

SPECIES TRAITS VERSUS ENVIRONMENTAL PROPERTIES AS FACTORS  
INFLUENCING SPECIES ABUNDANCE

by

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## **ABSTRACT**

A longstanding goal in ecological research is to explain the abundance of a species found in a particular place and time. To do so, researchers identify factors that influence species abundance and attempt to describe their relationship quantitatively. The main objective of my study was to compare the relative effects of intrinsic species traits (morphological, physiological, behavioral and life history attributes) and extrinsic environmental properties (climatic, biotic and geographic aspects) on species abundance. From a literature search, 915 independent abundance observations were compiled for 83 species from 170 survey locations distributed throughout the western United States. Besides abundance information, data on species traits associated with body size, reproductive capacity, diet, and geographic range were acquired along with properties of each survey location including climatic, spatial, and biotic (number of other rodent species and individuals) variables. To make the comparison, four composite variables (an intrinsic ecological variable, intrinsic geographic variable, extrinsic abiotic variable and extrinsic biotic variable) were created using Principal Components Analysis (PCA), and a fifth variable that was the distance between each species location (from a particular survey) and the center of that species geographic range was also included. Model comparison and model-averaging procedures were then conducted using all 31 possible linear regression models of the five predictor variables with standardized abundance (corrected for extraneous design variables) as the response variable. For the dataset consisting of all species, the intrinsic ecological variable was found to have the greatest



influence on abundance ( $N=915$ ,  $\beta_{eco} = 0.116$ ,  $SE= 0.042$ ). For datasets limited to certain genera (*Dipodomys*, *Neotoma*, *Perognathus*, and *Peromyscus*), different variables were identified as most influential. These results indicate that environmental properties and species traits can influence abundance independently and in combination with one another. Moreover, there is no single combination of extrinsic and intrinsic variables that most influences abundance in all genera. Nonetheless, the distinction between intrinsic and extrinsic variables is a useful dichotomy in studying the factors affecting species abundance.

# CHAPTER ONE

## SPECIES TRAITS VERSUS ENVIRONMENTAL PROPERTIES AS FACTORS INFLUENCING SPECIES ABUNDANCE

### Introduction

A longstanding goal in ecological research is to explain the abundance of a species found in a particular place and time. Abundance is typically measured as the density or the number of individuals of the same species residing within a specific area, usually as part of a system or community of co-occurring species. Abundance can vary among species found in the same location as well as for a single species across locations (Brown 1984). Commonly, to understand the mechanisms responsible for creating these differences, researchers identify factors that influence species abundance and attempt to describe their relationship with abundance quantitatively. In general these factors are the intrinsic characteristics of the species (e.g., morphological, physiological, and behavioral traits) and the extrinsic properties of the environment (i.e. climatic, biotic, and spatial aspects).

The intrinsic factors that influence abundance are associated with a species' ability to overcome limitations set by the environment and acquire enough resources for survival, growth, and reproduction. Essentially, these intrinsic factors are the morphological, physiological, behavioral, and life history attributes of the species. These characteristics provide the species with the capacity to withstand abiotic stressors of the environment (i.e., climatic extremes, stochastic disturbances, geographical restrictions), overcome increased mortality or reductions in necessary resources caused by biotic

interactions (i.e., predation and competition) or utilize the available resources efficiently (e.g., capacity for the population to persist through periods of resource scarcity). Clearly, the intrinsic factors do not act in isolation from or in a vacuum apart from the environment. The significance of species traits in determining abundance is dependent on the conditions of the environment.

The environmental factors (or extrinsic properties) of a site are often viewed as acting like filters or sieves in a community-assembly type of process whereby some species can exist at a site whereas others cannot (Keddy 1992; Poff 1997; Webb et al. 2010; Weiher et al. 2011). Community membership (and by extension, abundance) then is due presumably to an environment-trait interaction or perhaps a multidimensional spectrum of interactions. Multiple environmental properties work together to “filter out” species that cannot tolerate the local conditions and regulate the number of individuals of species that can. For example, as Keddy (1992) hypothetically described for a wetland plant community, the species that reached particular abundances were those that possessed specific attributes to utilize a wetland that dried and re-flooded as well as possessed some competitive advantage (Figure 1). Therefore, interaction between the intrinsic characteristics of a species (e.g., drought tolerance and competitive ability) and the extrinsic properties of the environment (e.g., drought and flooding periodicity) can be a major force in determining abundance. Essentially, the intrinsic-extrinsic interaction is natural selection in action on an ecological timescale (Vellend 2010).

Current conceptual and methodological approaches that draw upon the environment-trait interaction to understand and sometimes predict community composition typically combine species traits and environmental properties (intrinsic-

extrinsic interaction) to quantify the performance of species within specific environments. The “performance filter” leads to a trait distribution that has been filtered based on specific environmental properties (Webb et al. 2010). More specifically, for an area under study, the environment is defined along a gradient of either a single or several environmental properties that are anticipated to influence performance (in the sense of fitness) and hence species abundance. In this approach, empirical quantitative data on species traits are acquired for all species found within the locations of interest and used to construct the filtered distribution for either a single or multiple traits. This trait distribution then provides information on the species that should be able to exist at each location and also predicts their relative abundances (McGill et al. 2006; Shipley 2006; Cornwell and Ackerly 2010; Webb et al. 2010; Laughlin et al 2011; Labiérté et al 2012; Laughlin et al. 2012; Laughlin and Laughlin 2013). For example, a species whose observed trait value(s) is closest to the mean of the filtered distribution would be predicted to have the highest relative abundance (but see Laughlin et al. 2012). This approach has come to be known as trait-based assembly or niche-based environmental filtering (Weiher et al. 2011). As stated by Webb et al. (2010), there are three elements: trait distribution, performance filter, and projection of the filter along an environmental gradient. The idea of a filter is very prominent in this approach (e.g., Weiher et al. 2011). The filter, essentially manifested as a trait-environment interaction, acts to completely exclude some species from a local community and determine the relative abundances of the species that do pass through the filter. This filter-centric approach does not always explicitly recognize the distinction between intrinsic and extrinsic factors particularly as they might separately influence species abundances; this distinction is the focus of my

study. The relative influence of each type of factor can be examined by addressing the question: *Is a species abundance at different locales throughout its range determined more by intrinsic species traits or by the extrinsic environmental properties at each locale?* This is a fundamental question not often posed in previous studies [as exceptions see Krasnov et al. (2006) and Poulin (2006)]. Moreover, new insight into the processes affecting abundance could be gained by evaluating the importance of intrinsic vs. extrinsic factors outside of a specified mechanistic structure such as environmental filtering.

The main objective of my study was to compare the relative effects (or influence) of intrinsic species traits and extrinsic environmental properties on species abundance. To accomplish this, I compiled a continental-scale dataset of abundance, species traits, and environmental properties from previously published surveys of rodents (see next paragraph). If environmental properties and species traits work together in a deterministic and inseparable fashion then it would be expected that neither extrinsic nor intrinsic factors would be identified as more influential than the other. However, if either group of factors emerges more influential than the other then some unique insight into species abundance will have been obtained. That is, local abundance could be the outcome of particular traits of the species more so than environmental conditions, or vice-versa. In the first scenario, abundance itself might be an “inherent” trait of a species wherein the intrinsic characteristics of the species lead to relative constancy in abundance (throughout the geographic range) and the environment then has very little effect in causing variation in abundance from site to site (Krasnov et al. 2006). Alternatively, the environment might mostly determine local abundance such that certain hospitable

environments (locales) are favorable for all species whereas other environments are universally harsh.

For this conceptual study of local abundance, I focused on rodents for several reasons: (1) Rodents have long been used as a model system for understanding ecological structuring. For the last four decades rodent communities have been considered model systems to test theories of community assembly (Rosenzweig and Winakur 1969; Brown and Lieberman 1973; Fox and Brown 1993; Perri and Randall 1999; Kelt 2011; Brown 2012; Stevens and Tello 2012). (2) Rodents represent 42% of all living mammal species on earth, making them the largest order of mammals (Merritt 2010). With this high level of diversity it is clear that rodents are highly adaptive. They are found on every continent (except Antarctica) and have the ability to thrive in some of the harshest climates on earth (Stoddart 1979). (3) Rodents have high metabolic demands that make the acquisition of food a vital component of their day-to-day activities. However, in general, rodent species exhibit a substantial level of overlap in their resource use (Merritt 2010). This paradox creates a setting where community structure is regulated on the finest spatial and temporal scales. For example, granivorous rodent species in desert communities of western North America are highly adapted for eating seeds and because of this the species have little separation in their habitat and diet and yet often coexist (Brown 1989; Kelt 2011). Communities that exhibit features such as high resource and habitat overlap among species provide a setting where structuring processes (based on intrinsic or extrinsic factors) could be so fine-tuned as to affect abundances in addition to simple presence-absence.

