

Phylogenetic structure illuminates the mechanistic role of environmental heterogeneity in community organization

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Summary

1. Diversity begets diversity. Numerous published positive correlations between environmental heterogeneity and species diversity indicate ubiquity of this phenomenon. Nonetheless, most assessments of this relationship are phenomenological and provide little insight into the mechanism whereby such positive association results.
2. Two unresolved issues could better illuminate the mechanistic basis to diversity begets diversity. First, as environmental heterogeneity increases, both productivity and the species richness that contributes to that productivity often increase in a correlated fashion thus obscuring the primary driver. Second, it is unclear how species are added to communities as diversity increases and whether additions are trait based.
3. We examined these issues based on 31 rodent communities in the central Mojave Desert. At each site, we estimated rodent species richness and characterized environmental heterogeneity from the perspectives of standing primary productivity and number of seed resources. We further examined the phylogenetic structure of communities by estimating the mean phylogenetic distance (MPD) among species and by comparing empirical phylogenetic distances to those based on random assembly from a regional species pool.
4. The relationship between rodent species diversity and environmental heterogeneity was positive and significant. Moreover, diversity of resources accounted for more unique variation than did total productivity, suggesting that variety and not total amount of resource was the driver of increased rodent diversity. Relationships between environmental heterogeneity and phylogenetic distance were negative and significant; species were significantly phylogenetically over-dispersed in communities of low environmental heterogeneity and became more clumped as environmental heterogeneity increased.
5. Results suggest that species diversity increases with environmental heterogeneity because a wider variety of resources allow greater species packing within communities.

Key-words: diversity begets diversity, environmental heterogeneity, interspecific competition, phylogenetic diversity, rodent community, spatial analysis

Introduction

One of the most fundamental paradigms in ecology is a simple one: increased environmental heterogeneity promotes species richness (Hutchinson 1959). In a seminal publication, MacArthur & MacArthur (1961) were the first to quantify

the relationship between environmental heterogeneity and species diversity. They examined 13 different temperate forest communities in which foliage height diversity and bird species diversity were simultaneously measured and found that few bird species coexisted in simple environments, whereas more species coexisted in more complex environments. Such a relationship between environmental heterogeneity and consumer diversity is ubiquitous across the contemporary biota and appears to be robust to how environmental heterogeneity or consumer diversity is actually quantified (Tews *et al.* 2004).

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At least two distinct mechanisms potentially give rise to the relationship between environmental heterogeneity and species diversity. Both are based on energetic considerations of the distribution of resources and are related to how resources are added along diversity gradients. Often, as environmental heterogeneity increases, so does the amount (productivity) of resource (Waide *et al.* 1999). Thus, for consumers of such resources, effects of increases in productivity as well as number of resources are difficult to disentangle. Fortunately, such correlations between richness and productivity are typically only moderate (Mittelbach *et al.* 2001), and such variation can be used to determine which type of increase (i.e. amount or kinds) determines species richness of consumers. For example, that variety of resources accounts for variation over and beyond that of amount of resources (productivity) would implicate variety as playing a more important role than productivity in increasing species richness.

In addition to understanding what aspect of environmental heterogeneity drives increases in species richness, few studies have attempted to identify the actual mechanism responsible for this common relationship. One possibility is that species packing facilitates increases in diversity (MacArthur 1972). In particular, increases in resources should allow more subdivision and lead to increase in species richness of consumers. To this end, if energetic consequences of increases in environmental heterogeneity underlie increases in diversity, consumers should be more ecologically similar in communities of greater environmental heterogeneity.

