative medullary thickness (RMT) of the kidney (metric of urine concentrating ability)	Continuous	Kohli and Rowe 2019, Chapter 2
	Annual dormancy pattern (long-term) - obligate, facultative, none	Cat., nominal	Chapter 3; literature
	Geographic affinity (the location of a species' geographic range relative to the study area) - north, south, equivalent	Cat., nominal	Kohli et al. 2018, Chapter 1
	Habitat affinity (abiotic) - mesic, xeric, generalist	Cat., nominal	Rowe and Terry 2014, literature
	Daily activity time - nocturnal, diurnal, crepuscular	Cat., binary	Wilman et al. 2014
	Nest location - underground, ground level (<2m above ground), aboveground (>2m), rock crevices/cliffs	Cat., binary	Chapter 3; literature
Habitat response	Habitat Use (primary habitat types) - shrubland, woodland, forest, rock features, riparian/water features, sand dunes	Cat., binary	Chapter 3; literature
	Locomotion style - quadrupedal, bipedal	Cat., nominal	literature
	Foraging location - aquatic, ground level, above ground level	Cat., binary	Chapter 3; literature
	Diet guild - omnivore, herbivore, granivore, insectivore	Cat., nominal	Rowe and Terry 2014, literature
	Possess cheek pouches - yes or no	Cat., binary	literature

Rostrum length	Continuous	Kohli and Rowe 2019, Chapter 2
Rostrum width	Continuous	Kohli and Rowe 2019, Chapter 2
Upper incisor width	Continuous	Kohli and Rowe 2019, Chapter 2
Upper incisor depth (anterio-posterior)	Continuous	Kohli and Rowe 2019, Chapter 2
Molar (all cheekteeth) toothrow length	Continuous	Kohli and Rowe 2019, Chapter 2
Molar toothrow width	Continuous	Kohli and Rowe 2019, Chapter 2
Jaw fulcrum length (index of mandible robustness)	Continuous	Kohli and Rowe 2019, Chapter 2
Lower incisor width	Continuous	Kohli and Rowe 2019, Chapter 2

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Table 4-2. Paired *t*-test results comparing diversity metrics for small mammals captured at nine paired resurvey sites in the Snake Range, NV during historical (1929-1939) and modern (2015-2016) periods. Diversity metrics included two taxonomic measures, species richness (SR) and total abundance (effort-standardized), and four measures of functional diversity: functional richness (FRic), functional divergence (FDiv), functional dispersion (FDis) and functional evenness (FEve). Functional diversity metrics were calculated using all traits, only climate traits, and only habitat traits. For each test, effect size and power at two significance levels ( $\alpha$ ) are shown. Significant differences among time periods ( $p \leq 0.10$ ) are bolded and marked with an asterisk. For significant metrics, negative *t*-values indicate an increase in mean values from historical to modern surveys; positive values indicate a decrease over time.

Metric	<i>t</i>	df	<i>p</i> -value	Effect size (Cohen's <i>d</i> )	Power, $\alpha = 0.05$	Power, $\alpha = 0.1$
SR	-0.83863	8	0.426	0.280	0.115	0.198
Abundance	0.95306	8	0.369	0.318	0.135	0.226
<b>All traits</b>						
FRic	-0.8914	8	0.399	0.297	0.123	0.211
FDiv	0.63049	8	0.546	0.210	0.086	0.156
FDis	1.54	8	0.162	0.513	0.270	0.408
FEve	2.5213	8	<b>0.036*</b>	0.840	0.600	0.740
<b>Climate traits</b>						
FRic	-1.8978	8	<b>0.094*</b>	0.633	0.387	0.536
FDiv	-0.02399	8	0.982	0.008	0.050	0.100
FDis	0.74714	8	0.476	0.240	0.100	0.180
FEve	3.0225	8	<b>0.017*</b>	1.008	0.750	0.866
<b>Habitat traits</b>						
FRic	-0.34189	8	0.741	0.114	0.060	0.117
FDiv	1.9749	8	<b>0.084*</b>	0.658	0.412	0.564
FDis	1.7933	8	0.111	0.598	0.350	0.498
FEve	1.4043	8	0.198	0.468	0.236	0.361

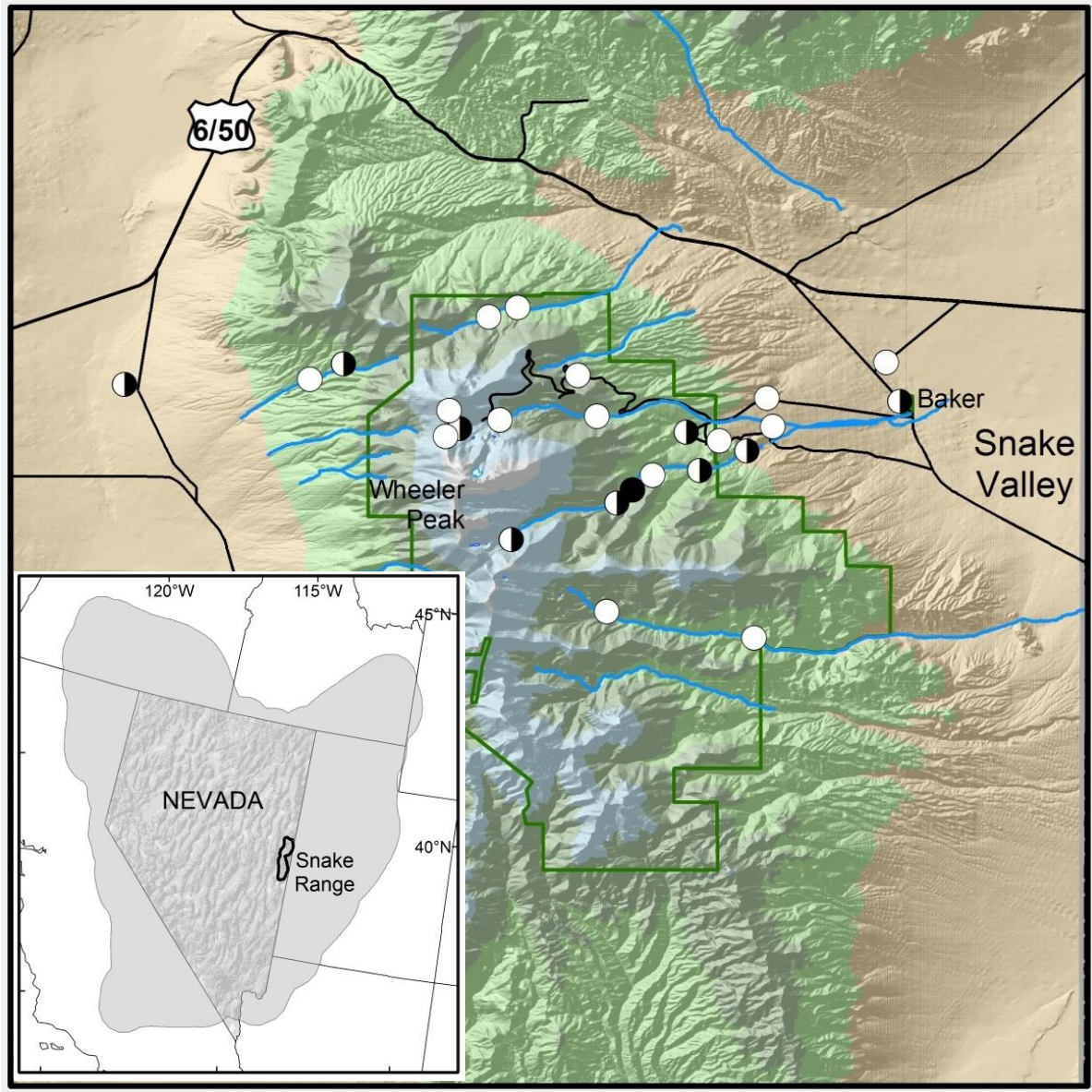


Figure 4-1. Map of sites surveyed in the Snake Range, NV for which functional diversity was evaluated over time. Black circles were surveyed historically (1929-1939,  $n = 10$ ), white circles were recently surveyed (2015-2016,  $n = 24$ ), and bi-colored circles indicate paired resurvey sites ( $n = 9$ ). Landscape coloration demarcates the general elevations of major vegetative zones. The boundary of Great Basin National Park is shown in green and permanent water bodies are blue. Inset shows the location of the study area within the Great Basin (shaded area).

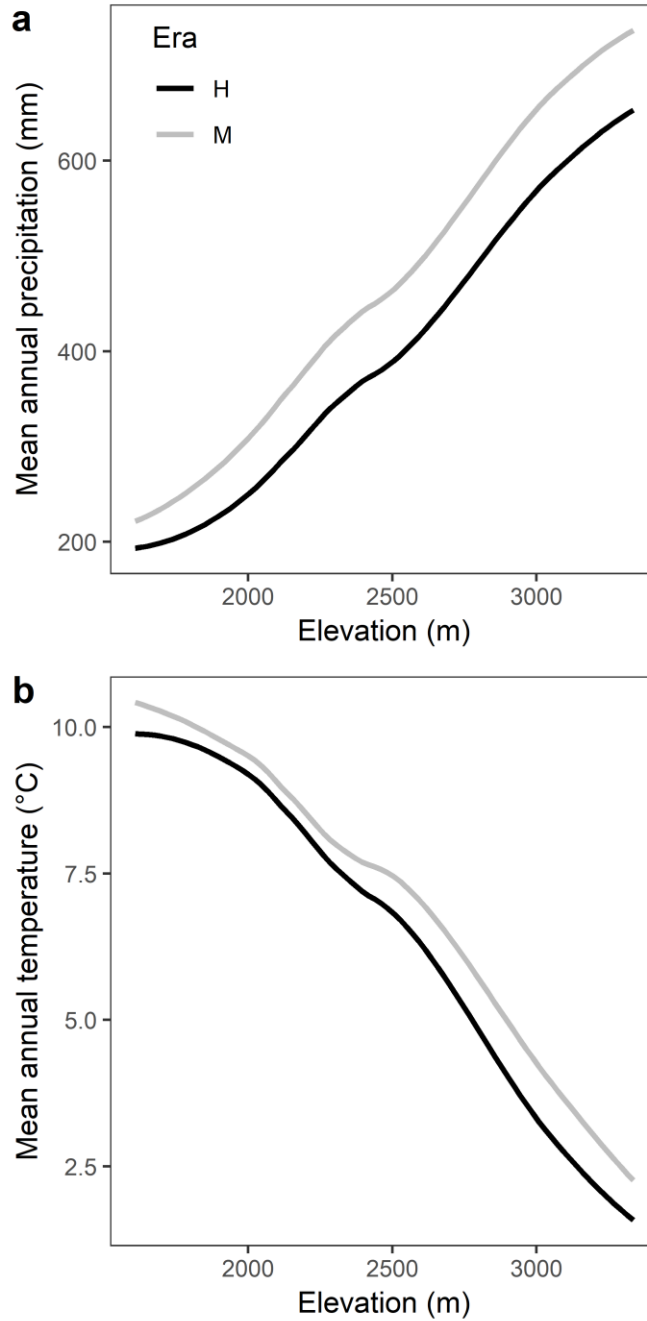


Figure 4-2. Change in (a) mean annual precipitation and (b) temperature along the elevational gradient of the Snake Range, Nevada between 1926-1929 and 2012-2016. Lines correspond to historical (H) or modern (M) data from all survey sites in both time periods.