## Methods

Data on rodent abundance were obtained from published surveys found using the Web of Science and Google Scholar databases and the following keywords: “small mammal”, “rodent”, “abundance”, “community structure”, and “survey”. I also set additional limitations to only include publications from 1970 to 2013 and to exclude non-wildlife related research (e.g., medical research, parasitology and veterinary sciences); this was done to reduce the resulting publication list to a manageable number as well as increase the likelihood of reviewed publications meeting the required trapping procedure (see below) and providing necessary information. To be included in the analysis the published surveys met specific requirements in terms of their location, trapping method, the species included, and information provided (e.g., trapping effort).

All included survey data were collected within continental North America west of the Mississippi River and north of Mexico (essentially an area bounded between 25° and 50° N and between 90° and 130° W). All studies used standard-sized Sherman live traps, thus ensuring that all abundance data represented small-bodied (typically < 500 g) species from the order Rodentia. A few studies reported data on other non-rodent species, however these data were not included in my analysis. Additionally, in order to be included in the analysis, surveys were required to provide specific information regarding the trapping procedure (e.g., layout of traps) and effort in the form of trapping nights (one trap set for one night = 1 trapping night). “Trapping nights” is a commonly-used way of reporting trapping effort in surveys of rodents. Because of these requirements all of the included studies were essentially collecting abundance data under the same basic protocol (i.e., Sherman traps deployed in either a grid, web, or line-transect layout). This helped

to reduce the amount of variation (error) in the data that would have arisen from non-biologically meaningful sources such as trap design and deployment.

From the literature search, I acquired 41 publications providing 170 independent site-specific surveys (Figure 2). Thus, some studies provided data for more than one location (range 1 – 35); separate unique locations were defined as trapping layouts that were more than 2 km apart, studies that summed abundance data across multiple locations were excluded from the analysis. Together the 170 surveys provided 915 abundance observations (i.e., recorded abundance of a given species at a given location) that formed the main dataset for subsequent analyses ( $N = 915$ ). The total abundance over all species within a single location ranged from 6 to 1,330 with an average of 170 individuals. The number of species found at a single location ranged from 2 to 14, with an average of 6.5 species. In total, 83 species of rodents from the families Cricetidae, Geomyidae, Heteromyidae, Muridae and Sciuridae were included.

For my analyses, the response variable was based on the abundance of each species found at a survey location, after some statistical adjustment (see “Analysis” section). Abundance was defined as the total number of individuals captured at a specific location and did not include known recaptures. If surveys were conducted multiple times at the same location then only a single measure of abundance (for each species) was included. That is, I summed the abundance data over multiple trapping periods; none of the 170 surveys represented more than one set of abundance data for a given location. Further, no survey was included that represented abundance measured after an experimental manipulation; again this restriction helped to control for additional influences on abundance estimates.



Although I eliminated much unwanted extraneous variation by setting criteria for study inclusion, there was still a need to account for non-biological sources of variation in abundance estimates due to differences in study design. Therefore I included five nuisance variables describing the trapping protocol of each study. First, to account for the spatial aspects of the trapping design, the size and shape of layout were defined as well as anthropogenic presence for each survey location. The “shape” fell into one of three categories based on the orientation of the traps either grid, web, or transect. If the shape of the trap layout was either a grid or web the area was approximated using standard area calculations, length  $\times$  width or  $\pi \times$  radius of the web squared, respectively. The area of the trapping layout covered by a transect was determined as the length of the transect line multiplied by 117 m<sup>2</sup>, which was the average area per trap for all grid and web surveys. Second, to account for the temporal aspects of the trapping design, the span of the trapping period and number of trap nights were included. Span of trapping period was the total number of months that abundance data were acquired, ranging from 1 to 18 months.

### **Intrinsic factors**

The intrinsic factors for this study were species-specific traits that have the potential to influence abundance. Included variables accounted for differences among species in body size, degree of diet specialization, reproductive capacity, and geographic range size and location. This life history information was obtained from either NatureServe ([www.natureserve.org](http://www.natureserve.org)) or Encyclopedia of Life ([www.eol.org](http://www.eol.org)). Both sources are online databases that are compiled over a series of publications and are consistently updated. If a variable for any species was not found in NatureServe,

Encyclopedia of Life, or through a literature search, the information for the closest known relative was used (this occurred in only a few instances).

Body size was included as a measure of mass given that it can influence a species competitive ability (Bowers and Brown 1982) as well as ability to escape predators (Kotler et al. 1988). Body mass was treated as a discrete variable and was quantified as the log-transformed mid-point of the maximum and minimum average mass reported for the species in North America. The maximum and minimum for body mass were inclusive of both males and females, usually males set the maximum values and females set the minimum. Mid-point of the average body mass among all included species ranged from 7 to 662.5 grams.

Diet was treated as a categorical variable ranging from 1 to 5 representing degree of specialization of resource use. The less specialized a species is in its resource use then the better is its ability to avoid resource limitations and utilize habitat that a more specialized species cannot. I recognized five categories based on the list provided through NatureServe: granivorous, herbivorous, carnivorous, frugivorous, and insectivorous. Each species was assigned a value from 1 through 5 with “1” indicating that the species is highly specialized on only a single resource category and “5” indicating that the species is a generalist and uses all dietary resource categories. Thus, the categorical variable was essentially converted into a discrete quantitative variable that likely would have more potential to explain differences in species abundances than would a series of separate categorical variables (coded as “0” or “1”) representing the identity of a species resource category. My interest was in examining whether degree of diet specialization was positively related to abundance rather than to testing whether abundance differences

existed among species in the different resource use categories.

Litter size, reproductive season, number of litters and age of onset of female sexual maturity were all included as indicators of reproductive capacity, which can directly influence a species' population growth rate and therefore its abundance. A species with a larger litter size, longer reproductive season, more litters per season and shorter time for onset of female reproductive maturity would be expected to have a higher growth rate and therefore potentially a greater abundance than a species that has otherwise. Granted, because of life history tradeoffs and physiological constraints, a species might not be able to maximize all of these reproductive traits. Litter size was a discrete variable quantified as the mid-point between the average maximum and minimum values reported for the species throughout its North American range. The maximum and minimum values were taken from both online sources and were quantified as the average number of offspring produced per litter. The range of mid-litter size for all included species was from 2 to 10 individuals. Span of reproductive season was a binary variable representing the proportion of the year a species has been found to be reproductively active. The length of time reported for all included species ranged from year round to as short as a three-month window. Species were recognized as year round if they were reported as being reproductively active in at least nine months of the year for any type of conditions, not just extremely good conditions (i.e. high resource availability). Species found to be reproductively active less than 75% of the year were considered seasonal breeders. Number of litters in a single reproductive season was a binary variable designated as "0" for one litter per season and "1" for two or more litters per season, again regardless of resource availability. This variable represents the common

reproductive potential for the species in nature and does not cover all instances for the species (e.g., captive animals). Age of female sexual maturity was a binary variable with age  $\leq 6$  months coded as “1” and “0” otherwise.

Geographic range size for each species was approximated as a continuous variable for the extent of the species range throughout North America. Geographic range size provides insight into the ability of the species to persist in different regions and its dispersal ability. A range map for each species was obtained from the IUCN Red List of threatened species website ([www.iucnredlist.org](http://www.iucnredlist.org)). Each map was then uploaded into ArcGIS version 10.1 as a shape file and converted to the North American Albers Equal Area Conic projected coordinate system. I then used the Geometry Calculator tool to obtain the area of the range. If the range (shape file) was broken up into multiple fragments (e.g., disjunct ranges) then the total area for all the fragments was used. I also used the Geometry Calculator tool to obtain the spatial center (centroid) of each species geographic range in North America. The geographic center captures the concept of the abundant geographic center hypothesis, in that species are more abundant at the center of their geographic range than towards the boundaries of their range due to better habitat suitability for the species at the center (Brown 1984). For each shape file, the geographic coordinate system was set to World Geodetic System 1984 in order to get latitudinal and longitudinal position of each centroid in decimal degrees. If the range was broken up into several fragments that varied substantially in size (i.e. most of the range was within one fragment) the center was approximated for the largest fragment only. If fragments were generally equal in size then the centermost fragment was used to get the centroid. Latitude and longitude of the centroid represented the spatial location of the species

overall geographic range, another general intrinsic factor that could be related to abundance. This variable was also used to calculate distance from range center for each survey location and species (see later section).

### **Extrinsic factors**

Environmental properties of each survey location were included as the extrinsic factors. These factors assessed the environmental aspects that could influence local species abundance. These variables represented regional, climatic, and habitat properties (both abiotic and biotic) of the survey locations. Variables were quantified either using information extracted from the published studies or from online databases.

The location (latitude and longitude) of a survey was either reported within the publication or approximated from a verbal description or map of the area where the study was conducted, occasionally also by referring to images in Google Earth. Elevation for each location was obtained using Google Earth (if not reported in published paper) and was included as a continuous variable. Habitat type was treated as a quantitative variable, roughly indicating the amount of vegetation found at the survey location based on the description provided by the publication. The variable ranged from 1 (substantial vegetation) to 5 (very little vegetation) determined by whether author identified the habitat as forest (1), grassland (2), agriculture/pasture (3), desert scrub (4), and barren (5).