One limitation to the test of such a mechanistic hypothesis is that the concept of ecological similarity is based on the Hutchinsonian niche (Hutchinson 1959) and thus hard to quantify with precision. Although an important heuristic tool for understanding the multifaceted nature of the ecology of organisms, the *n*-dimensionality of the Hutchinsonian niche is too open-ended for practical application because it is very difficult to know whether enough characteristics have been measured to adequately estimate the niche of a species or even whether the important characteristics of the niche have been measured at all (Paine 2010; Ricklefs 2010). One solution making estimation of niche differences more operational may be use of indirect measures of overall ecological similarity of species such as those based on phylogeny. Because sister taxa evolutionarily emanate from a common ancestor, they are expected to share many ecological characteristics, a phenomenon referred to as phylogenetic signal (Losos 2008) or phylogenetic niche conservatism (Harvey & Pagel 1991; Peterson 2011; Wiens *et al.* 2010; but see Losos 2008 for a clarification of terms). Often, phylogenetic proximity reflects ecological similarity, and thus, phylogenetic distance can provide a general surrogate measure of expected multidimensional ecological similarity among related species (Webb *et al.* 2002). For example, while morphological information may quite accurately estimate resource use (Ricklefs & Travis 1980; Winemiller 1991; Stevens & Willig 1999), phylogenetic information may provide an even more general estimate of the ecological niche because many other

ecologically important characteristics such as those related to morphology, behaviour and physiology are related to phylogeny as well (Harvey & Pagel 1991).

Herein, we examine the relationship between environmental heterogeneity and species richness of rodent communities in the Mojave Desert. In particular, we determine the relative contributions of resource productivity and resource variety in accounting for variation in species richness. Lastly, we examine the patterns of species packing based on the phylogenetic diversity of communities to illuminate how species richness increases owing to increases in environmental heterogeneity.

MATERIALS AND METHODS

Rodent species composition and environmental characteristics were determined in 31 communities distributed throughout the Mojave National Preserve (MNP, Fig. 1). The MNP comprises approximately 0.6 million hectares and is located roughly 80 km southwest of Las Vegas in San Bernardino County, California. Communities from eight of the most extensive macrohabitats were sampled: creosote bajada (seven sites), Joshua tree woodland (five), blackbrush woodland (four), Mojave yucca woodland (six), piñon-juniper woodland (three), lava bed (two), sand dune (two) and alkaline playa (two). Number of sites per macrohabitat was proportional to spatial extent of the particular macrohabitat in the study system. Moreover, because of heterogeneous and interdigitated macrohabitats, most sites' nearest neighbours were from different macrohabitat types, thus minimizing spatial autocorrelation of environmental characteristics of communities. Sites were selected so that sampling characterized a homogenous area. Specifically, sites were located away from roads (> 100 m) or washes that might introduce extraneous forms of heterogeneity. Sampling was conducted between September and November 2005. For each community, rodent species composition was sampled using paired 500-m transects. Sherman live traps were placed every 5 m for a total of 101 traps on each transect and 202 traps sampling each community each night. Sampling was conducted for three nights at each site, and animals were marked and released every morning. We used the number of species per site (species richness) as an estimate of rodent diversity. More details regarding rodent sampling can be found in Stevens & Tello (2009).

Vegetative features were used to characterize environmental heterogeneity of each community based on eight additional transects running perpendicular on each of the paired mammal transects. Vegetation transects were evenly spaced on each of the mammal transects and were located at the 0, 167, 333 and 500 m marks. These transects were 2 m wide and 25 m long. Species, length, width and height of each perennial plant occurring within this transect were determined to estimate the relative standing biomass of each species.

Rodents are predominantly primary consumers in these habitats, and thus, the vegetative component of the environment contributes greatly to resources available to them (Brown & Harney 1993). We measured two aspects of environmental heterogeneity based on the perennial flora: (i) species richness that estimates the relative number of different seed resources available and (ii) total plant volume that estimates the relative amount of standing plant biomass or productivity (Cox *et al.* 2006) as well as total amount of resource available to consumers.

We constructed a phylogeny for all nocturnal rodents whose geographic distribution overlapped the Mojave Desert as determined by contemporary distribution maps (Patterson *et al.* 2005).