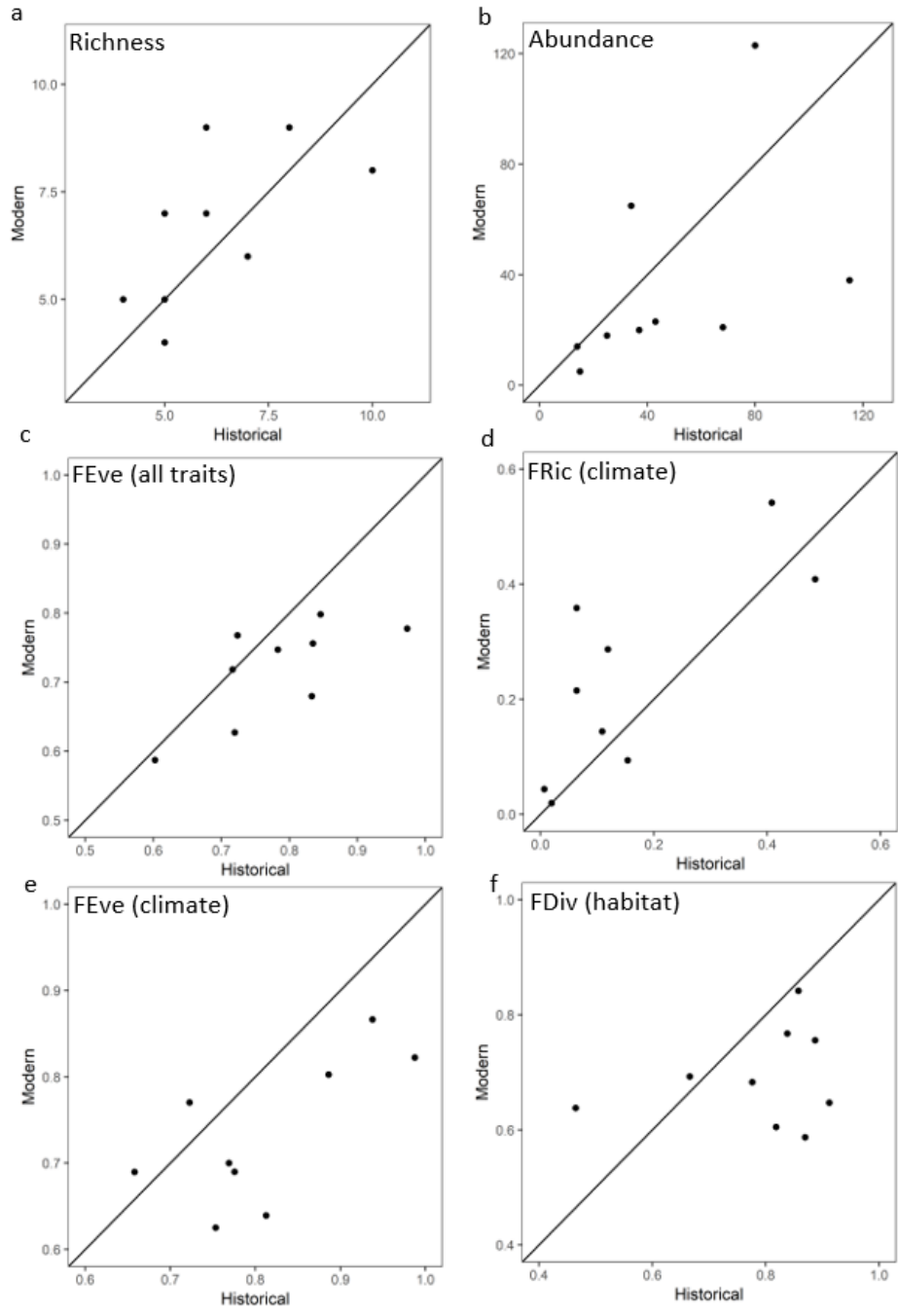


Figure 4-3. Comparisons of small mammal community diversity metrics between historical (1929-1939) and modern (2015-2016) survey periods in the Snake Range, NV. Historical values at nine paired resurvey sites are plotted against modern values. Diagonal lines represent the 1:1 line. Points falling below the line indicate a decrease over time at a site, points above the line indicate an increase, and points on the line indicate no change. Taxonomic diversity (a, species richness; b, total effort-standardized abundance) did not statistically change. The four measures of functional diversity that significantly changed over time ( $p \leq 0.10$ ) are shown: c, functional evenness (FEve) of all 23 traits; d, functional richness (FRic) of climate response traits; e, FEve of climate response traits; f, functional divergence (FDiv) of habitat response traits.



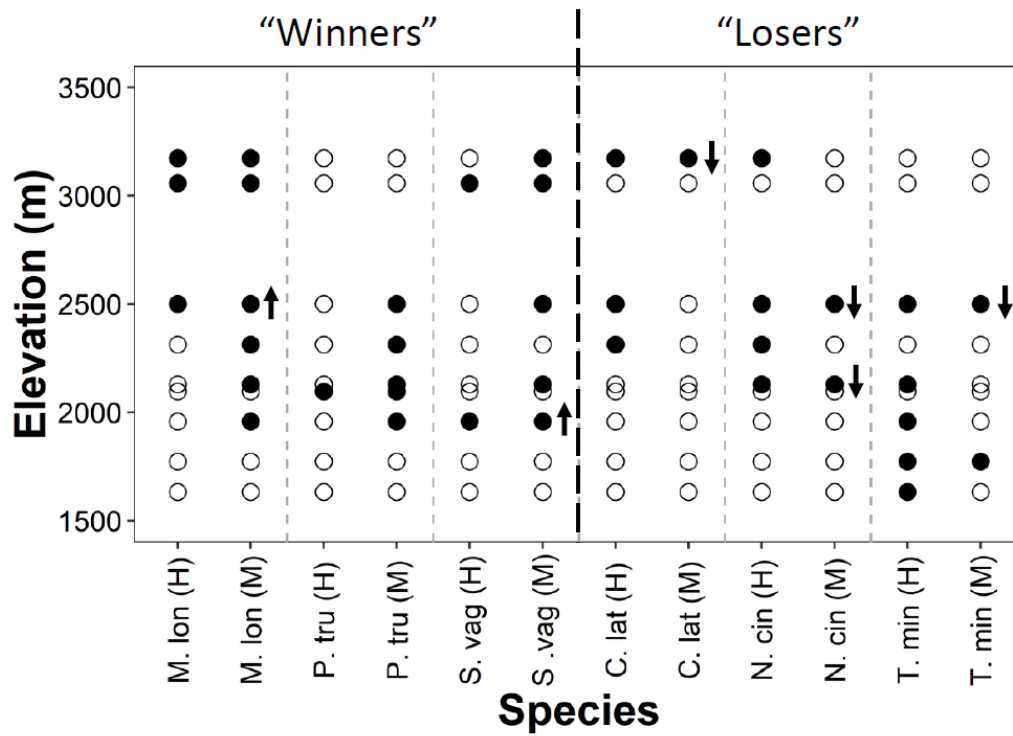


Figure 4-4. Occurrence and abundance changes for the size species experiencing the greatest magnitude of change over time at nine paired resurvey sites in the Snake Range, NV. The first three species (*Microtus longicaudus*, *M. lon*; *Peromyscus truei*, *P. tru*; *Sorex vagrans*, *S. vag*) were identified as the biggest “winners” over time. The last three species (*Callospermophilus lateralis*, *C. lat*; *Neotoma cinerea*, *N. cin*; *Tamias minimus*, *T. min*) were the biggest “losers”. Detection (filled circles) and non-detection (open circles) of each species is given for historical (H) modern (M) surveys. Arrows next to circles indicate a major shift in relative abundance over time at that site, either increasing (arrow pointing up) or decreasing (arrow pointing down) by >50% of its historical abundance.

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## APPENDICES

APPENDIX A

IACUC APPROVAL FOR RESEARCH CONDUCTED AS PART OF THIS DISSERTATION

University of New Hampshire

Research Integrity Services, Service Building  
51 College Road, Durham, NH 03824-3585  
Fax: 603-862-3564

07-Nov-2014

Rowe, Rebecca J  
Natural Resources & the Environment, James Hall Rm 136  
Durham, NH 03824

**IACUC #:** 141103A

**Project:** Great Basin Mammal Resurvey

**Category (if known):**

**Approval Date:** 07-Nov-2014

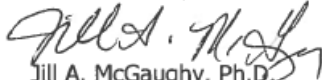
The Institutional Animal Care and Use Committee (IACUC) has administratively accepted the protocol for this study approved by the University of Utah IACUC. The IACUC made the following comment(s) on this protocol:

*The researcher needs to forward to the UNH IACUC the new University of Utah IACUC-approved application and approval letter upon receipt, but no later than the expiration date of the current protocol (January 24, 2015).*

Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

If you have any questions, please contact Julie Simpson at 862-2003.

For the IACUC,

  
Jill A. McGaughy, Ph.D.  
Chair

cc: File





AAALAC Accreditation (Health Sciences): 23 JUL 2012  
AAALAC Accreditation (College of Science): 23 JUL 2012  
PHS Assurance Registration Number: A3031-01  
USDA Registration Number: 87-R-0001

Principal Investigator: Eric Rickart  
Protocol Number: 15-02001  
Protocol Title: Great Basin Mammal Resurvey  
Date Protocol Received: 16 JAN 2015  
Date of Approval: 25 FEB 2015  
Date of Expiration: 24 FEB 2018

**Protocol Summary:**

This project involves comprehensive field surveys of small mammal communities (principally rodents and shrews) at localities in Nevada and Utah where similar historical surveys were conducted 50-100 years ago. These comparative data provide a baseline for investigating recent changes in regional biotic communities. The study is designed to quantify faunal changes that have occurred over the resurvey intervals and distinguish the effects of climate and non-climate factors in promoting these changes.

Your animal protocol was reviewed at a convened IACUC meeting and approved on the date listed above.

Please be aware that serious or repeated adverse events (e.g., a large number of postoperative complications, excessive or unexpected mortality rate) must be reported timely to the IACUC committee. The notification should include a brief summary of the adverse event and any corrective actions. It is further required to report if any of the adverse events lead to a change in pain categories (e.g., unalleviated pain or severe distress, category E).

For your convenience a copy of your approved protocol is enclosed.

  
\_\_\_\_\_  
IACUC

  
\_\_\_\_\_  
Date

cc: Thomas N. Parks, Ph.D.  
Vice President for Research

APPENDIX B

SUPPLEMENTARY DATA FOR CHAPTER 1

Table B1. Species included in study, their functional group assignments, taxonomic family, and mountain ranges captured in during field surveys, excluding opportunistic captures (see Methods).

Species	Habitat	Geog.	Diet	Mass (g)	Family	Mountains
<i>Ammospermophilus leucurus</i>	Xeric	S	Omnivore	103.92	Sciuridae	TS
<i>Callospermophilus lateralis</i>	Mixed	N	Omnivore	175.1	Sciuridae	RTS
<i>Chaetodipus formosus</i>	Xeric	S	Granivore	19.45	Heteromyidae	T
<i>Dipodomys deserti</i>	Xeric	S	Granivore	107.63	Heteromyidae	T
<i>Dipodomys merriami</i>	Xeric	S	Granivore	37.91	Heteromyidae	T
<i>Dipodomys microps</i>	Xeric	E	Herbivore	56.26	Heteromyidae	TS
<i>Dipodomys ordii</i>	Xeric	S	Granivore	50.4	Heteromyidae	RTS
<i>Lemmiscus curtatus</i>	Xeric	N	Herbivore	28.27	Muridae	TS
<i>Microdipodops megacephalus</i>	Xeric	E	Granivore	12.3	Heteromyidae	TS
<i>Microdipodops pallidus</i>	Xeric	S	Granivore	13.36	Heteromyidae	T
<i>Microtus longicaudus</i>	Mesic	N	Herbivore	44.8	Muridae	RTS
<i>Microtus montanus</i>	Mesic	E	Herbivore	42.85	Muridae	RTS
<i>Neotoma cinerea</i>	Mesic	N	Herbivore	285.89	Muridae	RTS
<i>Neotoma lepida</i>	Xeric	S	Herbivore	143.88	Muridae	TS
<i>Onychomys leucogaster</i>	Xeric	E	Insectivore	27.92	Muridae	RTS
<i>Onychomys torridus</i>	Xeric	S	Insectivore	21.68	Muridae	T
<i>Otospermophilus variegatus</i>	Mixed	S	Omnivore	714.58	Sciuridae	S
<i>Perognathus longimembris</i>	Xeric	S	Granivore	8.07	Heteromyidae	TS
<i>Perognathus mollipilosus</i>	Xeric	E	Granivore	21.56	Heteromyidae	RTS
<i>Peromyscus crinitus</i>	Xeric	S	Omnivore	16.32	Muridae	T
<i>Peromyscus maniculatus</i>	Mixed	E	Omnivore	19.98	Muridae	RTS
<i>Peromyscus truei</i>	Xeric	S	Omnivore	27	Muridae	RTS
<i>Reithrodontomys megalotis</i>	Mixed	S	Granivore	10.72	Muridae	RTS
<i>Sorex merriami</i>	Mesic	E	Insectivore	5.99	Soricidae	T
<i>Sorex monticolus</i>	Mesic	E	Insectivore	6.92	Soricidae	R
<i>Sorex palustris</i>	Mesic	N	Insectivore	13.07	Soricidae	RTS
<i>Sorex preblei</i>	Mixed	N	Insectivore	3.12	Soricidae	R
<i>Sorex tenellus</i>	Mesic	S	Insectivore	3.8	Soricidae	RTS
<i>Sorex vagrans</i>	Mesic	N	Insectivore	5.99	Soricidae	RTS
<i>Tamias dorsalis</i>	Xeric	S	Omnivore	63.66	Sciuridae	TS
<i>Tamias minimus</i>	Mixed	N	Omnivore	42.87	Sciuridae	RTS
<i>Tamias umbrinus</i>	Mixed	E	Omnivore	51.75	Sciuridae	RTS
<i>Urocitellus beldingi</i>	Mixed	E	Omnivore	272.53	Sciuridae	RT
<i>Zapus princeps</i>	Mesic	N	Omnivore	27.2	Dipodidae	RT