Two climatic properties (mean monthly air temperature and mean monthly precipitation) were included as continuous variables. For each survey location these variables were derived from data obtained through the land-based weather station mapping tool provided by the National Climatic Data Center ([www.ncdc.noaa.gov](http://www.ncdc.noaa.gov)).

Using this tool I identified all weather stations within 20 km of each survey location. I then downloaded temperature and precipitation data from the five closest stations that had data for the relevant time period. For a few survey locations, there were no stations within 20 km so I used the closest station beyond that distance; the furthest station used was 45 km from its associated survey location. Data were averaged among stations for those survey locations that had multiple weather stations. I then calculated mean monthly air temperature across the span of the trapping period plus an additional six months prior to the first month of trapping. I obtained total precipitation for each month within the trapping period plus the six months prior. These values were summed and then divided by the total number of months to get an average monthly precipitation amount.

For each species at each survey location, I also included two variables intended to represent the potential “competitive pressure” on resources. These variables were total abundance of all rodents and number of rodent species found at the survey location. Total abundance included all species except the particular focal species. Total number of species was the same value for all species at a given survey location.

### **Distance between geographic range center and survey location**

Distance between survey location and species geographic range center was the only variable included in the analysis that can be described as both an intrinsic and extrinsic factor. It is derived from an intrinsic factor (range center) and extrinsic factor (survey location) and thus is a characteristic of the species and a property of a particular site. I calculated this variable by first transforming the survey location and the range geographic center into radians. I then used the Haversine formula to quantify the distance

between the two locations.

## **Analysis**

To compare the influence of intrinsic versus extrinsic factors on species abundance, I used a model building and comparison procedure. More specifically, I constructed a series of regression models and compared them in an information-theoretic framework (Burnham and Anderson 2002). Given that a multitude of factors (many unaccounted for in the present study) can potentially influence the local abundance of any species, I expected the abundance data to have a substantial amount of variation (within and among species) arising from unknown sources. As such, an NHST (null hypothesis significance testing) approach to comparing intrinsic and extrinsic factors did not seem appropriate. Preliminary investigation of the data revealed that none of the independent (predictor) variables alone had a strong relationship with abundance. One strength of the information-theoretic approach is the capacity for directly comparing multiple different explanatory models that themselves differ in their predictor variables, without having to make arbitrary decisions regarding statistical significance.

The first step in the analysis was to correct the abundance data for differences in trapping methods among the different studies. To do this, a least-squares multiple regression was completed using abundance as the response variable and the five nuisance variables as the predictor variables. These variables accounted for differences in temporal and spatial aspects of the survey method and included: trap layout shape, trap layout area, anthropogenic influence, temporal span of the trapping period, and number of trap nights. The standardized residuals for each abundance observation were extracted from the

regression and used as the new survey-method-corrected abundance estimate (hereafter just referred to as “standardized abundance”).

Additionally, to reduce the number of predictor variables used in the model comparisons and to control for correlation among the variables, four summary (or composite) variables were generated using the factor scores or loadings from four principal component analyses. The PCAs were conducted on standardized (z-transformed) versions of the predictor variables. Extrinsic and intrinsic variables were grouped based on the type of information they described. For the intrinsic factors, traits of the species associated with its morphology, resource use, and reproductive capacity (body mass, diet, litter size, age of female reproductive maturity and reproductive season) were grouped. Species traits associated with geographic distribution (area of geographic range, latitude and longitude of the centroid of the geographic range) were combined into a second group and PCA. For the extrinsic factors, properties of the survey location associated specifically with the environmental conditions of the location (latitude, longitude, elevation, temperature, precipitation, and habitat) were grouped and referred to as abiotic conditions. The properties of the survey location associated with biotic conditions (total rodent abundance and total number of species present) were grouped. Distance between the center of each species geographic range and each survey location (where it was recorded), was not grouped into a summary PCA variable due to its unique nature as both an intrinsic and extrinsic variable. Thus, for model comparison, five predictor variables were available: (1) PCA-derived variable representing intrinsic morphology/reproductive traits (referred to as ecological variable), (2) PCA-derived variable representing intrinsic range size/location “traits” (referred to as geographic



variable), (3) PCA-derived variables representing extrinsic abiotic conditions (referred to as abiotic variable), (4) PCA-derived variable representing extrinsic biotic conditions (referred to as biotic), and (5) distance between survey location and range center (referred to as distance variable).

The first axis for morphology/reproduction or ecological PCA explained 30.96% of the variance and had an eigenvalue of 1.24. This factor was positively correlated with body mass and female maturity (factor loadings were 0.52 and 0.39 respectively) and negatively correlated with litter size, number of litters within a season and diet (factor loadings were -0.23, -0.66 and -0.32 respectively). The first axis for the PCA based on range size and location (termed geographic variable) explained 57.97% of the variance and had an eigenvalue of 1.31. This factor was positively correlated with both the latitudinal and longitudinal position of the range centroid and the area of the geographic range (factor loadings were 0.32, 0.62, and 0.72 respectively). The first axis for the extrinsic abiotic grouping explained 33.85% of the variance and had an eigenvalue of 1.42. This factor was positively correlated with the latitudinal position, elevation, and habitat (factor loadings were 0.50, 0.50 and 0.15 respectively) and was negatively correlated with longitudinal position, temperature, and precipitation (factor loadings were -0.38, -0.52 and -0.25 respectively). The first axis for the extrinsic biotic grouping explained 87.95% of the variance and had an eigenvalue of 1.32. This factor was negatively correlated with both total abundance and number of species (factor loadings were -0.71 and -0.71 respectively). The relatively large percentages of explained variation (31%, 58%, 34%, and 88%) indicate that the four composite variables derived from these PCAs were sufficient in capturing the variance and covariance among the

constituent variables; i.e., they were appropriate variables for use in subsequent models.

An exhaustive (complete) model building process was conducted on the full data set ( $N = 915$  abundance observations among 86 species) and on subsets representing select genera: *Dipodomys* ( $N = 107$  abundance observations among 8 species), *Neotoma* ( $N = 111$  abundance observations among 9 species), *Perognathus* ( $N = 67$  abundance observations among 7 species) and *Peromyscus* ( $N = 266$  abundance observations among 11 species). For the full data set and each of the genera subsets, I obtained all 31 models possible from a set of five predictor variables. For each of the genera-based data sets, the preliminary regression step of removing the effects of nuisance variables on abundance was repeated separately followed by new PCAs to generate the four summary variables. To make comparisons among the beta coefficients obtained from the model building procedure more meaningful I standardized all variable values separately. As with the full data set, the PCAs on the data subsets were useful in producing meaningful summary variables (explained variance and eigenvalues were comparable to the full data set).

For the full data set and the four data subsets separately, I examined all 31 possible models using the Akaike information criterion corrected for small sample size (AICc) and model weights. In particular, I was most interested in comparing models that included only intrinsic factors to those that included only extrinsic factors given that the extrinsic vs. intrinsic distinction was the main focus of the study. However, to further examine the influence of each predictor variable (relative to the other variables), I also compared their regression coefficients as weighted averages over all models for a given data set.

Regression coefficients were averaged using the R software package MuMIn.

From each model-averaging procedure I extracted the averaged coefficient without shrinkage, the unconditional standard error and the relative importance measure. Model averaging without shrinkage refers to averaging over only models in which the variable appears (Burnham and Anderson 2002). Unconditional standard error estimates include model selection uncertainty as well as an estimate of precision of the parameter not conditional on any particular model (Burnham and Anderson 2002). Finally, I also calculated the relative importance measure as the sum of the model weights for all models that included the variable of interest. I then compared each importance value to the random expectation value of 0.516. This represents the importance value that would obtain if all models had the same weight ( $1/31 = 0.032$ ) and given that each variable was included in 16 models ( $0.032 \times 16 = 0.516$ ). This expected value is also the long-run expectation if the weight of each model was from a random cumulative and uniform distribution between 0 and 1. Therefore, it is a useful benchmark for determining whether a given importance value is meaningful (i.e.,  $> 0.516$ ) in a probabilistic sense.

## Results

The standardized abundance estimates often varied considerably within a species (among survey locations) over two SD units and sometimes 6 SD units (Figure 3). There was a significant amount of variation in standardized abundance among the four most species-rich genera (ANOVA,  $F_{3,547}=9.13$ ,  $P < 0.0001$ ) and among species nested within these genera (ANOVA,  $F_{34,527}= 3.68$ ,  $P < 0.0001$ ). As expected, the mean and standard deviation values for the full dataset were close to zero (-0.009) and one (0.984), respectively. From the same regression using all species, the mean and standard deviation

were 0.594 and 1.659 for the *Dipodomys* species, -0.036 and 0.872 for the *Neotoma* species, -0.081 and 0.974 for the *Perognathus* species, and 0.017 and 0.888 for the *Peromyscus* species, respectively. This indicates that *Neotoma*, *Perognathus*, and *Peromyscus* species had a distribution of abundance values that was similar to the overall distribution for all species but the *Dipodomys* species had abundance estimates with a tendency to be higher than expected (Figure 4).