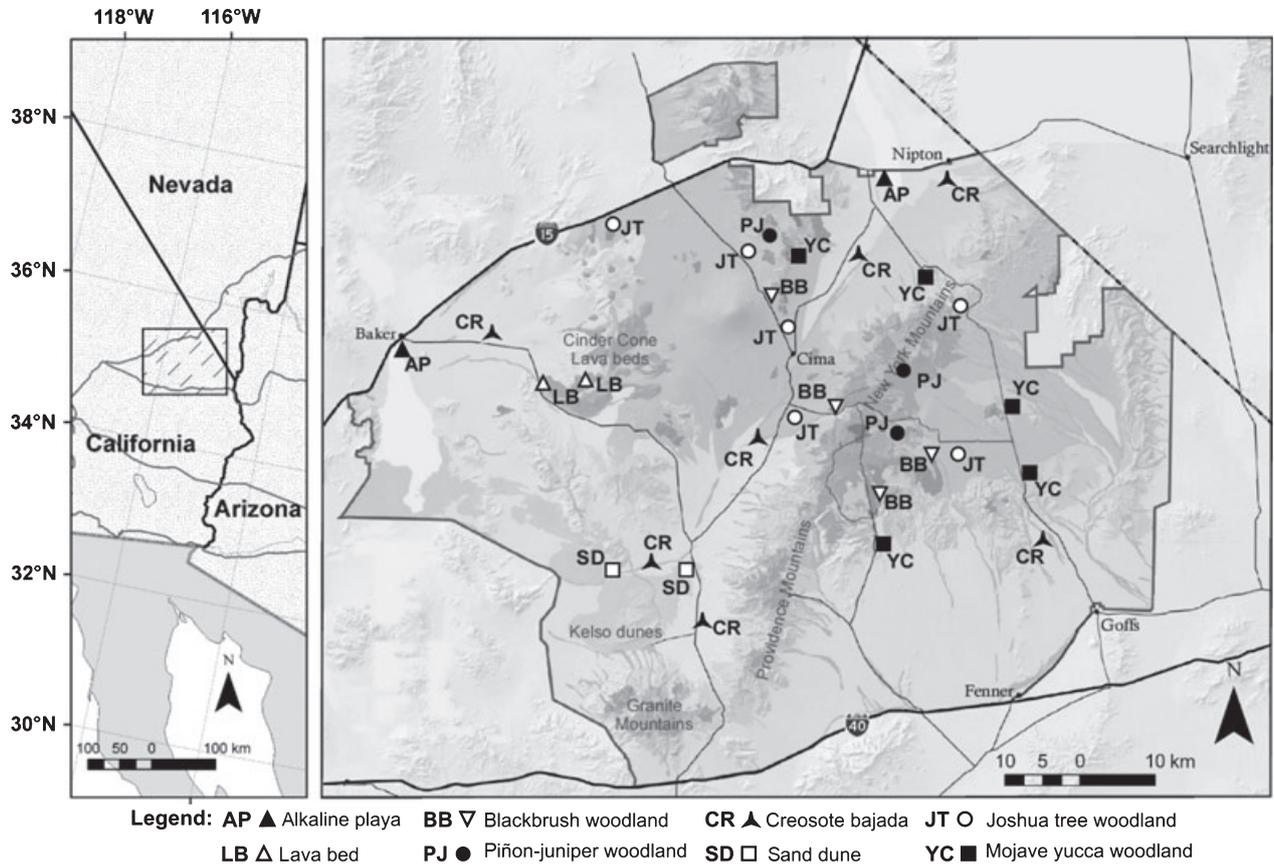


Fig. 1. Map of the Mojave National Preserve demonstrating sampled communities. Acronyms are as follows: AP, alkaline playa; BB, blackbrush woodland; CR, creosote bajada; JT, Joshua tree woodland; LB, lava bed; PJ, piñon-juniper woodland; SD, sand dune; YC, Mojave yucca woodland.

Mitochondrial cytochrome *b* sequences for each observed taxon were obtained from GenBank (Appendix S1, Supporting Information). Sequences were aligned using Muscle (Edgar 2004), and the resulting alignment was analysed using a hierarchical likelihood ratio test via Modeltest v3.7 (Posada & Crandall 1998) to determine the most appropriate model of evolution. Maximum-likelihood (ML) genetic distances were calculated based on a General Time Reversible (GTR) model with gamma-distributed rate heterogeneity ($\Gamma = 0.578$) and per cent invariable sites (I) equal to 0.4327 using PAUP* (Swofford 2002). PAUP* was also used to infer a ML tree from the data with 1000 bootstrap replicates (Fig. 2). We used an additive as opposed to an ultrametric tree. While commonly used, ultrametric trees treat all members within a clade as the same when calculating the time of divergence from taxa across clades. Nonetheless, additive trees account for evolutionary differences within clades when making between clade calculations of phylogenetic distance.