Table B2. Significant species pairs, Pairs Z-scores, functional similarity characteristics (intra-guild or inter-guild pair), mass differential, elevational distribution overlap within the mountain range, and the most parsimonious mechanism causing their association. Negative Z-scores indicate aggregations, positive are segregations. EF = Environmental Filtering, BI = Biotic Interactions (positive or negative). Dashes indicate duplication of the row above. Full species names can be found in Table S1. Asterisks next to Species 1 indicates the pair is also significantly associated in other mountain ranges.

Sp. 1	Sp. 2	Scale	Z-score	Functional trait similarity				Mass Diff. (g)	Ranges	Mechanism
				Habitat	Geog. Aff.	Diet	Body size			
<b>Ruby Mountains</b>										
<i>C.lat</i>	<i>M.lon</i>	Local	3.36	inter	intra	inter	inter	130.3	Overlap	EF
<i>C.lat</i>	<i>P.mol</i>	Local	2.63	inter	intra	inter	inter	153.54	Overlap	EF
<i>C.lat</i>	<i>T.umb</i>	Local	-2.69	intra	inter	intra	inter	123.35	Overlap	EF
<i>C.lat</i>	<i>U.bel</i>	Local	-2.75	intra	inter	intra	intra	97.43	Overlap	EF
<i>M.lon</i>	<i>S.vag</i>	Local	-2.5	intra	intra	inter	inter	38.81	Overlap	EF
<i>M.lon</i>	<i>Z.pri</i>	Local	-2.81	intra	intra	inter	inter	17.6	Overlap	EF
* <i>M.mon</i>	<i>S.vag</i>	Local	-3.16	intra	inter	inter	inter	36.86	Overlap	EF
<i>N.cin</i>	<i>P.mol</i>	Landscape	-2.06	inter	intra	inter	inter	264.33	Overlap	EF
<i>P.mol</i>	<i>P.tru</i>	Local	-2.77	intra	inter	inter	intra	5.44	Overlap	EF
<i>P.mol</i>	<i>S.mon</i>	Landscape	3.3	inter	inter	inter	inter	14.64	Overlap	EF
<i>P.mol</i>	<i>S.mon</i>	Local	3.62	inter	inter	inter	inter	14.64	Overlap	EF
<b>Snake Range</b>										
* <i>A.leu</i>	<i>D.mic</i>	Local	-4.84	intra	inter	inter	inter	47.66	Overlap	EF
<i>A.leu</i>	<i>D.ord</i>	Landscape	-2.73	intra	intra	inter	inter	53.52	Overlap	EF
<i>A.leu</i>	<i>D.ord</i>	Local	-4.67	intra	intra	inter	inter	53.52	Overlap	EF
<i>A.leu</i>	<i>P.mol</i>	Landscape	-2.44	intra	inter	inter	inter	82.36	Overlap	EF
<i>A.leu</i>	<i>P.mol</i>	Local	-4.71	intra	inter	inter	inter	82.36	Overlap	EF
<i>A.leu</i>	<i>T.umb</i>	Landscape	2.78	inter	inter	intra	inter	52.17	Non	EF
<i>C.lat</i>	<i>L.cur</i>	Landscape	-2.7	inter	intra	inter	inter	146.83	Overlap	EF/+BI

<i>C.lat</i>	<i>L.cur</i>	Local	-4.89	inter	intra	inter	inter	146.83	Overlap	EF/+BI
<i>C.lat</i>	<i>S.ten</i>	Landscape	-3	inter	inter	inter	inter	171.3	Overlap	EF/+BI
<i>C.lat</i>	<i>S.ten</i>	Local	-4.69	inter	inter	inter	inter	171.3	Overlap	EF/+BI
<i>D.mic</i>	<i>D.ord</i>	Local	-3.47	intra	inter	inter	intra	5.86	Overlap	EF
* <i>D.mic</i>	<i>M.lon</i>	Landscape	3.27	inter	inter	intra	intra	11.46	Abut	EF
<i>D.mic</i>	<i>P.mol</i>	Local	-3.46	intra	inter	inter	inter	34.7	Overlap	EF
<i>D.ord</i>	<i>P.mol</i>	Landscape	-2.34	intra	inter	intra	inter	28.84	Overlap	EF
<i>D.ord</i>	<i>P.mol</i>	Local	-3.28	intra	inter	intra	inter	28.84	Overlap	EF
<i>M.lon</i>	<i>P.mol</i>	Local	2.74	inter	intra	inter	inter	23.24	Overlap	EF
<i>M.lon</i>	<i>T.dor</i>	Local	2.5	inter	inter	inter	intra	18.86	Overlap	EF
* <i>M.mon</i>	<i>S.vag</i>	Landscape	-2.01	intra	inter	inter	inter	36.86	Overlap	EF
* <i>M.mon</i>	<i>S.vag</i>	Local	-3.92	intra	inter	inter	inter	36.86	Overlap	EF
<i>N.cin</i>	<i>O.var</i>	Landscape	-2.99	inter	inter	inter	intra	428.69	Overlap	EF
<i>P.mol</i>	<i>T.umb</i>	Landscape	3.43	inter	inter	inter	inter	30.19	Abut	EF
<i>P.mol</i>	<i>T.umb</i>	Local	3.07	inter	inter	inter	inter	30.19	Abut	EF
<i>P.tru</i>	<i>T.dor</i>	Local	-3.42	intra	intra	intra	inter	36.66	Overlap	EF
<i>T.dor</i>	<i>T.umb</i>	Landscape	2.82	inter	inter	intra	intra	11.91	Abut	-BI

### ***Toiyabe Range***

<i>A.leu</i>	<i>D.mer</i>	Landscape	-3.06	intra	intra	inter	inter	66.01	Overlap	EF
<i>A.leu</i>	<i>D.mer</i>	Local	-4.76	intra	intra	inter	inter	66.01	Overlap	EF
* <i>A.leu</i>	<i>D.mic</i>	Landscape	-2.76	intra	inter	inter	inter	47.66	Overlap	EF
* <i>A.leu</i>	<i>D.mic</i>	Local	-4.71	intra	inter	inter	inter	47.66	Overlap	EF
<i>A.leu</i>	<i>O.tor</i>	Landscape	-2.99	intra	intra	inter	inter	82.24	Overlap	EF
<i>A.leu</i>	<i>O.tor</i>	Local	-4.54	intra	intra	inter	inter	82.24	Overlap	EF
<i>C.for</i>	<i>N.lep</i>	Landscape	-2.75	intra	intra	inter	inter	124.43	Overlap	EF
<i>C.for</i>	<i>N.lep</i>	Local	-3.86	intra	intra	inter	inter	124.43	Overlap	EF
<i>C.for</i>	<i>P.cri</i>	Local	-3.7	intra	intra	inter	intra	3.13	Overlap	EF

<i>C.lat</i>	<i>T.min</i>	Local	-2.54	intra	intra	intra	inter	132.23	Overlap	EF
<i>D.mer</i>	<i>D.mic</i>	Landscape	-2.7	intra	inter	inter	intra	18.35	Overlap	EF
<i>D.mer</i>	<i>D.mic</i>	Local	-4.63	intra	inter	inter	intra	18.35	Overlap	EF
<i>D.mer</i>	<i>M.lon</i>	Local	2.55	inter	inter	inter	intra	6.89	Non	EF
<i>D.mer</i>	<i>O.tor</i>	Landscape	-2.95	intra	intra	inter	inter	16.23	Overlap	EF
<i>D.mer</i>	<i>O.tor</i>	Local	-4.68	intra	intra	inter	inter	16.23	Overlap	EF
<i>D.mer</i>	<i>P.lon</i>	Local	-3.38	intra	intra	intra	inter	29.84	Overlap	EF
<i>*D.mic</i>	<i>M.lon</i>	Landscape	3.23	inter	inter	intra	intra	11.46	Non	EF
<i>*D.mic</i>	<i>M.lon</i>	Local	2.87	inter	inter	intra	intra	11.46	Non	EF
<i>D.mic</i>	<i>O.tor</i>	Landscape	-2.7	intra	inter	inter	inter	34.58	Overlap	EF
<i>D.mic</i>	<i>O.tor</i>	Local	-4.55	intra	inter	inter	inter	34.58	Overlap	EF
<i>D.mic</i>	<i>P.lon</i>	Landscape	-2.6	intra	inter	inter	inter	48.19	Overlap	EF
<i>D.mic</i>	<i>P.lon</i>	Local	-3.93	intra	inter	inter	inter	48.19	Overlap	EF
<i>D.ord</i>	<i>M.lon</i>	Landscape	3.99	inter	inter	inter	intra	5.6	Non	EF
<i>D.ord</i>	<i>M.lon</i>	Local	2.84	inter	inter	inter	intra	5.6	Non	EF
<i>D.ord</i>	<i>P.lon</i>	Landscape	-2.35	intra	intra	intra	inter	42.33	Overlap	EF
<i>M.lon</i>	<i>P.lon</i>	Landscape	4.04	inter	inter	inter	inter	36.73	Non	EF
<i>M.lon</i>	<i>P.lon</i>	Local	3.11	inter	inter	inter	inter	36.73	Non	EF
<i>M.mon</i>	<i>N.cin</i>	Landscape	-1.92	intra	inter	intra	inter	243.04	Overlap	EF
<i>M.mon</i>	<i>P.cri</i>	Landscape	2.97	inter	inter	inter	inter	26.53	Overlap	EF
<i>*M.mon</i>	<i>S.vag</i>	Local	-3.41	intra	inter	inter	inter	36.86	Overlap	EF
<i>M.mon</i>	<i>Z.pri</i>	Local	-3.3	intra	inter	inter	inter	15.65	Overlap	EF
<i>N.lep</i>	<i>P.cri</i>	Landscape	-2.46	intra	intra	inter	inter	127.56	Overlap	EF
<i>O.tor</i>	<i>P.lon</i>	Local	-3.75	intra	intra	inter	inter	13.61	Overlap	EF
<i>P.lon</i>	<i>P.mol</i>	Landscape	3.27	intra	inter	intra	inter	13.49	Overlap	-BI
<i>R.meg</i>	<i>Z.pri</i>	Landscape	2.86	inter	inter	inter	inter	16.48	Overlap	EF
<i>S.pal</i>	<i>S.vag</i>	Local	-3.51	intra	intra	intra	inter	7.08	Overlap	EF

Table B3. Results of exact binomial tests showing the observed number of non-randomly associated pairs (Obs. no. pairs), the expected (Exp.) and observed (Obs.) proportions of intra-guild and inter-guild pairs based on the total number of pairs per mountain range ( $n$ ), and p-values. Tests were conducted separately for species assignments to four separate functional groups. Habitat affinity and geographic affinity related to the role of environmental filtering whereas diet group and body size class related to biotic interactions. Tests were conducted using the set of significant associations identified by Pairs for the Ruby Mountains, Toiyabe Range, and Snake Range, and for each scale and type of association (aggregation or segregation) separately. Expected proportions are the same for each trait within a mountain range. Bolded p-values indicate significant deviations from expected proportions ( $p < 0.05$ ).