### **Model comparison**

For the full dataset including all species and the four genera subsets, all 31 possible regression models of the four PCA summary variables and one distance variable (i.e., distance from the center of each species range) were used in the AIC model comparison procedure. For the full dataset approximately half (15) of the compared models were included within the group composing 95% cumulative Akaike weights and 16 of these models had  $\Delta\text{AICc} < 5$  (Table 1). In this set of models, the  $\Delta\text{AICc}$  values gradually increased to 4.27 and then jumped to 6.55 for the next model outside the set. The distinguishing and unique feature of the 16 models is that the intrinsic ecological summary variable (*eco*) was included in all of them. Also, the importance value for *eco* (0.97) was very high. Importance values for the extrinsic abiotic variable (0.57) and distance-to-center (0.61) were also greater than the random expectation value (0.516) (Figure 5).

For the subset consisting of *Dipodomys* species approximately half of all the models were within the group composing 95% cumulative Akaike weights, however only the top 8 models had  $\Delta\text{AICc} < 5$  (Table 2). Again, there was a jump in  $\Delta\text{AICc}$  values

from 4.31 to 6.16 between the last model in this top set and the first model outside the set. The intrinsic ecological variable (*eco*) and extrinsic biotic variable were both included in all the top models (Table 2) and were the only variables with importance values  $> 0.516$  (Figure 5).

For the subset consisting of *Neotoma* species 25 of the 31 models were within the group composing 95% cumulative Akaike weights and of those models the top 21 had  $\Delta AICc < 5$  (Table 3). There was a slight increase in  $\Delta AICc$  values from 4.67 to 5.04 between the last model in the top set and the first model outside the set. The distance-to-center variable (DC) was the only variable with an importance value  $> 0.516$  (Figure 5).

For the subset consisting of *Perognathus* species most of the models (24 of 31) were within the group composing 95% cumulative Akaike weights and 25 models had  $\Delta AICc < 5$  (Table 4). There is no definitive set of top models in that there was a gradual increase in  $\Delta AICc$  values among the models (Table 4). The best-supported model had a weight of only 0.118. None of the variables had an importance value  $> 0.516$  (Figure 5).

For the subset of the *Peromyscus* species only the top three models were within the group composing the 95% cumulative Akaike weights and only the top four models had  $\Delta AICc < 5$  (Table 5). There was a jump from 2.77 to 12.88 between the last model of the top set and the first model outside of the top set. The intrinsic geographic variable (*geo*), extrinsic abiotic variable and distance-to-center variable (DC) were found in the top four models (Table 5) and all three of these variables had importance values of approximately 1 (Figure 5).

### Model-averaged regression coefficients

Using all 31 models, a model-averaged regression coefficient and unconditional standard error were calculated for each of the five variables in the full dataset and four genera subsets separately. All models were used because no one or two models stood out as superior and no variable was found exclusively in the top supported models during the model comparison phase. Furthermore, the averaging procedure was based on Akaike weights which ensured models with little support had only a small contribution to the model-averaged regression coefficient. Of the model-averaged regression coefficients for the full dataset, the coefficient for the intrinsic ecological variable ( $\beta_{eco} = 0.116$ ) was the greatest and had the lowest unconditional standard error relative to the coefficient's magnitude (Table 6) and it was the only variable that had a relative importance value near 1.0 (Figure 5). The model-averaged regression coefficients for the other four variables were close to zero, had large unconditional standard errors relative to the averaged coefficients (in the case of *geo* and the extrinsic biotic variable, standard error values were greater than the averaged regression coefficients; Table 6) and had much lower relative importance than *eco* (Figure 5).

For the subset of *Dipodomys* species, the model-averaged regression coefficients for the intrinsic ecological variable ( $\beta_{eco} = -0.271$ ) and the extrinsic biotic variable ( $\beta_{biotic} = -0.258$ ) were the most different from zero, had the lowest unconditional standard errors relative to the magnitude of the coefficients (Table 6) and were the only two variables that had relative importance values near 1.0 (Figure 5). The model-averaged coefficients for the remaining three variables (intrinsic geographic variable, extrinsic abiotic variable and distance-to center variable) were small, had large unconditional standard errors

relative to the averaged coefficients (in the case of DC the standard error value was greater than the averaged regression coefficient; Table 6) and the relative importance values were lower than *eco* and extrinsic biotic (Figure 5).

For the subset of the *Neotoma* species, the model-averaged regression coefficient for distance-to-center ( $\beta_{DC} = -0.172$ ) was the largest in magnitude, had the lowest standard error relative to the regression coefficient (Table 6) and had the highest relative importance value (Figure 5). The other four variables had either model-averaged regression coefficients close to zero or unconditional standard errors greater than or equal to the magnitude of the averaged coefficient, and relative importance values much lower than the DC variable (Figure 5).

For the subset of the *Perognathus* species, the model-averaged regression coefficient for the extrinsic biotic variable was most different from zero ( $\beta_{biotic} = -0.165$ ) and had the only standard error less than the regression coefficient value (Table 6). However, its relative importance value was less than the random expectation (Figure 5). The remaining four variables had averaged coefficients closer to zero, had unconditional standard errors greater than the coefficient estimate (Table 6), and relative importance values even less than the random expectation (Figure 5).

For the subset of the *Peromyscus* species, the model-averaged regression coefficients for the extrinsic abiotic variable, intrinsic geographic variable and distance-to-center variable were the most different from zero, had low unconditional standard error estimates relative to the magnitude of the coefficients (Table 6), and had very high relative importance values (Figure 5). The other two variables (*eco* and the extrinsic biotic variable) had lower averaged regression coefficients, high unconditional standard

errors relative to the magnitude of the coefficients (Table 6) and relative importance values less than the random expectation (Figure 5). It is worth noting that for all datasets and variables, the results for the model-averaged regression coefficients agreed very well with those for the importance values. That is, variables with high importance values also had large regression coefficients with relatively small standard errors.

### Discussion

Based on the model-comparison and model-averaging procedures, each of the five variables (two intrinsic, two extrinsic, and distance-to-range-center) had a substantial influence on rodent abundance in the full dataset or at least one of the genera subsets. This indicates that neither intrinsic species traits nor extrinsic environmental properties are universally more important than the other in influencing the abundance of rodent species. For most species, abundance is likely determined by site-specific environmental properties (extrinsic factors) whose influence is constrained by the inherent reproductive and resource use traits (intrinsic factors) of the species. The variables identified as having the most support in the model comparison and evaluation of importance values were different for the full dataset and genera subsets – this further emphasizes the complexity and pluralistic nature of factors that determine species abundance.

The full dataset was the only one in which the intrinsic ecological variable was the single most supported factor influencing abundance. This variable represented the morphology, life history, and resource use of the species, such that differences between the species in their ability to acquire resources, utilize the environment and reproduce were represented. The importance of the intrinsic ecological variable for the full dataset



suggests that when considering a mix of non-ecologically similar species (i.e., the entire rodent assemblage), abundance is related more to the identity of the species than to spatial location or conditions of the environment. However, the ecological identity of the species was not as important when considering species that were more closely related (i.e. genera subsets).

For the species of the genus *Dipodomys* the intrinsic ecological variable as well as the extrinsic biotic variable were identified as the most influential. For this subset, the model-averaged regression coefficients for these factors were equal in magnitude and direction (both had an inverse relationship with abundance; Table 6). This suggests that there may be a relationship between the identity of the *Dipodomys* species (i.e., the species morphological, reproductive, and diet characteristics) and the amount of competition present within the environment (i.e., the extrinsic biotic factor based on number of individuals and species found within the environment) in influencing abundance. In addition, *Dipodomys* was the only genus in which species abundances were greater than expected. This could indicate that *Dipodomys* species reach high enough local densities for intra- and interspecific competition to occur whether such competition suppresses population sizes or not. Of course, my study was not designed to test for competition (or its ecological consequences) and thus the negative effect of the intrinsic ecological variable could represent some other process.

For the species of the genus *Neotoma* the distance between the center of the geographic range and survey location was identified as the most informative factor. This variable was the only one that combined an intrinsic aspect of the species (range size and location) as well as an extrinsic property of the local environment (its location). Also, this

factor, more specifically, was a direct test of the ‘abundant center’ distribution hypothesis, which states that species will have the highest abundance at the center of their range and decreasing abundance towards the range edges (Sagarin and Gaines 2002). Commonly, this form of distribution is assumed to be associated with locations near the center of the range having environmental conditions most suitable for the species (Brown 1984). The importance and direction of the ‘DC’ variable in this analysis for the genus *Neotoma* aligns with the expectation of the hypothesis (i.e. strong, negative relationship). Moreover, the lack of support for the extrinsic abiotic variable (PCA combination of latitude, longitude, elevation, temperature, precipitation, and habitat) indicates that the distance-to-center effect is not simply an artefact of geographic location or local environmental conditions.