To estimate the degree of ecological similarity and hence the amount of species packing within communities, we determined the mean phylogenetic distance (MPD, Webb 2000) among all species within a community. MPD ranges from 0 to infinity whereby small values represent communities composed of species that are closely related, whereas large values represent communities with species that are distantly related. Given a positive relationship between resource diversity and species diversity, decreases in MPD with increases in resource diversity indicate species packing.

We also determined how different from random expectation values of MPD were by comparing them to distributions of MPD based on randomly assembled communities. Such a comparison can elucidate

which communities are more over-dispersed or under-dispersed than expected by chance and those that do not differ from a random assemblage of rodents. For our null model, we randomized the species by site incidence matrix. We did so using the Gotelli Swap Algorithm (Gotelli 2000) that randomly rearranges occurrences in the matrix (i.e. those species of Mojave Desert rodents encountered by our effort and their observed distribution across sites) but doing so based on the constraint that species richness and incidence of species across sites remain the same. This particular algorithm has good statistical properties, in particular maintaining type-1 error rates. This is true in general as demonstrated by Gotelli (2000) as well as for MPD in particular as demonstrated by Hardy (2008). We determined *P*-values by comparing the magnitude of the actual measure of MPD to a distribution of 1000 MPDs based on random assembly and used standardized effect sizes generated from each null distribution as variables in quantitative analyses. Each *P*-value and standardized effect size was based on a unique null distribution determined for a particular community. Standardized effect sizes (SES-MPD) for each community were calculated by subtracting the mean of the distribution of simulated MPDs from the observed value of MPD and then dividing this difference by the standard deviation of the distribution of simulated MPDs. SES-MPD ranges from negative to positive infinity whereby negative values represent under-dispersion (communities composed of species that are more related than that based on a null model) and positive values represent over-dispersion (communities composed of species that are less related than that based on a null model). Use of SES-MPD has a number of advantages. First, because values of MPD are standardized relative to the distribution of

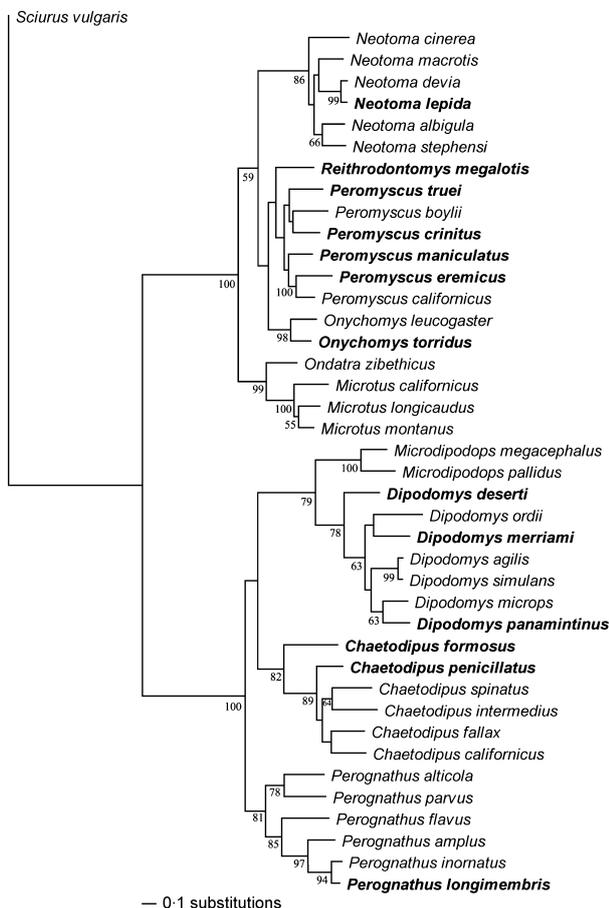


Fig. 2. Maximum-likelihood tree summarizing phylogenetic relationships of all nocturnal rodents occurring in the Mojave Desert. Species encountered across the Mojave National Preserve by our sampling efforts are indicated by bold print. Numbers above branches refer to the amount of bootstrap support for the node to the right.