Functional group	Ruby Mountains ( $n=105$ )				Toiyabe Range ( $n=351$ )				Snake Range ( $n=190$ )			
	Aggregations		Segregations		Aggregations		Segregations		Aggregations		Segregations	
	Landscape	Local	Landscape	Local	Landscape	Local	Landscape	Local	Landscape	Local	Landscape	Local
<i>Obs. no. pairs</i>	1	6	1	3	11	15	6	4	7	10	4	3
<b>Habitat Affinity</b>												
<i>Exp. Intra/Inter</i>	0.35/0.65	0.35/0.65	0.35/0.65	0.35/0.65	0.36/0.64	0.36/0.64	0.36/0.64	0.36/0.64	0.31/0.69	0.31/0.69	0.31/0.69	0.31/0.69
<i>Obs. Intra/Inter</i>	0.00/1.00	1.00/0.00	0.00/1.00	0.00/1.00	1.00/0.00	1.00/0.00	0.17/0.83	0.00/1.00	0.57/0.43	0.8/0.2	0.00/1.00	0.00/1.00
<i>p-value</i>	1	<b>0.00019</b>	1	0.56	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.43	0.3	0.21	<b>0.00018</b>	0.32	0.56
<b>Geographic Affinity</b>												
<i>Exp. Intra/Inter</i>	0.35/0.65	0.35/0.65	0.35/0.65	0.35/0.65	0.32/0.68	0.32/0.68	0.32/0.68	0.32/0.68	0.31/0.69	0.31/0.69	0.31/0.69	0.31/0.69
<i>Obs. Intra/Inter</i>	0.00/1.00	0.33/0.67	1.00/0.00	0.67/0.33	0.55/0.45	0.6/0.4	0.00/1.00	0.00/1.00	0.29/0.71	0.4/0.6	0.25/0.75	0.33/0.67
<i>p-value</i>	1	1	0.35	0.29	0.11	<b>0.0025</b>	0.19	0.32	1	0.51	1	1
<b>Diet Group</b>												
<i>Exp. Intra/Inter</i>	0.27/0.73	0.27/0.73	0.27/0.73	0.27/0.73	0.24/0.76	0.24/0.76	0.24/0.76	0.24/0.76	0.26/0.74	0.26/0.74	0.26/0.74	0.26/0.74
<i>Obs. Intra/Inter</i>	0.00/1.00	0.33/0.67	0.00/1.00	0.00/1.00	0.18/0.82	0.2/0.8	0.33/0.67	0.25/0.75	0.14/0.86	0.2/0.8	0.75/0.25	0.00/1.00
<i>p-value</i>	1	0.66	1	0.57	1	1	0.64	1	0.69	1	0.0055	0.57
<b>Body Size Class</b>												
<i>Exp. Intra/Inter</i>	0.21/0.79	0.21/0.79	0.21/0.79	0.21/0.79	0.25/0.75	0.25/0.75	0.25/0.75	0.25/0.75	0.23/0.77	0.23/0.77	0.23/0.77	0.23/0.77
<i>Obs. Intra/Inter</i>	0.00/1.00	0.33/0.67	0.00/1.00	0.00/1.00	0.009/0.91	0.13/0.87	0.33/0.67	0.75/0.25	0.14/0.86	0.1/0.9	0.5/0.5	0.33/0.67
<i>p-value</i>	1	0.66	1	1	0.31	0.38	0.65	0.0053	1	0.47	0.23	0.55

Figure B1.

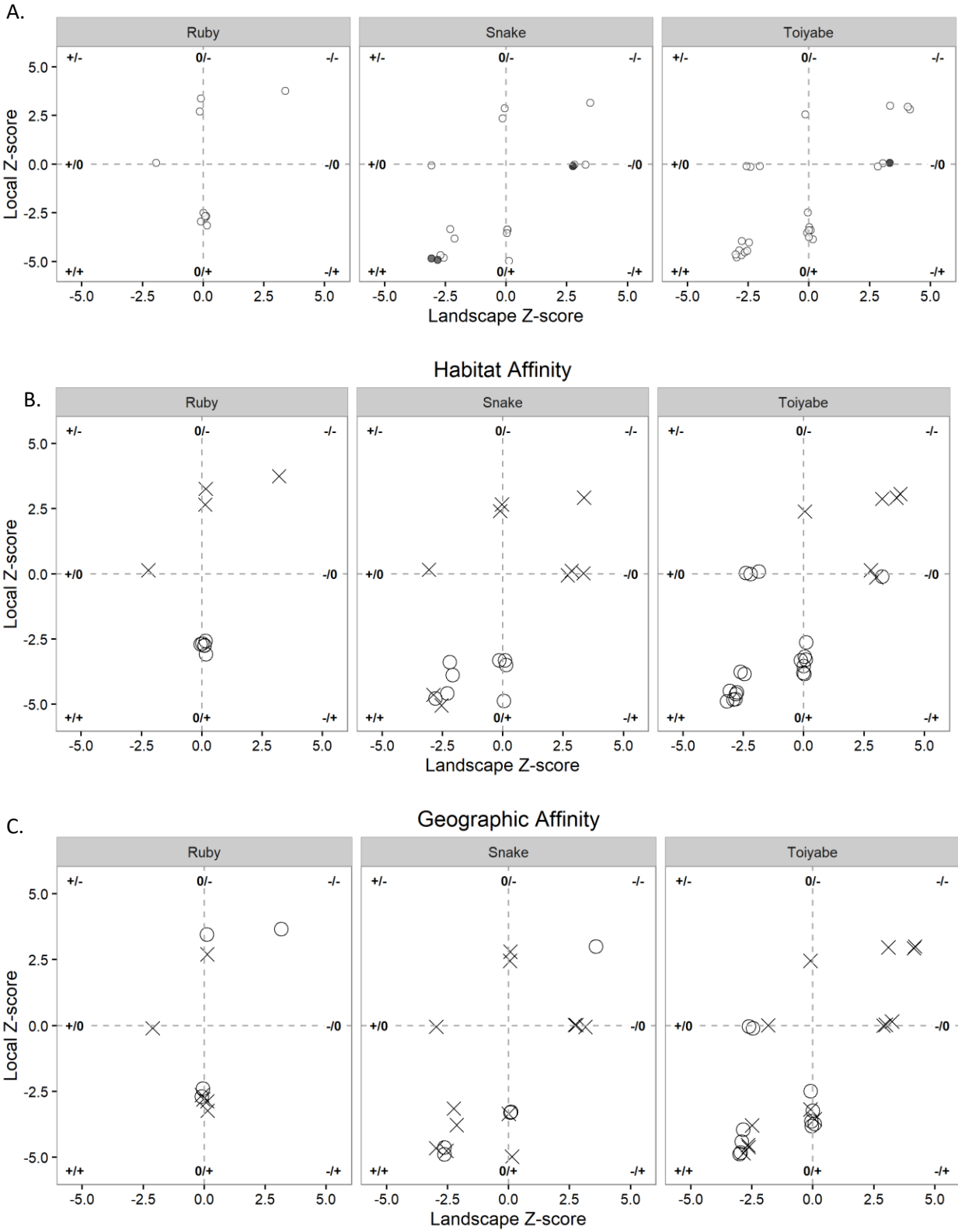


Fig. B1 continued.

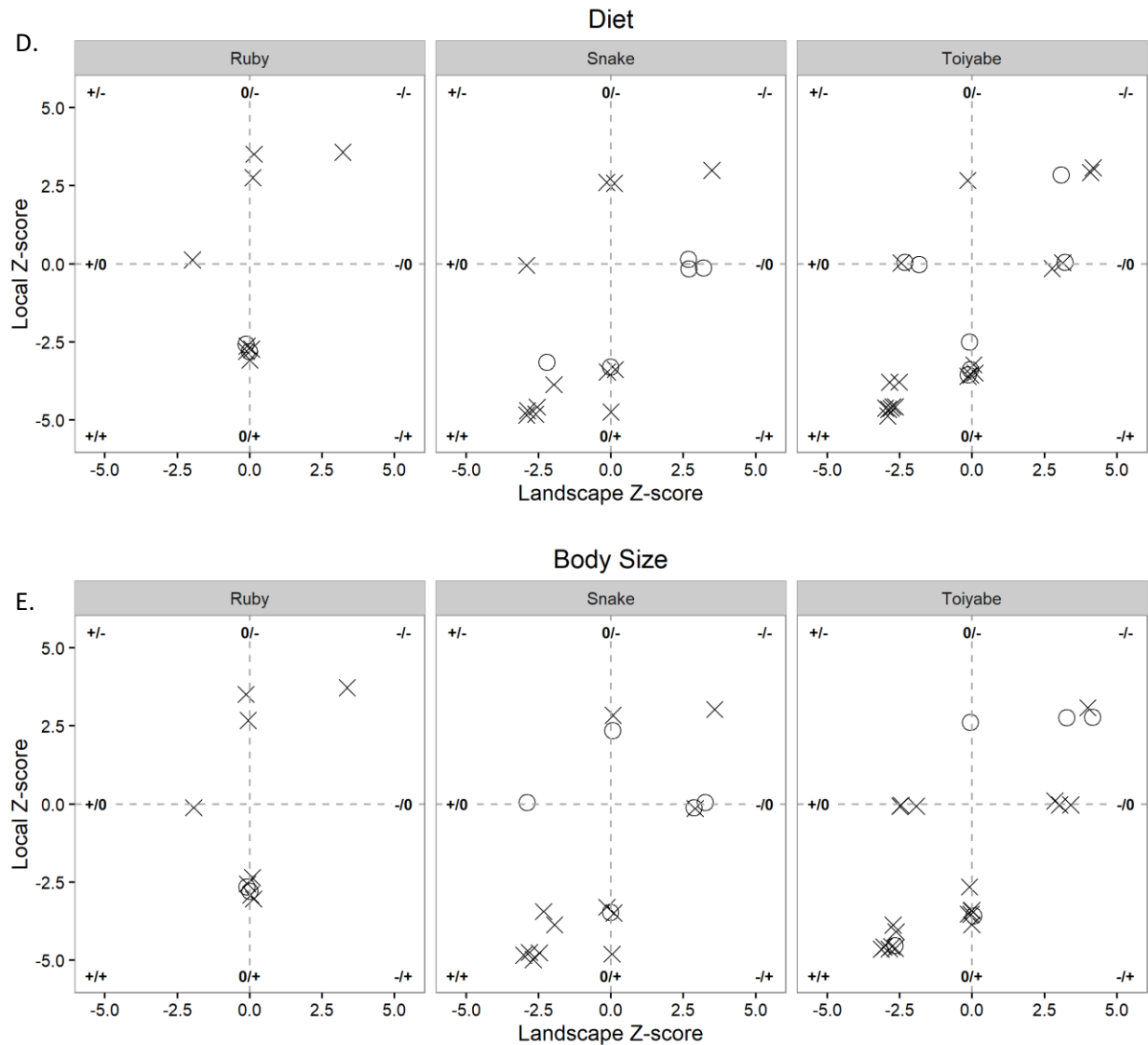


Figure B1. A.) Nonrandom species association patterns and their most parsimonious ecological mechanism for each mountain range. Signs (+/-) indicate the combination of association types each quadrant contains, for landscape and local scales, respectively. Due to the method of calculation, significant aggregations (+) correspond to negative Z-scores and segregations (-) have positive Z-scores. Points falling along a zero line indicate a pair that showed a random pattern (Bayes Mean  $Z = 0$ ) at one scale. Shading correspond to the likely underlying mechanism for the co-occurrence pattern, as determined by trait-based testing: white, environmental filtering (EF); light gray, facilitation or environmental filtering (+BI/EF); dark gray, competition (-BI). Points are jittered for ease of visualization. B-E.) The functional similarity (circles, intra-guild; crosses, inter-guild) of significantly associated species pairs for four traits: B.) habitat affinity, C.) geographic affinity, D.) diet group, and E.) body size class.