For the species of the genus *Perognathus* none of the five variables (two intrinsic, two extrinsic, and distance-to-center) were identified as more supported in influencing the standardized abundance. This could be due to the small sample size for this genus ( $N = 67$ ) compared to the other genera ( $N = 107, 111, \text{ and } 269$ ). The relatively low number of observations may not have provided enough information for a strong relationship between any of the factors and abundance to be revealed.

Finally, for the *Peromyscus* species the intrinsic geographic variable, extrinsic abiotic variable, and distance-to-center variable were identified as the most supported factors in influencing abundance and all had a positive relationship with abundance (Table 6). This suggests that the abundances of *Peromyscus* species are mostly influenced by spatial and physical aspects of their environment (that perhaps result in highly tolerant species being more widespread), rather than by intrinsic traits related to reproduction and

resource use.

There was a lack of consistency between the full dataset and the genera subsets in the magnitude of the regression coefficients, direction of the relationship between the variables and abundance (positive or negative regression coefficient) and the relative importance of each variable. These differences further indicate that rodent species may have very unique interactions between their traits and the environment. This is further supported by the importance of the intrinsic ecological variable for the full dataset. This variable captures the identity of each species by assigning a value to represent the unique combination of ecologically-based traits possessed by each species, in the context of an analysis that includes all the species. When the analysis does not include all the species (and hence less variation as in the genera-specific data subsets) the intrinsic ecological variable is no longer seen to be important, except for *Dipodomys*. When analysis is confined to single genera, other factors are revealed as having an influence on abundance.

The lack of repeatability in the abundance for a species across sites indicates that the identity of the species alone is not an obvious contributor to their abundance, unlike the pattern observed in flea populations across regions in Krasnov et al. (2006). In my study, there was a significant amount of variation in abundance within species and within genera (Figure 3). Krasnov et al. (2006) consider abundance to be an actual trait of flea species; however, for rodents there is no evidence to suggest that abundance is a trait. Even considering that the intrinsic ecological variable was identified as the most influential for the full dataset, extrinsic factors likely play a substantial role in adjusting local abundances of species given that no species had constant local abundance at all survey sites.

The results of my study (and consideration of ecological processes in general) imply that there is a great deal of complexity associated with identifying the factors that influence the abundance of species living within a community. More specifically, each species has a different relationship with the environment and species vary in the importance of factors that may influence their abundance. In the past, ecological research often sought out universal mechanisms that could govern the abundance of all or most species within a community, such as competition (Hutchinson 1957; Schoener 1974; Tilman 1994), predation (Brooks and Dodson 1965; Holt 1977), mutualism (Callaway et al. 2002), dispersal/colonization (Hubbell 2001), niche differentiation (Brown et al. 1995), and metabolism (Brown et al. 2004). Although there is some merit to this approach and searching for unifying principles and mechanisms, each species likely has a somewhat unique set of intrinsic and extrinsic factors that influence abundance both spatially and temporally. Results of my study support this perspective in that there was no one set of intrinsic or extrinsic factors that consistently had greater influence on abundance across all examined genera. My study also demonstrates an empirical and analytical approach that could be applied to other taxa in further comparing the relative influences of intrinsic and extrinsic factors on local species abundance measured for a wide variety of species across broad spatial extents.

The informative quality of environmental properties and species traits in understanding abundance has been made clear through the ‘Trait-based Approach’ (McGill et al. 2006). This strategy utilizes the relationship between these factors to quantify an expected trait-distribution and by extension predicted species presence and abundance for any particular environment. Environmental properties and traits of a

species do interact in influencing abundance. However, when combining species traits and environmental properties into a single performance distribution (see Webb et al. 2010) subtleties of how this interaction works across a system may be overlooked. First, there are differences among species in the importance of specific factors and this is lost when applying the same relationship across all the species found in a single location. Second, there is information to be gained in identifying factors of the environment that influence species abundances to different extents. Third, the intrinsic-extrinsic dichotomy is important and can lead to new insight when explicitly incorporated into an analysis of abundance.

As natural communities experience significant biodiversity loss, increased exotic invasions, climate change, habitat fragmentation, and anthropogenic habitat alterations, there is a growing need for information about how communities will respond. This need goes beyond predicting abundance. The more we can understand how species will react to changing environments the more likely we will make quality management decisions in preserving natural systems. A combination of environmental properties and species traits influence abundance and more generally community structure. However, it is useful to know what environmental properties are most influential for each species in a community or what traits allow species to be less influenced by environmental changes. The separation of the environment from the traits of species when attempting to understand abundance (i.e., analyzing abundance under the intrinsic-extrinsic dichotomy) may allow an opportunity to obtain better knowledge of the species that will be most affected by environmental changes and how they will be affected.

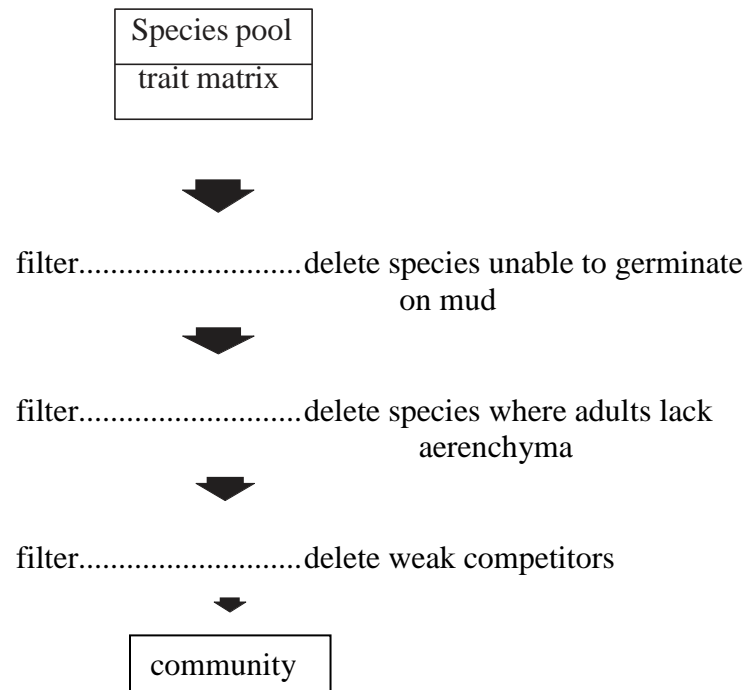


Figure 1. Hypothetical example of environmental filtering. Species composition in a wetland plant community is based on the traits of the species. Figure is adapted from Keddy (1992).

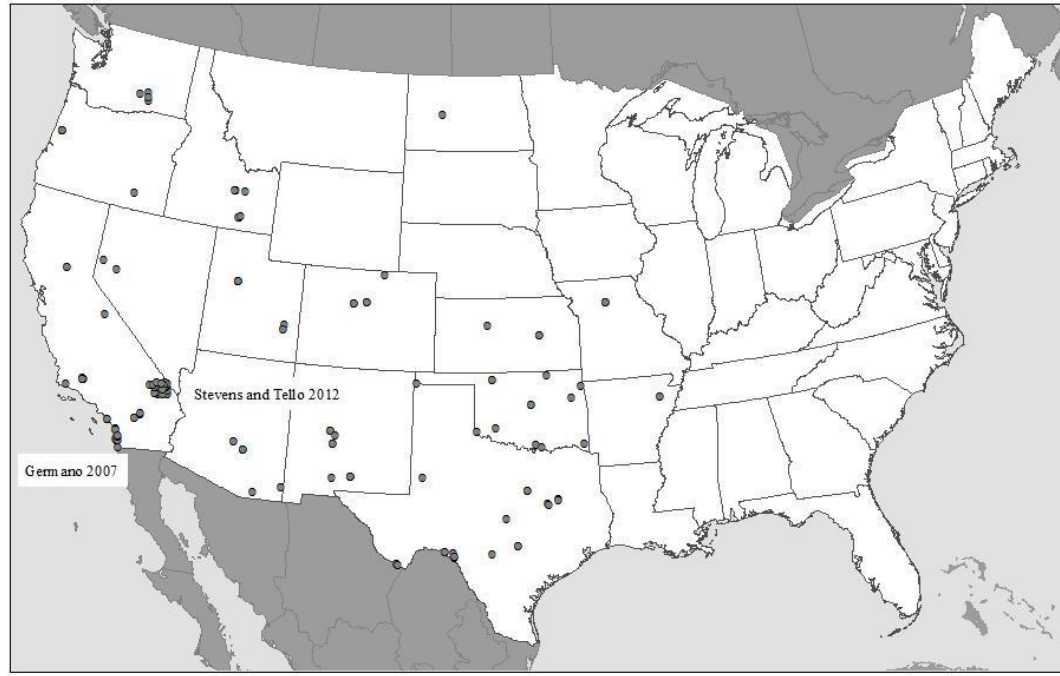


Figure 2. Map of the 170 survey locations. Locations are distributed throughout the western United States, all being west of the Mississippi River and north of Mexico (an area between  $25^{\circ}$  and  $50^{\circ}$  N and between  $90^{\circ}$  and  $130^{\circ}$  W). Thirty-one of the survey locations clustered in southern California were from Stevens and Tello (2012) and seven of the survey locations in coastal southern California were from Germano (2007).