expected MPDs, SES-MPD provides a comparable, relative measure of how significant (i.e. nonrandom) a particular community is in terms of phylogenetic structure. Perhaps more important is the fact that in some cases, the magnitude of MPD can be strongly related to the magnitude of species richness (Anderson, Shaw & Olff 2011), especially when communities range from a subset of a phylogeny to the entire phylogeny in terms of species composition (not a characteristic of these data). Use of SES-MPD ameliorates this problem. Null model results and the calculations of MPD and SES-MPD were performed using the package Picante (Kembel *et al.* 2010) in the statistical software R (R Development Core Team 2008).

We used permutation based analysis of variance (ANOVA, Sokal & Rohlf 1995) to evaluate significant differences among macrohabitats in terms of SES-MPD. Macrohabitat affiliation was permuted and F-statistics recalculated. This was repeated 1000 times to generate a distribution of permuted F-statistics. A *P*-value was calculated based on the position of the empirical F-statistics relative to the distribution of permuted statistics. ANOVA was followed by a Hochberg GT2 *a posteriori* mean separation test (Hochberg 1974) to determine location of significant differences among macrohabitats. To evaluate whether overall, sites within a particular macrohabitat exhibited significant phylogenetic structure, we conducted Fisher's tests of combined probabilities (Sokal & Rohlf 1995) on output (*P*-values) from null models.

We determined simultaneous autoregressive models (SAR, Haining 1990; Cressie 1993) for relationships among rodent diversity and resource heterogeneity, and these were conducted in Spatial Analysis in Macroecology, version 3 (Rangel, Diniz-Filho & Bini 2006). SARs determine the relationship between dependent and independent variables similarly as with ordinary least squares multiple regression but are different in that they include an extra term that incorporates spatial structure of data. In particular, when residuals are strongly spatially structured, this analysis decomposes residuals into variation that is spatially structured and that which is pure error (Kissling & Carl 2007). In our case, both dependent variables of rodent diversity (rodent richness, MPD or SES-MPD) and independent variables of environmental heterogeneity (perennial species richness, total perennial volume) are potentially spatially structured across this metacommunity. Accordingly, to maintain type-1 error at 5%, modelling of spatial structure was incorporated into both sets of variables.

We conducted three regressions. The first evaluated whether species richness of rodents was significantly related to environmental heterogeneity. This was followed by a regression on MPD to evaluate whether systematic changes in species packing were related to environmental heterogeneity. We conducted a third regression on standardized effect sizes to evaluate whether the degree of significant species packing as compared to a null model changed systematically along this environmental heterogeneity gradient as well. To maintain experiment-wise error rate at $\alpha = 0.05$, we deemed regressions significant only if *P*-values were smaller than that determined by a false discovery rate (FDR) procedure (Ventura, Paciorek & Risby 2004).

Results

We conducted 18 756 trap nights of effort to sample 31 rodent communities that generated 6541 individual captures from 13 species. Species were quite variable across sites with communities on average possessing six species of rodents (range = 2–9 species). Additionally, species of rodents occurred in an average of 15 different communities (range = 2–30 sites). At these same sites, we sampled 81 species of perennial shrubs with each community possessing on average 16 perennial species and each perennial species occurring on an average of six sites.

Regression analysis indicated a positive relationship between environmental heterogeneity and rodent species richness (Table 1). Environmental heterogeneity accounted for 26% of the variation among sites regarding species richness. Only for perennial species richness was the partial regression coefficient significant, indicating that variety of resources as measured by perennial species richness is more related to rodent diversity than is productivity.

Forty species of nocturnal rodents occur in the Mojave Desert. Relationships among and within the major lineages are well reconstructed by our phylogeny (Fig. 2). The largest break separates the Heteromyidae from the Cricetidae. Within these families, major groups can be distinguished as well. For example, large genera such as *Dipodomys*, *Chaetodipus*, *Perognathus*, *Peromyscus* and *Neotoma* are all distinguishable and monophyletic. Overall MPD for all species of nocturnal rodents in the Mojave Desert was 0.226, whereas MPD for the 13 species captured at the MNP was 0.220.