APPENDIX C

SUPPLEMENTARY MATERIAL FOR CHAPTER 2

Table C1. Species included in analyses (in alphabetical order), the abbreviations used to identify them in figures, their taxonomic family, average body mass in grams, and assigned guilds for habitat guild (Habitat), geographic affinity (Geog.), and diet.

Species	Abbrev.	Family	Mass (g)	Habitat	Geog.	Diet
<i>Ammospermophilus leucurus</i>	<i>A. leu</i>	Sciuridae	103.92	Xeric	South	Omnivore
<i>Callospermophilus lateralis</i>	<i>C. lat</i>	Sciuridae	175.10	Generalist	North	Omnivore
<i>Chaetodipus formosus</i>	<i>C. for</i>	Heteromyidae	19.45	Xeric	South	Granivore
<i>Dipodomys deserti</i>	<i>D. des</i>	Heteromyidae	107.63	Xeric	South	Granivore
<i>Dipodomys merriami</i>	<i>D. mer</i>	Heteromyidae	37.91	Xeric	South	Granivore
<i>Dipodomys microps</i>	<i>D. mic</i>	Heteromyidae	56.26	Xeric	Neither	Herbivore
<i>Dipodomys ordii</i>	<i>D. ord</i>	Heteromyidae	50.40	Xeric	South	Granivore
<i>Lemmiscus curtatus</i>	<i>L. cur</i>	Cricetidae	28.27	Xeric	North	Herbivore
<i>Microdipodops megacephalus</i>	<i>M. meg</i>	Heteromyidae	12.30	Xeric	Neither	Granivore
<i>Microdipodops pallidus</i>	<i>M. pal</i>	Heteromyidae	13.36	Xeric	South	Granivore
<i>Microtus longicaudus</i>	<i>M. lon</i>	Cricetidae	44.80	Mesic	North	Herbivore
<i>Microtus montanus</i>	<i>M. mon</i>	Cricetidae	42.85	Mesic	Neither	Herbivore
<i>Neotoma cinerea</i>	<i>N. cin</i>	Cricetidae	285.89	Mesic	North	Herbivore
<i>Neotoma lepida</i>	<i>N. lep</i>	Cricetidae	143.88	Xeric	South	Herbivore
<i>Onychomys leucogaster</i>	<i>O. leu</i>	Cricetidae	27.92	Xeric	Neither	Insectivore
<i>Onychomys torridus</i>	<i>O. tor</i>	Cricetidae	21.68	Xeric	South	Insectivore
<i>Otospermophilus variegatus</i>	<i>O. var</i>	Sciuridae	714.58	Generalist	South	Omnivore
<i>Perognathus longimembris</i>	<i>P. lon</i>	Heteromyidae	8.07	Xeric	South	Granivore
<i>Perognathus mollipilosus</i>	<i>P. mol</i>	Heteromyidae	21.56	Xeric	Neither	Granivore
<i>Peromyscus crinitus</i>	<i>P. cri</i>	Cricetidae	16.32	Xeric	South	Omnivore
<i>Peromyscus maniculatus</i>	<i>P. man</i>	Cricetidae	19.98	Generalist	Neither	Omnivore
<i>Peromyscus truei</i>	<i>P. tru</i>	Cricetidae	27.00	Xeric	South	Omnivore
<i>Reithrodontomys megalotis</i>	<i>R. meg</i>	Cricetidae	10.72	Generalist	South	Granivore
<i>Sorex monticolus</i>	<i>S. mon</i>	Soricidae	6.92	Mesic	Neither	Insectivore
<i>Sorex navigator</i>	<i>S. nav</i>	Soricidae	13.07	Mesic	North	Insectivore
<i>Sorex tenellus</i>	<i>S. ten</i>	Soricidae	3.80	Mesic	South	Insectivore
<i>Sorex vagrans</i>	<i>S. vag</i>	Soricidae	5.99	Mesic	North	Insectivore
<i>Tamias dorsalis</i>	<i>T. dor</i>	Sciuridae	63.66	Xeric	South	Omnivore
<i>Tamias minimus</i>	<i>T. min</i>	Sciuridae	42.87	Generalist	North	Omnivore
<i>Tamias umbrinus</i>	<i>T. umb</i>	Sciuridae	51.75	Generalist	Neither	Omnivore
<i>Urocitellus beldingi</i>	<i>U. bel</i>	Sciuridae	272.53	Generalist	Neither	Omnivore
<i>Zapus princeps</i>	<i>Z. pri</i>	Dipodidae	27.20	Mesic	North	Omnivore

Table C2. Specimens examined for the three morphological traits investigated. The 32 species included are listed in alphabetical order. Individuals are listed by the acronym and catalog number of the natural history museum they are housed in (UMNH: Natural History Museum of Utah, Salt Lake City; MSB: Museum of Southwestern Biology, Albuquerque). Detailed location, age, and collection date information for all specimens can be accessed online in the Arctos database (<http://arctos.database.museum>).

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**Relative medullary thickness (RMT) of the kidney:** *Ammospermophilus leucurus* - UMNH 30625, 30627, 35875, 35876, 35877; *Callospermophilus lateralis* - UMNH 39174, 39179, 39180, 39184, 39185; *Chaetodipus formosus* - UMNH 30579, 30643, 39188, 39193, 39196; *Dipodomys deserti* - UMNH 34508, MSB 105322, 105323, 105324, 105325; *Dipodomys merriami* - UMNH 34546, 34548, 34549, 34554, 35418; *Dipodomys microps* - UMNH 30577, 30596, 30631, 30766, 30797; *Dipodomys ordii* - UMNH 32346, 32350, 32353, 32354, 32355; *Lemmiscus curtatus* - UMNH 31922, 31923, 31924, 31925, 39202; *Microdipodops megacephalus* - MSB 35593, 37746, 37748, 37759; *Microdipodops pallidus* - MSB 38179, 38180, 38182; *Microtus longicaudus* - UMNH 30455, 30652, 30658, 30659, 39223; *Microtus montanus* - UMNH 30450, 30453, 30819, 39232, 39236; *Neotoma cinerea* - UMNH 29794, 31873, 32187, 32468, 32867; *Neotoma lepida* - UMNH 30638, 30640, 31514, 31515, 31937; *Onychomys leucogaster* - UMNH 30578, 30814, 32112, 32995, 35438; *Onychomys torridus* - UMNH 34571, 34572, 34573, MSB 37134, 37135; *Otospermophilus variegatus* - UMNH 29355, 31016, 32707; *Perognathus longimembris* - UMNH 33996, 33997, 34004, 34012, 34013; *Perognathus mollipilosus* - UMNH 32092, 32093, 32096, 32100, 32102; *Peromyscus crinitus* - UMNH 30580, 30648, 32714, 32715, 32722; *Peromyscus maniculatus* - UMNH 32027, 32030, 32034, 32036, 36435; *Peromyscus truei* - UMNH 31856, 31857, 39409, 39410, 39417; *Reithrodontomys megalotis* - UMNH 29761, 29762, 39418, 39419, 39421; *Sorex monticolus* - UMNH 31708, 31709, 31740, 31789, 31790; *Sorex navigator* - UMNH 31561, 31636, 32401, 32403, 32404; *Sorex tenellus* - UMNH 39491, 39924, 39925, 39927, 40549; *Sorex vagrans* - UMNH 31982, 31983, 31984, 31989, 31992; *Tamias dorsalis* - UMNH 30530, 30674, 30824, 34028, 34029; *Tamias minimus* - UMNH 32953, 32955, 32956, 32961, 32962, 32966; *Tamias umbrinus* - UMNH 30522, 30523, 30525, 30657, 30720; *Urocitellus beldingi* - UMNH 31710, 32052, 32130, 32245, 32246; *Zapus princeps* - UMNH 36498, 36499, 36503, 36504, 36563.

**Hair density:** *Ammospermophilus leucurus* - UMNH 30627, 35875, 35876, 35877; *Callospermophilus lateralis* - UMNH 39174, 39179, 39180, 39184, 39185; *Chaetodipus formosus* - UMNH 39187, 39188, 39191, 39193, 39196; *Dipodomys deserti* - UMNH 34508, MSB 105322, 105323, 105324, 105325; *Dipodomys merriami* - UMNH 34546, 34547, 34548, 34549, 34554; *Dipodomys microps* - UMNH 30577, 30596, 30631, 30766, 30797; *Dipodomys ordii* - UMNH 32346, 32350, 32353, 32354, 32355; *Lemmiscus curtatus* - UMNH 31922, 31923, 31924, 31925, 39202; *Microdipodops megacephalus* - MSB 35593, 37746, 37748, 37759; *Microdipodops pallidus* - MSB 38179, 38180, 38181, 38182; *Microtus longicaudus* - UMNH 30455, 30652, 30658, 30659, 39223; *Microtus montanus* - UMNH 30450, 30453, 30819, 39232, 39236; *Neotoma cinerea* - UMNH 29794, 31873, 32187, 32468, 32867; *Neotoma lepida* - UMNH 30638, 30640, 31514, 31515, 31937; *Onychomys leucogaster* - UMNH 30578, 30814, 32112, 32995, 35438; *Onychomys torridus* - UMNH 34571, 34572, 34573, MSB 37134, 37135; *Otospermophilus variegatus* - UMNH 29355, 31016, 32707; *Perognathus longimembris* - UMNH 33996, 33997, 34004, 34012, 34013; *Perognathus mollipilosus* - UMNH 32092, 32093,

32096, 32100, 32102; *Peromyscus crinitus* - UMNH 30580, 30648, 32714, 32715, 32722; *Peromyscus maniculatus* - UMNH 32027, 32030, 32034, 32036, 32037; *Peromyscus truei* - UMNH 31856, 31857, 39409, 39410, 39417; *Reithrodontomys megalotis* - UMNH 29761, 29762, 39418, 39419, 39421; *Sorex monticolus* - UMNH 31708, 31709, 31740, 31789, 31790; *Sorex navigator* - UMNH 31561, 31636, 32401, 32403, 32404; *Sorex tenellus* - UMNH 39435, 39491, 39924, 39925, 40549; *Sorex vagrans* - UMNH 31982, 31983, 31984, 31989, 31992; *Tamias dorsalis* - UMNH 30530, 30674, 30824, 34028, 34029; *Tamias minimus* - UMNH 32957, 32961, 32962, 32966, 39438; *Tamias umbrinus* - UMNH 30522, 30523, 30525, 30657, 30720; *Uroditellus beldingi* - UMNH 31710, 32052, 32130, 32245, 32246; *Zapus princeps* - UMNH 36498, 36499, 36503, 36504, 36563.

**Craniodental measurements:** *Ammospermophilus leucurus* - UMNH 38158, 38159, 38165, 38166, 38167; *Callospermophilus lateralis* - UMNH 23328, 24803, 35649, 35831, 35833; *Chaetodipus formosus* - UMNH 37148, 37149, 37150, 37181, 37184; *Dipodomys deserti* - UMNH 27380, 34646, 34647, 34648, 34649; *Dipodomys merriami* - UMNH 35503, 35511, 35513, 35518, 35519; *Dipodomys microps* - UMNH 37191, 37193, 37194, 37195; *Dipodomys ordii* - UMNH 37199, 37200, 37205, 37206, 37207; *Lemmiscus curtatus* - UMNH 39492, 39580, 39581, 39582, 39583; *Microdipodops megacephalus* - UMNH 25395, 25397, 25398, 25400, 25402; *Microdipodops pallidus* - UMNH 840, 2251, 28187, 28188, 34667; *Microtus longicaudus* - UMNH 36613, 36623, 36628, 36630, 36631; *Microtus montanus* - UMNH 33482, 33484, 33488, 33490, 33494; *Neotoma cinerea* - UMNH 28211, 32653, 33495, 33496, 33497; *Neotoma lepida* - UMNH 36008, 36009, 36012, 36013, 36014; *Onychomys leucogaster* - UMNH 35303, 35348, 35529, 35530, 35531; *Onychomys torridus* - UMNH 24912, 24914, 24915, 34670, 34671; *Otospermophilus variegatus* - UMNH 1320, 7664, 7665, 7666, 7667; *Perognathus longimembris* - UMNH 25498, 25499, 25500, 25502, 25504; *Perognathus mollipilosus* - UMNH 32608, 32612, 32613, 32629, 32656; *Peromyscus crinitus* - UMNH 32773, 32776, 32777, 34183, 34184; *Peromyscus maniculatus* - UMNH 37491, 37492, 37513, 37515, 37517; *Peromyscus truei* - UMNH 37241, 37245, 37526, 37533, 37535; *Reithrodontomys megalotis* - UMNH 37550, 37552, 37556, 37561, 37564; *Sorex monticolus* - UMNH 33813, 36508, 36578, 36579, 36580; *Sorex navigator* - UMNH 36510, 36582, 36583, 36584, 36585; *Sorex tenellus* - UMNH 39815, 39816, 39817, 39818, 40550; *Sorex vagrans* - UMNH 32631, 37246, 37372, 37375, 37378; *Tamias dorsalis* - UMNH 39539, 39540, 39541, 39542, 39543; *Tamias minimus* - UMNH 32804, 32806, 34816, 34817, 34818; *Tamias umbrinus* - UMNH 38523, 38524, 39858, 39860, 39893; *Uroditellus beldingi* - UMNH 8954, 8957, 36511, 36512, 36526; *Zapus princeps* - UMNH 32556, 32557, 32560, 32589, 32594.