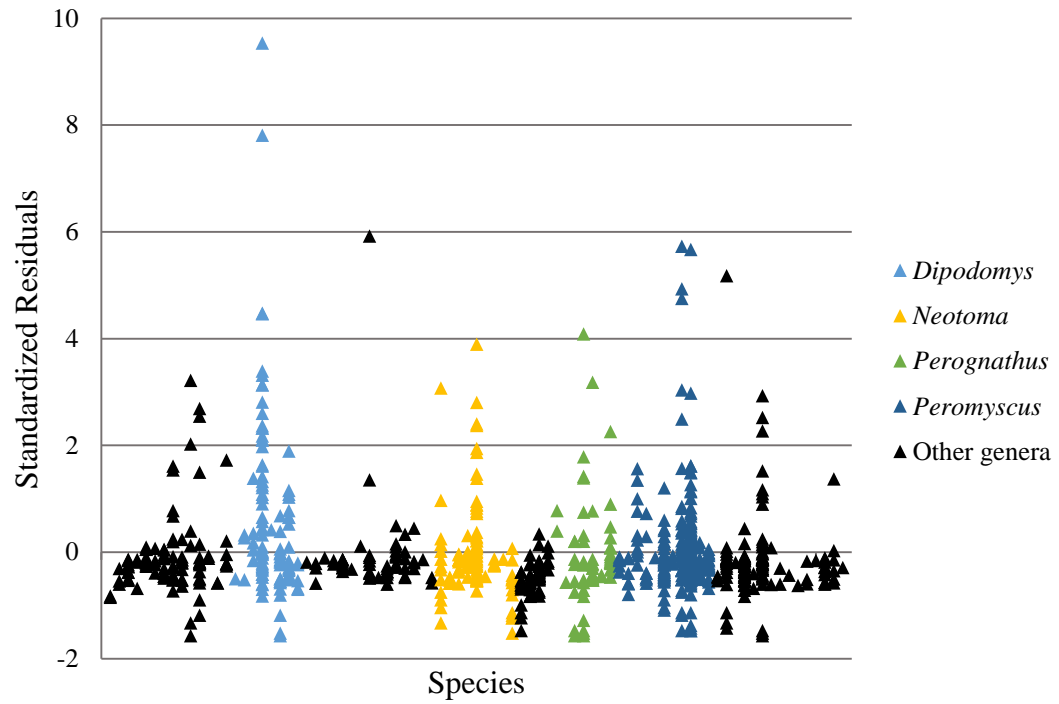


Figure 3. Standardized residuals of abundance corrected for nuisance variables.

Nuisance variables represent differences in survey procedure. Points are organized by species ( $N = 83$ ) in alphabetical order. Each vertical stack of points represents all of the survey locations where the particular species was recorded.



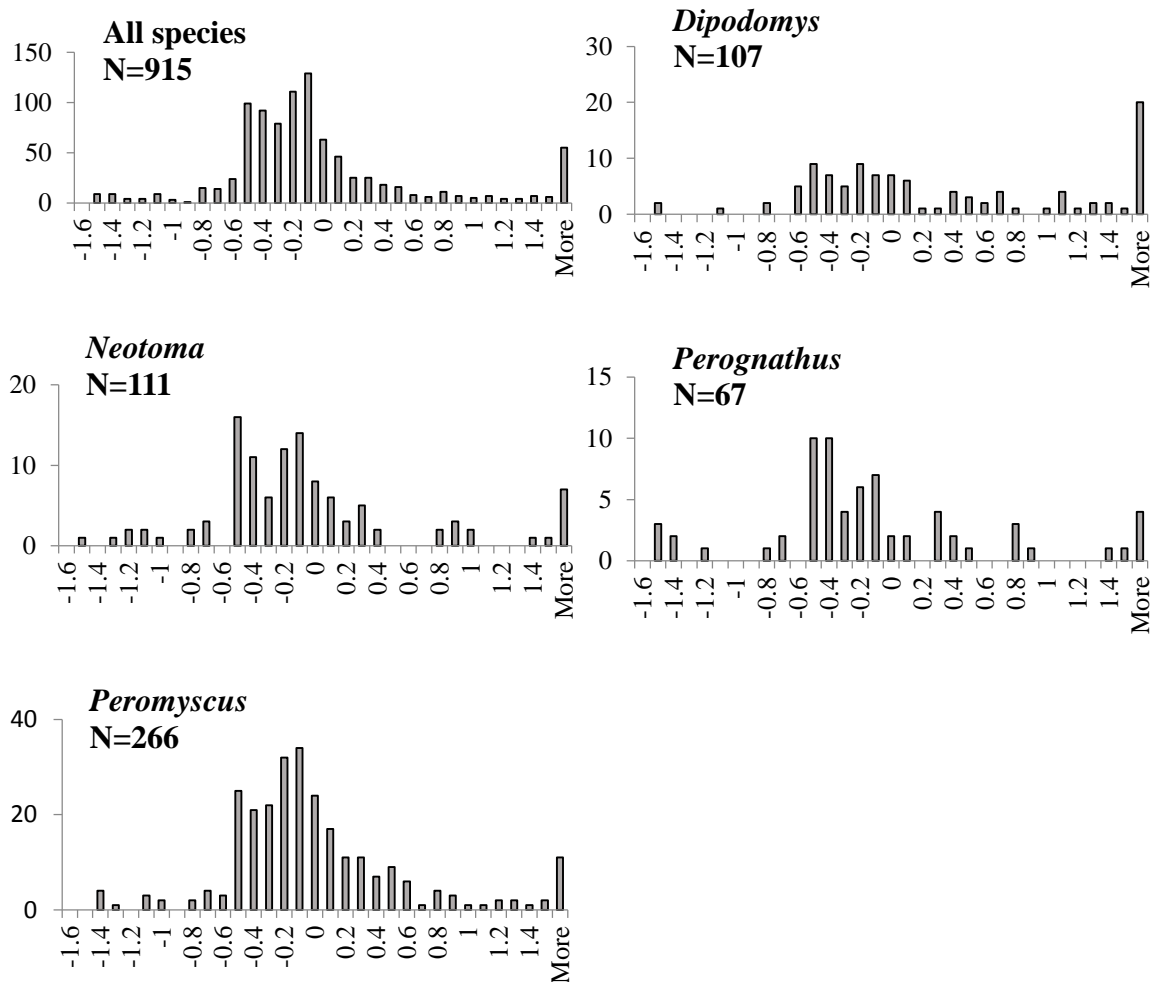


Figure 4. Frequency distributions of the standardized residuals of abundance. Abundance was corrected for the study design nuisance variables. Distributions are shown for the full dataset (all species) and each of the four species-rich genera. Standardized residuals are from a single regression involving all species so as to allow comparison among the genera. For the abundance regression models conducted separately on each genera, a different set of abundance residuals (not shown) was obtained based solely on the data for the particular genus.

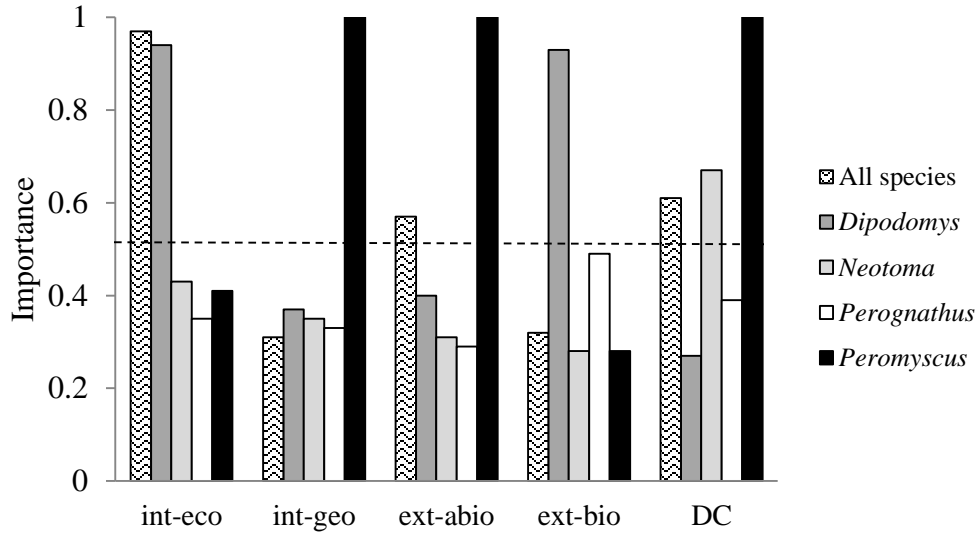


Figure 5. Relative importance values of each variable. Intrinsic ecological (*int-eco*), intrinsic geographic (*int-geo*), extrinsic abiotic (*ext-abio*), extrinsic biotic (*ext-bio*), and distance-to-range-center (DC) calculated as the sum of all Akaike weights of the models that the variable was included in (see text for more details). The dashed line (importance = 0.516) represents the expected importance value if all models had the same or a random weight and given that each variable was included in 16 models. Variables with importance values > 0.516 had a greater than randomly expected influence on standardized abundance.