Table 1. Results of applying simultaneous autoregressive models to characterize relationships between aspects of environmental heterogeneity and diversity of rodents in the Mojave Desert

Dependent variable	Independent variable	Student's <i>t</i>	<i>P</i>	<i>R</i> ² entire model	<i>P</i> entire model
Rodent richness	VegRich	3.04	0.005	0.264	0.014
	VegVol	-0.48	0.631		
Mean phylogenetic distance	VegRich	-2.72	0.011	0.250	0.018
	VegVol	0.38	0.710		
SES-MPD	VegRich	-3.21	0.003	0.304	0.006
	VegVol	0.61	0.548		

SES-MPD refers to the standard effect size of mean phylogenetic distance based on null model simulations. Student's *t* refers to magnitude of the test statistic characterizing the difference of the observed slope from one of zero. All three regressions were significant after comparison with a critical region defined by the FDR procedure (Ventura, Paciorek & Risby 2004).

Substantial variation existed in MPD across communities as well as in the degree of nonrandomness of these distances (Appendix S2, Supporting Information). In general, communities ran the entire gamut of degrees of phylogenetic structure: two sites approached significant phylogenetic under-dispersion, two sites exhibited significant phylogenetic over-dispersion and 25 sites exhibited phylogenetic structure that did not differ from random expectations. Fisher's test of combined probabilities indicated that environmentally simple systems such as dune and creosote sites exhibited significant phylogenetic over-dispersion overall ($P = 0.0001$ and $P = 0.0009$, respectively) and heterogeneous sites such as Joshua tree woodlands exhibited significant phylogenetic under-dispersion overall ($P = 0.0406$) even after maintaining experiment-wise error rate at $\alpha = 0.05$ based on the FDR procedure. Indeed, degree of phylogenetic structuring as indicated by standardized effect sizes (SES-MPD) is strongly related to macrohabitat affiliation of sites (permutation based ANOVA, $F_{7,23} = 5.57$, $P < 0.001$). *A posteriori* tests indicated that the biggest difference was between phylogenetically under-dispersed piñon-juniper and Joshua tree woodlands and phylogenetically over-dispersed creosote bajada and sand dune habitats (Fig. 3).

Absolute (MPD) and relative (SES-MPD) measures of MPD were negative and significant functions of environmental heterogeneity with again perennial species richness accounting for significant unique variation (Fig. 4), whereas productivity did not (Table 1). We found no significant regression between MPD and species richness ($r^2 = 0.062$, $P = 0.178$), suggesting that associations of species richness and MPD with environmental heterogeneity are two independent outcomes of the same diversifying mechanism. Moreover, independent characteristics of species richness and MPD describing community organization exhibit complementary gradients coincident with environmental heterogeneity that indicate that as diversity increases, species are packed more tightly into more species-rich communities.

Discussion

Understanding the mechanistic basis of origin and maintenance of biodiversity is a central challenge to biogeographers, conservation biologists and ecologists alike. That diversity

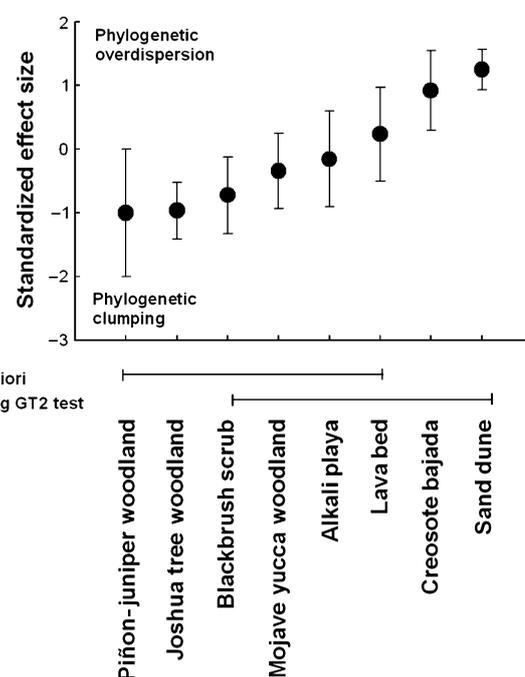


Fig. 3. Means and 95% confidence intervals of standardized effect sizes for communities in each macrohabitat sampled in the Mojave National Preserve. Horizontal bars below x-axis indicate groups of macrohabitats that are not statistically different from each other.