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Table C3. Uncorrected species means and standard deviations (in parentheses) for all measurements used in analyses as well as 2 other commonly reported kidney morphology metrics. Hair density and the month(s) specimens were collected from the wild are reported. For months outside the typical summer season, sample sizes are in parentheses. One *Sorex tenellus* (UMNH 40549) listed as collected "before Oct" was salvaged from a building, and thus the precise date of death is not known. Detailed information can be obtained on the Arctos museum database. For kidneys, relative medullary thickness, kidney volume (length\*width\*thickness), percent medullary thickness (PMT), and medulla to cortex thickness ratio (M:C) are included. All craniodental measurements are in mm. CBL = condylobasal length, RL = rostrum length, RW = rostrum width, UIW = upper incisor width, UID = upper incisor depth, CRL = cheek teeth row length, CRW = cheek teeth row width, JFL = jaw fulcrum length (mandible robustness), LIW = lower incisor width.

Species	Hair		Kidney				Craniodental								
	Density (hairs/mm <sup>2</sup> )	Month(s) collected	RMT	Volume (mm <sup>3</sup> )	PMT (%)	M:C	CBL	RL	RW	UIW	UID	CRL	CRW	JFL	LIW
<i>Ammospermophilus leucurus</i>	76.88 (6.94)	Sept, Oct (3)	9 (0.47)	512.9 (131.4)	86.21 (1.25)	6.3 (0.63)	35.12 (1.29)	11.72 (0.58)	4.34 (0.36)	2.74 (0.2)	2.01 (0.19)	6.4 (0.45)	2.14 (0.16)	12.69 (0.39)	0.97 (0.14)
<i>Callospermophilus lateralis</i>	68.96 (7.24)	July, Aug	6.28 (0.33)	1030.73 (258.6)	78.12 (2.64)	3.63 (0.66)	39.16 (1.15)	14.04 (0.96)	6.12 (0.42)	3.3 (0.44)	2.11 (0.12)	7.99 (0.3)	2.67 (0.14)	14.12 (0.5)	1.25 (0.15)
<i>Chaetodipus formosus</i>	65.84 (6.17)	June	12.89 (0.37)	130.58 (22.41)	90.7 (1.35)	9.93 (1.51)	23.94 (0.69)	10.67 (0.26)	2.76 (0.09)	1.64 (0.04)	1.14 (0.03)	3.42 (0.13)	1.25 (0.06)	6.75 (0.23)	0.63 (0.03)
<i>Dipodomys deserti</i>	57.22 (15.54)	June, Sept	9.69 (1.2)	387.09 (167.82)	89.9 (1.22)	9.01 (1.1)	36.67 (0.7)	16.67 (0.55)	3.99 (0.16)	2.35 (0.14)	1.85 (0.04)	4.86 (0.19)	2.07 (0.11)	10.24 (0.19)	0.92 (0.06)
<i>Dipodomys merriami</i>	95.38 (8.14)	Sept	10.54 (0.5)	267.48 (26.1)	89.2 (1.95)	8.48 (1.57)	28.17 (0.63)	12.95 (0.31)	3.16 (0.12)	1.89 (0.05)	1.46 (0.03)	3.66 (0.24)	1.55 (0.11)	8.11 (0.05)	0.65 (0.02)
<i>Dipodomys microps</i>	85.04 (11.97)	May-Sept, Oct (1)	9.23 (0.72)	628.05 (67.27)	89.45 (0.74)	8.52 (0.69)	29.26 (0.51)	12.95 (0.5)	3.49 (0.19)	2.54 (0.08)	1.44 (0.03)	3.87 (0.08)	1.67 (0.09)	8.7 (0.12)	1.15 (0.04)
<i>Dipodomys ordii</i>	86.57 (7.31)	May	9.13 (0.25)	359.74 (38.27)	86.51 (1.57)	6.49 (0.92)	28.52 (0.69)	13.13 (0.52)	3.4 (0.2)	1.89 (0.07)	1.4 (0.04)	3.58 (0.14)	1.41 (0.08)	7.93 (0.27)	0.75 (0.06)
<i>Lemmys curtatus</i>	126.57 (19.54)	May, July	7.48 (0.74)	226.67 (33.94)	85.42 (2.15)	5.99 (1.14)	22.79 (0.69)	5.9 (0.43)	2.77 (0.25)	2.03 (0.12)	1.06 (0.09)	5.24 (0.16)	1.13 (0.04)	8.26 (0.26)	0.82 (0.05)
<i>Microdipodops megacephalus</i>	113.16 (6.36)	April (1), Sept	12.25 (0.54)	90.28 (22.27)	90.88 (0.23)	9.96 (0.28)	20.57 (0.27)	8.85 (0.48)	2.04 (0.06)	1.56 (0.15)	1.08 (0.02)	2.77 (0.09)	1.03 (0.08)	5.44 (0.27)	0.65 (0.05)
<i>Microdipodops pallidus</i>	128.07 (8.83)	Sept, Nov (1)	11.88 (0.7)	96.01 (15.03)	89.14 (0.43)	8.22 (0.37)	20.78 (0.54)	9.53 (0.38)	2.15 (0.04)	1.55 (0.15)	1.08 (0.06)	2.83 (0.06)	1.18 (0.09)	5.52 (0.22)	0.55 (0.02)
<i>Microtus longicaudus</i>	133.01 (14.29)	June, Aug	5.7 (0.47)	401.34 (79.25)	82.94 (2.87)	5 (1.07)	26.51 (0.52)	7.68 (0.46)	3.2 (0.23)	2.23 (0.14)	1.35 (0.06)	6.09 (0.21)	1.3 (0.05)	8.85 (0.38)	0.98 (0.05)
<i>Microtus montanus</i>	134.16 (14.7)	April (1), July-Aug	6.08 (0.52)	293.73 (60.63)	83.78 (2.11)	5.25 (0.81)	27.1 (1.17)	7.67 (0.36)	3.13 (0.21)	2.53 (0.07)	1.55 (0.08)	6.35 (0.23)	1.34 (0.04)	9.62 (0.36)	1.07 (0.02)
<i>Neotoma cinerea</i>	79.49 (23.7)	July, Aug	7.09 (0.55)	2271.39 (509.37)	82.86 (3.22)	5.02 (1.21)	47.68 (3.56)	19.47 (1.74)	5.41 (0.33)	3.65 (0.37)	2.37 (0.25)	9.05 (0.54)	2.47 (0.31)	17.46 (1.37)	1.47 (0.11)
<i>Neotoma lepida</i>	95.7 (14.58)	May-Sept	7.41 (0.26)	1927.47 (285.96)	83.15 (2.69)	5.06 (1.03)	36.81 (0.45)	14.56 (0.47)	4.63 (0.15)	2.64 (0.19)	1.85 (0.06)	7.32 (0.11)	2.03 (0.07)	14.08 (0.34)	1.3 (0.09)
<i>Onychomys leucogaster</i>	132.5 (17.02)	May, June	7.7 (0.75)	281.2 (50.35)	83.74 (1.8)	5.22 (0.69)	24.58 (0.6)	9.43 (0.27)	2.85 (0.22)	1.76 (0.14)	1.35 (0.01)	3.71 (0.1)	1.24 (0.06)	8.38 (0.14)	0.77 (0.07)
<i>Onychomys torridus</i>	107.11 (11.69)	Feb (1), Sept	8.27 (0.55)	151.45 (30.55)	86.47 (0.9)	6.42 (0.5)	22.64 (0.92)	8.98 (0.44)	2.55 (0.12)	1.67 (0.04)	1.32 (0.03)	3.6 (0.14)	1.16 (0.06)	7.64 (0.36)	0.71 (0.04)
<i>Otospermophilus variegatus</i>	49.55 (3.38)	Mar (1), July-Aug	6.38 (0.33)	2089.55 (272.7)	75.72 (1.48)	3.13 (0.26)	56.48 (0.82)	22.13 (1.2)	8.68 (0.55)	4.94 (0.24)	3.21 (0.12)	11.6 (0.32)	3.56 (0.14)	20.95 (1.21)	1.85 (0.05)
<i>Perognathus longimembris</i>	107.37 (6.32)	May	13.61 (0.77)	68.58 (13.15)	89.13 (0.89)	8.25 (0.77)	18.55 (0.28)	7.97 (0.3)	2.19 (0.11)	1.42 (0.03)	0.99 (0.02)	2.65 (0.18)	1 (0.02)	5.37 (0.27)	0.54 (0.04)
<i>Perognathus mollipilosus</i>	82.94 (2.92)	June	10.86 (0.69)	172.29 (40.79)	89.51 (0.7)	8.56 (0.65)	23.03 (0.87)	10.28 (0.61)	2.79 (0.19)	1.92 (0.21)	1.11 (0.08)	3.49 (0.09)	1.28 (0.03)	6.76 (0.48)	0.74 (0.09)
<i>Peromyscus crinitus</i>	145.71 (16.97)	July, Sept	9.02 (0.65)	154.13 (17.15)	85.25 (2.11)	5.91 (1.18)	21.9 (0.43)	9.35 (0.17)	2.27 (0.09)	1.34 (0.06)	1.21 (0.07)	3.19 (0.11)	1.05 (0.03)	7.38 (0.23)	0.62 (0.1)
<i>Peromyscus maniculatus</i>	148.58 (10.89)	May	8.15 (0.33)	191.34 (58.85)	84.31 (2.43)	5.52 (1.23)	22.73 (0.34)	10.17 (0.51)	2.5 (0.09)	1.49 (0.04)	1.21 (0.08)	3.6 (0.14)	1 (0.04)	7.9 (0.16)	0.64 (0.05)
<i>Peromyscus truei</i>	122.23 (15.35)	June-Aug	8.45 (0.52)	224.01 (41.36)	84.63 (1.59)	5.56 (0.72)	24.59 (0.79)	10.1 (0.55)	2.43 (0.1)	1.39 (0.11)	1.41 (0.06)	4 (0.13)	1.11 (0.06)	8.72 (0.19)	0.55 (0.06)
<i>Reithrodontomys megalotis</i>	146.86 (13.3)	July	9.5 (0.6)	128.58 (14.3)	86.46 (1.68)	6.47 (0.82)	18.35 (0.11)	7.62 (0.53)	1.84 (0.1)	1.2 (0.09)	1.11 (0.05)	3.06 (0.09)	0.84 (0.03)	6.06 (0.11)	0.62 (0.04)
<i>Sorex monticolus</i>	150.62 (8.33)	Aug	6.21 (0.34)	39.61 (4.32)	82.91 (2.42)	4.94 (0.81)	16.6 (0.3)	6.78 (0.48)	1.44 (0.08)	1.01 (0.09)	0.43 (0.13)	4.3 (0.09)	1.44 (0.08)	4.43 (0.14)	0.36 (0.04)
<i>Sorex navigator</i>	161.47 (13.36)	July, Aug	5.07 (0.24)	90.6 (24.09)	77.96 (2.86)	3.6 (0.6)	20.26 (0.42)	8.53 (0.4)	1.54 (0.06)	1.07 (0.05)	0.58 (0.08)	4.77 (0.1)	1.74 (0.06)	4.92 (0.33)	0.47 (0.04)
<i>Sorex tenellus</i>	166.76 (13.76)	Aug, before Oct	6.29 (0.76)	27.01 (3.95)	84.79 (2.42)	5.71 (1.09)	14.71 (0.18)	5.94 (0.26)	1.1 (0.05)	0.75 (0.03)	0.33 (0.04)	3.63 (0.1)	1.18 (0.11)	3.62 (0.18)	0.34 (0.03)
<i>Sorex vagrans</i>	150.69 (14.74)	May	6.36 (0.41)	52.17 (11.68)	81.99 (1.95)	4.61 (0.61)	16.67 (0.32)	7.08 (0.47)	1.34 (0.08)	0.9 (0.05)	0.49 (0.04)	4.11 (0.13)	1.31 (0.07)	4.74 (0.31)	0.36 (0.03)
<i>Tamias dorsalis</i>	93.4 (9.56)	April (1), June	8.25 (0.41)	283.28 (40.71)	86.2 (4.19)	6.89 (2.74)	31.58 (0.45)	10.5 (0.58)	4.42 (0.09)	2.58 (0.16)	1.76 (0.06)	5.37 (0.22)	1.71 (0.06)	11.6 (0.23)	0.9 (0.07)
<i>Tamias minimus</i>	143.67 (16.45)	July	9.83 (0.97)	235.41 (27.36)	88.59 (2.29)	8.08 (1.87)	26.67 (0.85)	8.85 (0.22)	3.63 (0.23)	1.95 (0.06)	1.34 (0.05)	4.74 (0.23)	1.54 (0.03)	9.42 (0.34)	0.8 (0.06)
<i>Tamias umbrinus</i>	133.4 (16.24)	June, Aug	7 (0.5)	368.52 (34.72)	84.85 (2.54)	5.75 (1.12)	31.59 (0.82)	11.38 (0.54)	4.49 (0.29)	2.56 (0.07)	1.73 (0.06)	5.29 (0.32)	1.75 (0.06)	11.86 (0.42)	0.97 (0.11)
<i>Urocyon beldingi</i>	67.24 (13.88)	June-Aug	7.15 (0.54)	1202.22 (321.9)	81.63 (2.55)	4.53 (0.73)	44.13 (0.54)	16.76 (0.67)	7.11 (0.38)	3.69 (0.25)	2.15 (0.12)	9.76 (0.2)	3.01 (0.13)	16.49 (0.38)	1.57 (0.04)
<i>Zapus princeps</i>	107.69 (9.09)	July	5.93 (0.32)	242.13 (42.13)	81.54 (2.91)	4.53 (0.89)	22.51 (0.72)	9.95 (0.2)	2.97 (0.09)	1.7 (0.11)	1.4 (0.06)	4.19 (0.26)	1.23 (0.05)	7.3 (0.38)	0.7 (0.06)