Table 1. AICc model comparison for the full dataset (N = 915).

Variables included in model*					$\log(L)$	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$	$cum. w$			
Intrinsic		Extrinsic											
eco		+	abiotic		+	DC	-1305.10	4	2620.27	0.00	0.179	0.179	
eco					+	DC	-1306.56	3	2621.17	0.90	0.115	0.294	
eco		+	abiotic				-1306.83	3	2621.71	1.44	0.087	0.381	
eco		+	abiotic	+	+	DC	-1304.89	5	2621.87	1.60	0.081	0.462	
eco							-1308.00	2	2622.02	1.75	0.075	0.537	
eco	+	geo	+	abiotic		+	DC	-1305.09	5	2622.28	2.01	0.066	0.603
eco				+	+	DC	-1306.19	4	2622.45	2.17	0.060	0.663	
eco	+	geo	+	abiotic			-1306.42	4	2622.91	2.64	0.048	0.711	
eco	+	geo			+	DC	-1306.52	4	2623.11	2.84	0.043	0.754	
eco	+	geo					-1307.54	3	2623.11	2.84	0.043	0.797	
eco		+	abiotic	+	+		-1306.65	4	2623.37	3.09	0.038	0.835	
eco				+	+		-1307.68	3	2623.41	3.13	0.037	0.872	
eco	+	geo	+	abiotic	+	+	DC	-1304.88	6	2623.88	3.61	0.030	0.902
eco	+	geo		+	+	DC	-1306.15	5	2624.39	4.12	0.023	0.925	
eco	+	geo		+	+		-1307.20	4	2624.47	4.20	0.022	0.947	
eco	+	geo	+	abiotic	+	+	-1306.23	5	2624.54	4.27	0.021	0.968	
			abiotic				-1310.40	2	2626.83	6.55	0.007	0.975	
	geo	+	abiotic				-1310.11	3	2628.27	8.00	0.003	0.978	
	geo						-1311.31	2	2628.64	8.37	0.003	0.981	
			abiotic	+	+		-1310.30	3	2628.65	8.37	0.003	0.984	
				biotic			-1311.36	2	2628.74	8.47	0.003	0.987	
			abiotic		+	DC	-1310.38	3	2628.81	8.53	0.003	0.990	
						DC	-1311.56	2	2629.14	8.87	0.002	0.992	
	geo	+	abiotic		+	DC	-1309.80	4	2629.67	9.40	0.002	0.994	
	geo	+	abiotic	+	+		-1310.01	4	2630.09	9.82	0.001	0.995	
	geo			+	+		-1311.10	3	2630.24	9.97	0.001	0.996	
	geo				+	DC	-1311.14	3	2630.32	10.05	0.001	0.997	
			abiotic	+	+	DC	-1310.28	4	2630.64	10.36	0.001	0.998	
				biotic	+	DC	-1311.36	3	2630.76	10.48	0.001	0.999	
	geo	+	abiotic	+	+	DC	-1309.70	5	2631.49	11.22	0.001	0.999	
	geo			+	+	DC	-1310.92	4	2631.91	11.64	0.001	1.000	

\*Variables included in models are all composites variables calculated using Principle Components Analysis (PCA) of several closely related variables except 'DC'. *eco* (intrinsic ecological aspects of species): median body size, reproductive capacity and degree of diet specialization, *geo* (intrinsic geographic aspects of species): geographic range size and location of center of the range, *abiotic* (extrinsic non-living features of the site): climate, elevation, habitat type and location of trapping site, *biotic* (extrinsic living features of the trapping site): abundance and diversity of competitors. DC: Distance between center of species geographic range locations and the survey location.

Table 2. AICc model comparison for the subset of *Dipodomys* species (N = 107)

Variables included in model*					$\log(L)$	$K$	$AIC_c$	$\Delta_i AIC_c$	$w_i$	$cum. w$					
Intrinsic		Extrinsic													
eco			+	biotic			-1305.10	3	295.53	0.00	0.252	0.252			
eco		+	abiotic	+	biotic		-1306.56	4	296.28	0.75	0.173	0.424			
eco	+	geo		+	biotic		-1306.83	4	296.60	1.07	0.147	0.572			
eco	+	geo	+	abiotic	+	biotic	-1304.89	5	297.65	2.12	0.087	0.659			
eco				+	biotic	+	DC	-1308.00	4	297.73	2.20	0.084	0.742		
eco		+	abiotic	+	biotic	+	DC	-1305.09	5	298.53	3.00	0.056	0.799		
eco	+	geo		+	biotic	+	DC	-1306.19	5	298.68	3.15	0.052	0.851		
eco	+	geo	+	abiotic	+	biotic	+	DC	-1306.42	6	299.84	4.31	0.029	0.880	
eco	+	geo					-1306.52	3	301.69	6.16	0.012	0.891			
eco	+			abiotic			-1307.54	3	301.82	6.29	0.011	0.902			
					biotic	+	DC	-1306.65	3	301.93	6.40	0.010	0.913		
					biotic		-1307.68	2	301.99	6.46	0.010	0.923			
eco	+	geo	+	abiotic			-1304.88	4	301.99	6.46	0.010	0.932			
eco							-1306.15	2	302.15	6.62	0.009	0.942			
					abiotic	+	biotic		-1307.20	3	302.24	6.71	0.009	0.950	
					abiotic	+	biotic	+	DC	-1306.23	4	302.47	6.94	0.008	0.958
		geo			+	biotic	+	DC	-1310.40	4	302.88	7.34	0.006	0.965	
eco	+	geo					+	DC	-1310.11	4	303.13	7.60	0.006	0.970	
eco	+	geo	+	abiotic			+	DC	-1311.31	5	303.69	8.16	0.004	0.975	
		geo	+	abiotic	+	biotic	+	DC	-1310.30	5	303.79	8.26	0.004	0.979	
eco			+	abiotic			+	DC	-1311.36	4	303.98	8.45	0.004	0.982	
		geo			+	biotic			-1310.38	3	303.99	8.46	0.004	0.986	
eco							+	DC	-1311.56	3	304.23	8.70	0.003	0.989	
		geo	+	abiotic	+	biotic			-1309.80	4	304.36	8.83	0.003	0.992	
		geo	+				+	DC	-1310.01	3	305.67	10.14	0.002	0.994	
						abiotic			-1311.10	2	306.00	10.47	0.001	0.995	
		geo	+	abiotic			+	DC	-1311.14	4	306.06	10.53	0.001	0.997	
						abiotic	+	DC	-1310.28	3	306.08	10.55	0.001	0.998	
							DC		-1311.36	2	306.48	10.95	0.001	0.999	
		geo	+	abiotic					-1309.70	3	307.56	12.03	0.001	0.999	
		geo							-1310.92	2	307.95	12.42	0.001	1.000	

\*Variables included in models are all composites variables calculated using Principle Components Analysis (PCA) of several closely related variables except 'DC'. *eco* (intrinsic ecological aspects of species): median body size, reproductive capacity and degree of diet specialization, *geo* (intrinsic geographic aspects of species): geographic range size and location of center of the range, *abiotic* (extrinsic non-living features of the site): climate, elevation, habitat type and location of trapping site, *biotic* (extrinsic living features of the trapping site): abundance and diversity of competitors. DC: Distance between center of species geographic range locations and the survey location.

Table 3. AICc model comparison for the subset of *Neotoma* species (N = 111)

Variables included in model*					$\log(L)$	$K$	$AIC_c$	$\Delta_i AIC_c$	$w_i$	$cum. w$
Intrinsic		Extrinsic								
				DC	-155.19	2	316.60	0.00	0.159	0.159
eco				+ DC	-154.79	3	317.95	1.35	0.081	0.240
	geo			+ DC	-154.80	3	317.98	1.37	0.080	0.320
eco					-156.09	2	318.40	1.80	0.065	0.384
		abiotic		+ DC	-155.12	3	318.62	2.02	0.058	0.442
			+ biotic	+ DC	-155.18	3	318.74	2.13	0.055	0.497
eco	+ geo			+ DC	-154.31	4	319.19	2.59	0.044	0.541
eco		+ abiotic			-155.63	3	319.64	3.04	0.035	0.575
eco		+ abiotic		+ DC	-154.59	4	319.76	3.15	0.033	0.608
		abiotic			-156.79	2	319.81	3.21	0.032	0.640
	geo				-156.82	2	319.86	3.25	0.031	0.671
eco	+ geo				-155.78	3	319.93	3.33	0.030	0.701
	geo		+ biotic	+ DC	-154.73	4	320.04	3.44	0.028	0.730
	geo	+ abiotic		+ DC	-154.76	4	320.09	3.48	0.028	0.758
			biotic		-156.94	2	320.10	3.50	0.028	0.785
eco			+ biotic	+ DC	-154.77	4	320.11	3.50	0.028	0.813
eco			+ biotic		-156.01	3	320.40	3.79	0.024	0.837
		abiotic	+ biotic	+ DC	-155.12	4	320.81	4.21	0.019	0.856
eco	+ geo	+ abiotic		+ DC	-154.16	5	321.12	4.51	0.017	0.873
eco	+ geo		+ biotic	+ DC	-154.21	5	321.22	4.62	0.016	0.889
eco	+ geo	+ abiotic			-155.35	4	321.28	4.67	0.015	0.904
	geo	+ abiotic			-156.63	3	321.65	5.04	0.013	0.917
	geo		+ biotic		-156.69	3	321.75	5.14	0.012	0.929
eco	+ geo		+ biotic		-155.59	4	321.75	5.15	0.012	0.941
eco		+ abiotic	+ biotic		-155.61	4	321.79	5.19	0.012	0.953
		abiotic	+ biotic		-156.77	3	321.91	5.31	0.011	0.964
eco		+ abiotic	+ biotic	+ DC	-154.59	5	321.98	5.38	0.011	0.975
	geo	+ abiotic	+ biotic	+ DC	-154.71	5	322.23	5.63	0.010	0.984
eco	+ geo	+ abiotic	+ biotic	+ DC	-154.10	6	323.28	6.67	0.006	0.990
eco	+ geo	+ abiotic	+ biotic		-155.26	5	323.33	6.73	0.005	0.995
	geo	+ abiotic	+ biotic		-156.56	4	323.69	7.09	0.005	1.000