begets diversity is a foundational paradigm in ecology. Nonetheless, few direct tests of particular mechanisms underlying such a pattern have been conducted despite the ubiquity of the positive relationships between species diversity and environmental heterogeneity. Complicating matters are the dual nature of mechanistic effects of increases in environmental heterogeneity. Additions of greater amounts of the same resources or additions of different types of resources could both generate diversity gradients. Indeed, in the Mojave Desert, diversity of rodent consumers increases as number of resources within communities increases. Moreover, such increases in rodent richness are facilitated by packing more ecologically similar species into more diverse communities.

Environmental heterogeneity captured by perennial species richness is multifaceted over and beyond the complementary aspects of productivity and diversity of

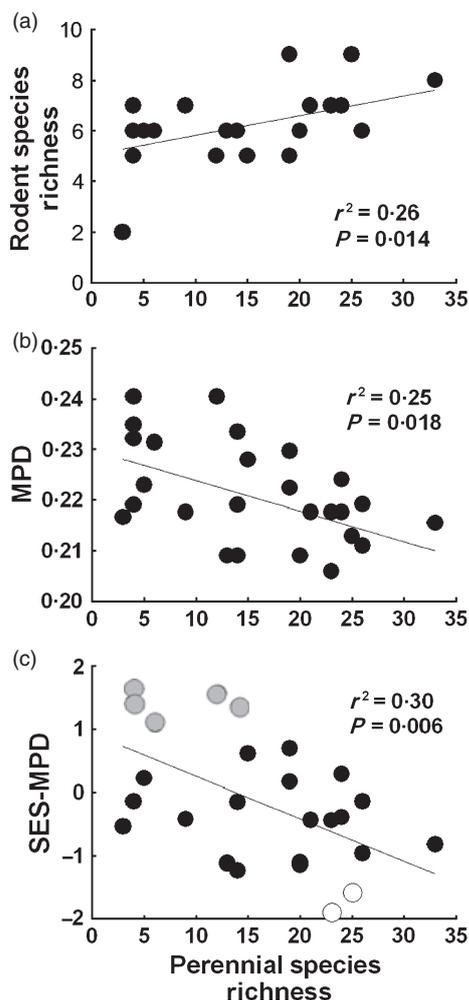


Fig. 4. Scatter plots describing relationships between perennial species richness and (a) rodent species richness, (b) mean phylogenetic diversity and (c) the standard effect size of mean phylogenetic diversity. Regression lines indicate statistically significant relationships. (c) Grey dots correspond to communities that tended towards phylogenetic over-dispersion, white dots correspond to communities that tended towards phylogenetic under-dispersion and black dots correspond to communities that do not differ from a random collection of species taken from the metacommunity in terms of phylogenetic dispersion.

resources because it also coincides with variation in both the physical structure of the environment provided by plants as well as the amount and variety of seed types provided to these predominantly seed-eating rodents. Results presented here extend prior conclusions regarding relative roles of structural and resource diversity in determining community organization (Stevens & Tello 2011). Heterogeneity can increase species diversity in two very different ways. First, increases in heterogeneity of structural aspects of the environment could allow more physical spaces for species to exploit the same resource thereby enhancing coexistence (MacArthur & MacArthur 1961). Of similar effect, greater heterogeneity in food resources can increase the number of niches and enhance diversity. In this rodent metacommunity, resource characteristics accounted for much more of the variation in rodent

diversity than did structural characteristics (measured as diversity of substrate sizes and variability of physical structure provided by plants, Stevens & Tello 2011). Moreover, once correlated effects were accounted for, only resource diversity accounted for significant variation in rodent diversity. Here, we find that resource diversity is not only related to numbers of species but also related to species packing whereby more similar species are packed more tightly into communities with greater numbers of perennial species. Such congruence supports the notion that spatial variation in community organization across this metacommunity is strongly resource mediated.