Table C4. Non-phylogenetic discriminant function (DF) analysis loadings for the 8 craniodental characters measured and the total variation accounted for by each discriminant function.

Measurement	DF1	DF2	DF3
Rostrum length	-0.56	-0.26	-0.51
Rostrum width	-0.52	-0.14	0.59
Upper incisor width	0.06	-0.49	0.45
Upper incisor depth	-0.45	-0.43	0.62
Cheek teeth row length	0.54	0.64	-0.07
Cheek teeth row width	0	0.51	-0.74
Jaw lever length (JFL)	0	0.36	0.81
Lower incisor width	0.37	-0.45	0.52
<b>% Variation accounted for</b>	<b>63.5</b>	<b>30.27</b>	<b>6.19</b>

Table C5. Non-phylogenetic discriminant function analysis classification table. *A priori* diet classifications are rows, predicted classifications (the diet category predicted by morphology) are columns. Overall, 84% of species were correctly classified by the original DFA, and 63% when applying leave-one-out cross-validation.

	<i>A priori</i> group	Predicted group				% correct
		Graniv.	Herbiv.	Insectiv.	Omniv.	
Original	Granivore ( $n = 9$ )	8	0	0	1	89
	Herbivore ( $n = 6$ )	0	5	1	0	83
	Insectivore ( $n = 6$ )	0	0	4	2	67
	Omnivore ( $n = 11$ )	1	0	0	10	91
Cross-validated	Granivore	7	1	0	1	78
	Herbivore	1	3	2	0	50
	Insectivore	0	0	4	2	67
	Omnivore	3	0	2	6	55

Table C6. Residuals for craniodental features used in discriminant function analyses, generated by regressions of mean log-transformed measurements of each against log body mass. RL = rostrum length, RW = rostrum width, UIW = upper incisor width, UID = upper incisor depth, CRL = cheek teeth row length, CRW = cheek teeth row width, JFL = jaw lever length (mandible robustness), LIW = lower incisor width. Residuals from each regression were normally distributed except for RL ( $p = 0.002$ ) and UID ( $p = 0.009$ ), as assessed with a Shapiro-Wilks test. Species abbreviations correspond to Table C1.

Species	RL	RW	UIW	UID	CTL	CTW	JFL	LIW
<i>A. leu</i>	-0.0539	-0.0179	0.0016	0.0295	0.0195	0.0448	0.0223	-0.0505
<i>C. lat</i>	-0.0278	0.0444	0.0066	-0.0325	0.0562	0.0861	-0.0072	-0.0165
<i>C. for</i>	0.074	0.0612	0.0259	0.0459	-0.0618	-0.012	-0.0072	-0.0006
<i>D. des</i>	0.0956	-0.0606	-0.0699	-0.0116	-0.1046	0.0268	-0.0757	-0.0815
<i>D. mer</i>	0.0909	0.0098	-0.0123	0.0478	-0.1079	0.0116	-0.0251	-0.0804
<i>D. mic</i>	0.0513	-0.0112	0.0586	-0.021	-0.1292	0.0019	-0.0523	0.1088
<i>D. ord</i>	0.0685	-0.0043	-0.0519	-0.0167	-0.1504	-0.06	-0.0765	-0.063
<i>L. cur</i>	-0.2212	0.0025	0.0627	-0.0467	0.0817	-0.0944	0.0256	0.0579
<i>M. meg</i>	0.039	0.0065	0.0697	0.0938	-0.1007	-0.0476	-0.0342	0.0766
<i>M. pal</i>	0.0627	0.0163	0.0548	0.0787	-0.101	0.0036	-0.0402	-0.0095
<i>M. lon</i>	-0.1524	-0.0111	0.0352	-0.014	0.0942	-0.082	-0.0112	0.073
<i>M. mon</i>	-0.1489	-0.0136	0.0979	0.0543	0.1174	-0.0652	0.0312	0.1145
<i>N. cin</i>	0.0648	-0.0896	-0.0208	-0.0568	0.054	0.0	0.0134	-0.0151
<i>N. lep</i>	0.0078	-0.044	-0.0617	-0.058	0.0405	-0.0124	0.0202	0.0292
<i>O. leu</i>	-0.0162	0.0163	0.0024	0.0614	-0.0673	-0.052	0.0341	0.0332
<i>O. tor</i>	-0.0117	0.0102	0.017	0.0909	-0.0519	-0.0542	0.0304	0.0319
<i>O. var</i>	0.0282	-0.0358	-0.024	-0.0686	0.057	0.0623	-0.041	-0.0446
<i>P. lon</i>	0.036	0.1067	0.0909	0.1208	-0.0714	-0.0145	0.0217	0.0581
<i>P. mol</i>	0.0477	0.0491	0.0791	0.0165	-0.0638	-0.0105	-0.0217	0.0499
<i>P. cri</i>	0.0342	0.0055	-0.0383	0.096	-0.0718	-0.0691	0.0571	0.0155
<i>P. man</i>	0.0506	0.0142	-0.0213	0.0656	-0.0417	-0.1108	0.0572	0.0006
<i>P. tru</i>	0.0171	-0.0473	-0.0938	0.0846	-0.0311	-0.0991	0.0561	-0.1067
<i>R. meg</i>	-0.012	-0.0165	-0.0226	0.1253	-0.0413	-0.1203	0.0328	0.0728
<i>S. mon</i>	-0.0191	-0.0487	-0.0363	-0.222	0.1561	0.1607	-0.0398	-0.1003
<i>S. nav</i>	0.017	-0.1269	-0.1016	-0.1903	0.1287	0.1741	-0.0865	-0.0774
<i>S. ten</i>	-0.0159	-0.0662	-0.075	-0.2333	0.1518	0.1346	-0.0393	-0.037
<i>S. vag</i>	0.0144	-0.0573	-0.0636	-0.1411	0.153	0.1332	0.0106	-0.0831
<i>T. dor</i>	-0.0521	0.0703	0.0481	0.0471	-0.0011	0.0002	0.055	-0.0132
<i>T. min</i>	-0.0865	0.0504	-0.0156	-0.0082	-0.0099	-0.0053	0.0223	-0.0101
<i>T. umb</i>	0.0034	0.1119	0.0748	0.0733	0.016	0.0308	0.0947	0.048
<i>U. bel</i>	0.0046	0.037	-0.0093	-0.0922	0.0922	0.091	-0.0043	0.021
<i>Z. pri</i>	0.0101	0.0385	-0.0076	0.0814	-0.0117	-0.0526	-0.0225	-0.0016