\*Variables included in models are all composites variables calculated using Principle Components Analysis (PCA) of several closely related variables except 'DC'. *eco* (intrinsic ecological aspects of species): median body size, reproductive capacity and degree of diet specialization, *geo* (intrinsic geographic aspects of species): geographic range size and location of center of the range, *abiotic* (extrinsic non-living features of the site): climate, elevation, habitat type and location of trapping site, *biotic* (extrinsic living features of the trapping site): abundance and diversity of competitors. DC: Distance between center of species geographic range locations and the survey location.

Table 4. AICc model comparison for the subset of *Perognathus* species (N = 67)

Variables included in model*						$\log(L)$	$K$	$AIC_c$	$\Delta_i AIC_c$	$w_i$	$cum. w$		
Intrinsic		Extrinsic											
eco	geo	+	biotic	+	DC	-93.94	2	194.25	0.00	0.118	0.118		
						-94.31	2	195.01	0.75	0.081	0.199		
						-94.33	2	195.04	0.78	0.080	0.278		
						-93.26	3	195.16	0.90	0.075	0.353		
						-94.43	2	195.25	0.99	0.072	0.425		
eco	geo	+	abiotic	+	DC	-94.55	2	195.49	1.24	0.064	0.489		
						-93.64	3	195.92	1.66	0.051	0.540		
						biotic	+	-93.85	3	196.34	2.08	0.042	0.581
						biotic	+	-93.94	3	196.52	2.26	0.038	0.619
						biotic	+	-92.81	4	196.61	2.35	0.036	0.656
eco	+	geo	+	+	DC	-94.11	3	196.87	2.62	0.032	0.688		
						-94.16	3	196.97	2.72	0.030	0.718		
						-94.17	3	196.99	2.74	0.030	0.748		
						abiotic	+	-94.30	3	197.25	2.99	0.026	0.774
						abiotic	+	-93.15	4	197.28	3.02	0.026	0.800
eco	+	geo	+	abiotic	+	-94.33	3	197.30	3.05	0.026	0.826		
						abiotic	+	-93.25	4	197.48	3.23	0.023	0.849
						abiotic	+	-94.43	3	197.50	3.25	0.023	0.873
						biotic	+	-93.61	4	198.21	3.95	0.016	0.889
						biotic	+	-93.63	4	198.24	3.99	0.016	0.905
eco	+	geo	+	abiotic	+	-93.84	4	198.67	4.42	0.013	0.918		
						+	-93.96	4	198.90	4.64	0.012	0.929	
						+	-92.76	5	198.92	4.67	0.011	0.941	
						+	-92.79	5	198.98	4.72	0.011	0.952	
						+	-94.11	4	199.20	4.95	0.010	0.962	
eco	+	geo	+	abiotic	+	-94.16	4	199.31	5.05	0.009	0.971		
						+	-94.17	4	199.33	5.07	0.009	0.981	
						+	-93.14	5	199.68	5.43	0.008	0.988	
						+	-93.61	5	200.62	6.36	0.005	0.993	
						+	-93.96	5	201.31	7.06	0.003	0.997	
eco	+	geo	+	abiotic	+	-92.74	6	201.38	7.13	0.003	1.000		

Table 5. AICc model comparison for the subset of *Peromyscus* species (N = 266)

Variables included in model*						$\log(L)$	$K$	$AIC_c$	$\Delta_i AIC_c$	$w_i$	$cum. w$
Intrinsic		Extrinsic									
	geo	+	abiotic		+ DC	-239.04	4	488.31	0.00	0.423	0.423
eco	+	geo	+	abiotic	+ DC	-238.34	5	489.01	0.69	0.299	0.722
	geo	+	abiotic	+	biotic	+ DC	5	490.12	1.81	0.171	0.893
eco	+	geo	+	abiotic	+	biotic	+ DC	6	491.09	2.77	0.999
eco			+	abiotic	+ DC	-245.48	4	501.19	12.88	0.001	0.999
eco			+	abiotic	+	biotic	+ DC	5	502.68	14.37	1.000
eco	+	geo	+	abiotic		-246.88	4	504.00	15.68	0.000	1.000
eco	+	geo	+	abiotic	+	biotic		5	505.35	17.04	1.000
				abiotic	+ DC	-249.97	3	508.09	19.78	0.000	1.000
				abiotic	+	biotic	+ DC	4	510.13	21.82	1.000
	geo	+	abiotic			-253.68	3	515.51	27.19	0.000	1.000
				abiotic		-254.87	2	515.82	27.51	0.000	1.000
	geo	+	abiotic	+	biotic	-253.68	4	517.58	29.27	0.000	1.000
eco			+	abiotic		-254.81	3	517.77	29.45	0.000	1.000
				abiotic	+	biotic		3	517.85	29.53	1.000
eco			+	abiotic	+	biotic		4	519.77	31.46	1.000
					biotic	-375.24	2	756.57	268.26	0.000	1.000
	geo			+	biotic	-375.07	3	758.30	269.98	0.000	1.000
					biotic	+ DC	3	758.30	269.99	0.000	1.000
eco				+	biotic	-375.24	3	758.63	270.32	0.000	1.000
	geo			+	biotic	+ DC	4	758.92	270.61	0.000	1.000
eco	+	geo		+	biotic	-374.40	4	759.03	270.72	0.000	1.000
	geo					-376.64	2	759.36	271.05	0.000	1.000
	geo				+ DC	-375.75	3	759.66	271.34	0.000	1.000
					DC	-376.78	2	759.66	271.34	0.000	1.000
eco						-376.88	2	759.85	271.53	0.000	1.000
eco			+	biotic	+ DC	-374.89	4	760.01	271.69	0.000	1.000
eco					+ DC	-376.15	3	760.45	272.14	0.000	1.000
eco	+	geo		+	biotic	+ DC	5	760.66	272.35	0.000	1.000
eco	+	geo				-376.38	3	760.92	272.60	0.000	1.000
eco	+	geo			+ DC	-375.75	4	761.73	273.42	0.000	1.000

\*Variables included in models are all composite variables calculated using Principle Components Analysis (PCA) of several closely related variables except 'DC'. *eco* (intrinsic ecological aspects of species): median body size, reproductive capacity and degree of diet specialization, *geo* (intrinsic geographic aspects of species): geographic range size and location of center of the range, *abiotic* (extrinsic non-living features of the site): climate, elevation, habitat type and location of trapping site, *biotic* (extrinsic living features of the trapping site): abundance and diversity of competitors. DC: Distance between center of species geographic range locations and the survey location.

Table 6. Model-averaged regression coefficients and unconditional standard errors for each of the five variables. Coefficients were averaged from the AICc model comparisons of the full (all species) dataset and the four genera subsets (*Dipodomys*, *Neotoma*, *Perognathus* and *Peromyscus*).

Dataset	Model-Averaged Regression Coefficient (Standard Error)				
	Intrinsic		Extrinsic		DC
	eco	geo	abiotic	biotic	
Full	0.116 (0.042)	0.020 (0.046)	-0.054 (0.034)	0.024 (0.034)	0.069 (0.041)
<i>Dipodomys</i>	-0.271 (0.097)	0.104 (0.100)	-0.110 (0.094)	-0.258 (0.094)	0.035 (0.121)
<i>Neotoma</i>	0.114 (0.101)	0.081 (0.097)	0.055 (0.010)	0.027 (0.098)	-0.172 (0.096)
<i>Perognathus</i>	0.090 (0.127)	-0.117 (0.141)	-0.004 (0.126)	-0.165 (0.137)	-0.071 (0.129)
<i>Peromyscus</i>	-0.105 (0.093)	0.255 (0.071)	0.809 (0.037)	0.015 (0.040)	0.250 (0.054)



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