Additional insights are evident regarding the basic structure of communities based on phylogenetic approaches used here. For example, from a phylogenetic perspective, the structure of Mojave Desert rodent communities runs the entire gamut of significance. Although most sites exhibit structure not differing phylogenetically from a random collection of the same number of species, some sites tended towards being phylogenetically clumped and some are significantly phylogenetically over-dispersed. Although significant spatial variation in degree of phylogenetic structure was detected from our comparative analysis, a notable pattern was the paucity of communities that actually exhibit significant over-dispersion. Typically, rodent communities are viewed as strongly deterministically structured systems that are a hallmark of competition theory (Brown & Harney 1993; Stevens & Willig 2000; Ernest *et al.* 2008). Historically, most work has demonstrated that North American deserts possess rodent communities of low diversity that are over-dispersed based on body size (Brown 1973; Brown & Kurzius 1987). These studies do represent primarily simple systems with few rodent species (1–9) and sites with such potentially low resource diversity as dunes and creosote bajadas. Our results indicate that the degree of phylogenetic structure is dependent on habitat type. While dune and creosote dominated systems have considerable spatial extent in North America, other systems dominated by other flora have appreciable spatial extents as well. For example, Joshua tree woodlands (64 750 km², Hickman 1993), black brush (30 000 km², Pendleton & Meyer 2004) and piñon-juniper woodlands (240 000 km², Miller & Wigand 1994) have large geographic extents in North American arid lands. Thus, perhaps the typical state across North American arid lands is not of over-dispersion, and this particular community state may be more the exception than the rule given that the degrees of structure in terms of over-dispersion may be habitat specific as demonstrated here. Indeed, over-dispersion varying in a habitat-specific way places a premium on understanding what determines the strength of interactions, how spatially variable community phylogenetic structure is and what is the particular context that gives rise to significant over-dispersion.

The recent surge of use of phylogenetic approaches in ecology has transformed understanding of community organization (Cavender-Bares *et al.* 2009; Kembel 2009), primarily because these approaches allow examination of

not only the proximate but also the ultimate determinants of community structure. Typically, phylogenetic approaches have been used to address questions of how species composition differs among communities or to partition variation because of contemporary ecology from that owing to historical processes (Losos 1994; Losos *et al.* 2003; Elias *et al.* 2008). Furthermore, phylogenetic tools are proving to be potentially more powerful than more traditional approaches to better understand the patterns of coexistence that characterize variation in community structure. Traditional approaches of estimating similarity based on ecological characteristics such as diet, activity, morphology and habitat, to name only a few, potentially underestimate ecological similarity of species. Nonetheless, because much of the ecological niche is phylogenetically conserved (Harvey & Pagel 1991), estimates of similarity based on phylogeny may be much more comprehensive. Indeed, for desert rodents, phylogenetic similarity associates numerous aspects of the ecological niche (Riddle, Hafner & Alexander 2000; Alexander & Riddle 2005). Use of phylogenetic distance as a measure of the ecological similarity of species agrees with other studies demonstrating that differences among species are an important characteristic of community assembly (Kelt *et al.* 1996, Goheen *et al.* 2005; Thibault, Ernest & Brown 2010). Moreover, distribution of interspecific differences indicates that increased environmental heterogeneity allows more similar species to be added to communities along a diversity gradient. Indeed, the mechanism whereby diversity begets diversity at least in this particular system is by decreases in MPD (increase in ecological similarity) as resource diversity and species richness increase. This particular result represents a single snapshot in both space and time for a single but important taxonomic group. Future work examining the consistency of these results across extensive spatial, temporal and evolutionary extents will greatly illuminate the generality of this particular mechanism of coexistence in natural communities.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Taxa and accession number from GenBank of specimens used to construct phylogeny of Mojave Desert nocturnal rodents.

Appendix S2. Species richness, average phylogenetic distance and *P*-value from null model analysis for each of 31 communities distributed throughout the Mojave National Preserve.

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