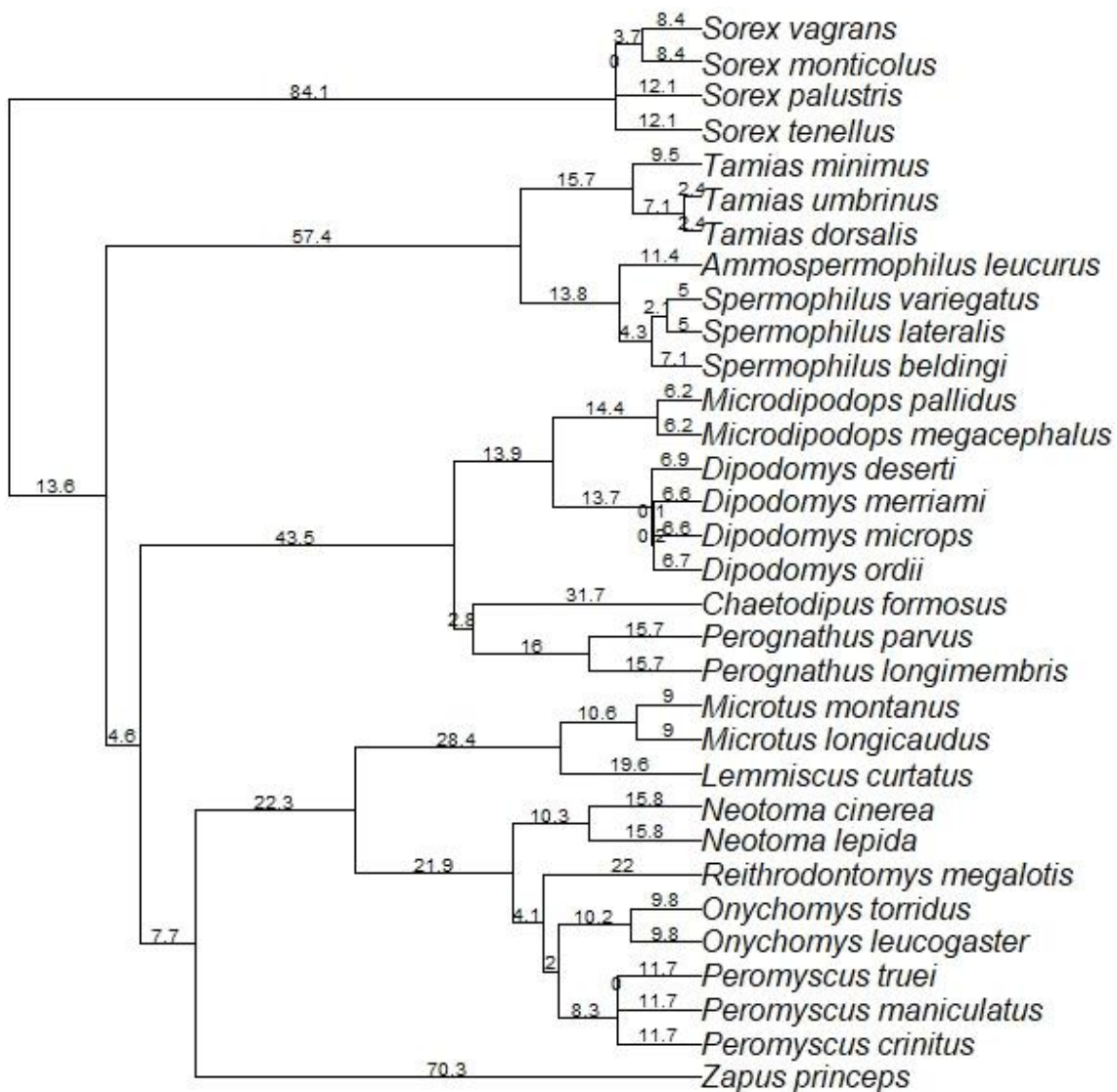


Figure C1. Phylogenetic tree used in phylogenetically informed methods and assessments of phylogenetic signal in traits. Branch lengths are time in millions of years. Two polytomies that were present in the source tree (Fritz et al. 2009) have been resolved here: 1 among *Sorex*, another among *Peromyscus* species. Taxonomy in this tree follows Wilson & Reeder (2005) with the exception of the replacement of *Perognathus parvus* with *P. mollipilosus* (Riddle et al. 2014a), *Sorex palustris* with *Sorex navigator* (Hope et al. 2014), and recent revisions to the genus *Spermophilus* (Helgen et al. 2009), including *Callospermophilus lateralis*, *Otospermophilus variegatus*, and *Urocitellus beldingi*.



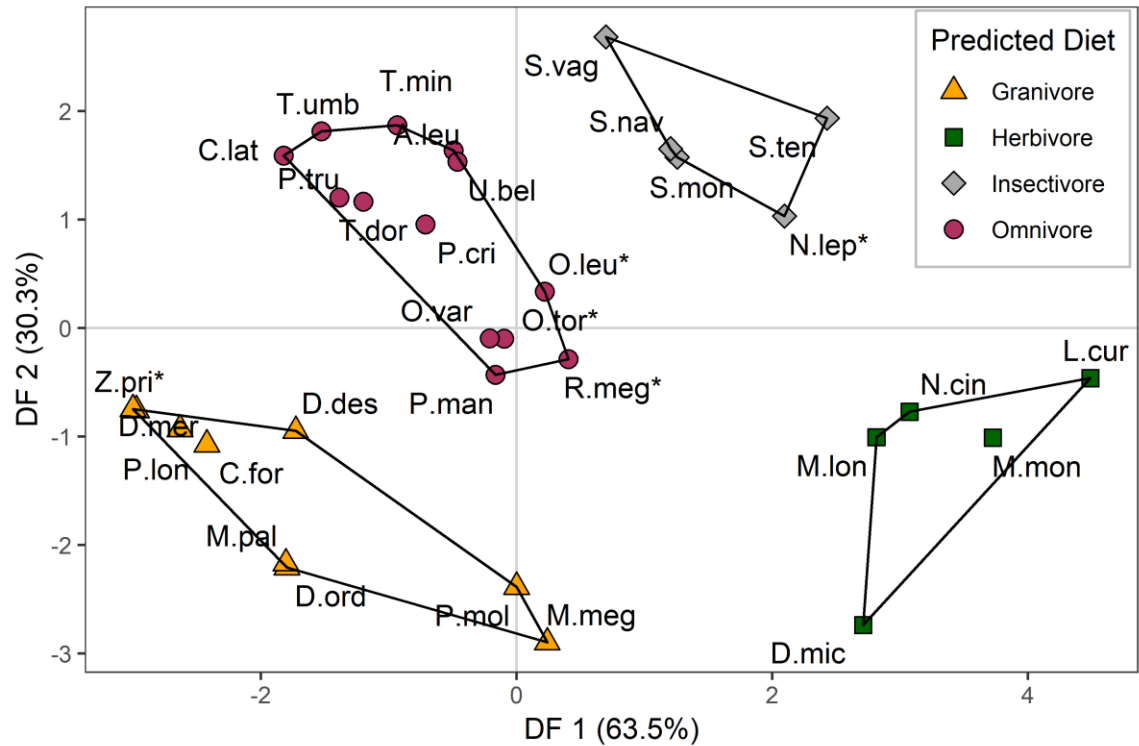


Figure C2. Non-phylogenetic DFA plot, constructed based on body-size corrected residuals of craniodental measurements. The total variation accounted for by each discriminant function (DF) are included within parentheses. Misclassified species are identified with asterisks. Strong correlations ( $r > 0.94$ ) among conventional and phylogenetic discriminant scores indicates that relative positioning of species in morphospace was very similar between the methods, but classification success decreased in the phylogenetic DFA.

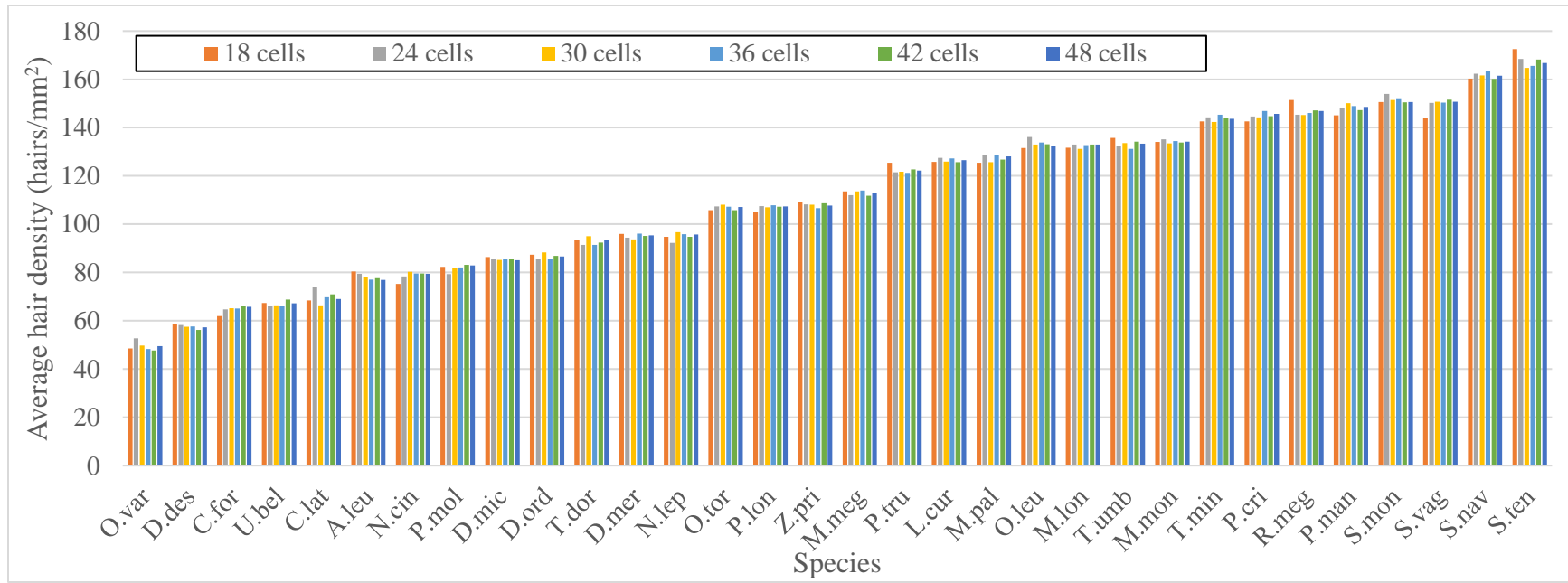


Figure C3. Comparison of mean hair density calculated using the maximum number of ocular grid cells sampled (48 cells) and various subsamples (18-42 cells) of that full data set. Species are ordered from least to most dense hair (left to right). Species abbreviations correspond to Table C1.

## APPENDIX D

### SUPPLEMENTARY MATERIAL FOR CHAPTER 4

Table D1. Field Notes used to reconstruct historical small mammal sampling in the Snake Range, NV, 1929-1939.

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Alcorn, J.R. Field Notebook. 1936-1941. Volume 487, sections 1-2. Museum of Vertebrate Zoology Archives, University of California, Berkeley.

Alcorn, J.R. Field Notebook. 1936-1940. Volume 488, section 1. Museum of Vertebrate Zoology Archives, University of California, Berkeley.

Hall, E.R. Field Notebook (Itineraries). 1928-1941. Volume 1339, section 1, pages 13-33, 247-251. Museum of Vertebrate Zoology Archives, University of California, Berkeley.

Hall, E.R. Field Notebook (Specimen Catalog). 1928-1941. Volume 1338, section 1, pages 22-39. Museum of Vertebrate Zoology Archives, University of California, Berkeley.

Hall, E.R. Field Notebook (Species Accounts). 1928-1941. Volume 1341, section 1, pages 22-39. Museum of Vertebrate Zoology Archives, University of California, Berkeley.

Moore, R.D. Field Notebook. 1929-1930. Volume 1749, section 4, pages 1-64. Museum of Vertebrate Zoology Archives, University of California, Berkeley.

Longhurst W.M. Field Notebook. 1939-40. Volume 1458, section 2. Museum of Vertebrate Zoology Archives, University of California, Berkeley.

Russell, W.C. Field Notebook. 1929. Volume 1570, section 4, pages 10-55. Museum of Vertebrate Zoology Archives, University of California, Berkeley.

Russell, W.C. Field Notebook. 1930. Volume 1570, section 6, pages 1-23. Museum of Vertebrate Zoology Archives, University of California, Berkeley.

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Table D2. Small mammal species ( $n = 22$ ) captured at paired resurvey sites in the Snake Range, NV. Era(s) captured in and the number of site-level extirpations, introductions, and >50% relative abundance changes are listed.

Species	Abbrev.	Era captured	Extirp.	Introd.	Major decline	Major increase
<i>Ammospermophilus leucurus</i>	<i>A. leu</i>	HM	1	1		1
<i>Callospermophilus lateralis</i>	<i>C. lat</i>	HM	2		1	
<i>Dipodomys microps</i>	<i>D. mic</i>	HM	1		1	
<i>Dipodomys ordii</i>	<i>D. ord</i>	M		2		
<i>Lemmiscus curtatus</i>	<i>L. cur</i>	HM	1	2		
<i>Microtus longicaudus</i>	<i>M. lon</i>	HM		3		2
<i>Microdipodops megacephalus</i>	<i>M. meg</i>	HM			1	
<i>Microtus montanus</i>	<i>M. mon</i>	HM		1	1	
<i>Neotoma cinerea</i>	<i>N. cin</i>	HM	2		2	
<i>Neotoma lepida</i>	<i>N. lep</i>	HM	1	1	1	
<i>Onychomys leucogaster</i>	<i>O. leu</i>	H	2			
<i>Peromyscus crinitus</i>	<i>P. cri</i>	H	1			
<i>Peromyscus maniculatus</i>	<i>P. man</i>	HM			2	5
<i>Perognathus mollipilosus</i>	<i>P. mol</i>	HM		1	1	1
<i>Peromyscus truei</i>	<i>P. tru</i>	HM		4		
<i>Reithrodontomys megalotis</i>	<i>R. meg</i>	HM	1		1	
<i>Sorex navigator</i>	<i>S. nav</i>	HM				
<i>Sorex tenellus</i>	<i>S. ten</i>	M		1		
<i>Sorex vagrans</i>	<i>S. vag</i>	HM		3		2
<i>Tamias dorsalis</i>	<i>T. dor</i>	HM	1	1		1
<i>Tamias minimus</i>	<i>T. min</i>	HM	3		1	
<i>Tamias umbrinus</i>	<i>T. umb</i>	HM			1	3