Journal of Mammalogy, 92(2):387–395, 2011

Diversity begets diversity: relative roles of structural and resource heterogeneity in determining rodent community structure

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Environmental heterogeneity is an important determinant of the diversity of natural communities. Effects of heterogeneity can emanate from complementary effects of resource heterogeneity (variation in the number of resources) and structural heterogeneity (variation in the physical structure of the environment). We examined relative effects of structural and resource heterogeneity on the diversity of 31 desert rodent communities in the Mojave Desert. Both structural and resource heterogeneity significantly accounted for rodent species diversity. Nonetheless, when unique and shared effects were examined, only resource heterogeneity exhibited a significant unique effect, accounting for more variation than structural heterogeneity in diversity of rodent communities. When compared with results of previous studies the possibility emerges that effects of either structural or resource heterogeneity might be context dependent and determined by the taxon of focus and relative variation of these two forms of heterogeneity. Accordingly, future studies should distinguish between these two important forms of environmental heterogeneity to improve understanding of their relative impacts on diversity.

Key words: community structure, desert rodent community, habitat heterogeneity, species diversity, structural diversity

DOI: 10.1644/10-MAMM-A-117.1

One of the most fundamental paradigms in ecology is that increased environmental heterogeneity increases the diversity of local communities (Hutchinson 1959; MacArthur 1972; Rosenzweig 1995; Tilman 1986). Increased environmental heterogeneity allows a greater number of ecological niches and thus coexistence of a greater diversity of taxa. This idea was formalized first by MacArthur and MacArthur (1961) to explain patterns of diversity of birds in coniferous and deciduous forests of North America. Similar results implicating the importance of environmental heterogeneity to species diversity have been described in numerous systems (Tews et al. 2004). Despite its wide acceptance, it is less appreciated that more than one mechanism underlies the effects of environmental heterogeneity on diversity.

As originally described, structural heterogeneity was the driving mechanism. Namely, increased foliage height diversity within forests allowed more physical spaces for species to forage, and species were able to subdivide the forest vertically and more were able to coexist (MacArthur and MacArthur 1961). Thus, spatial heterogeneity can allow organisms to subdivide a limiting food resource, leading to the coexistence of greater numbers of species. The positive relationship between structural heterogeneity and species diversity is ubiquitous. It has been documented empirically in systems ranging from terrestrial forests to coral reefs (Gratwicke and Speight 2005), kelp forests (Christie et al. 2007), and soils (Sessitsch et al. 2001).

Another formulation of the heterogeneity–diversity paradigm, however, has highlighted the importance of energy resources, in particular those involving food or nutrients and their variety (MacArthur and Levins 1964; Siemann 1998; Tilman 1986). This formulation is based on an implication of the competitive exclusion principle (Gause 1934) that the number of coexisting species is determined by the number of limiting resources; thus, a greater variety of resources promotes higher diversity. Support for the resource heterogeneity formulation is also strong and frequent (Elmberg et al. 1994; Hovemeyer 1999; Murdoch et al. 1972; Ribas et al. 2003; Siemann 1998).

Despite their similarity, these two formulations are fundamentally distinct, and differences warrant specific consideration when attempting to understand how heterogeneity enhances diversity. The structural heterogeneity formulation involves environmental variation, specifically the physical characteristics of the environment. A greater variety of spaces allows species to specialize on those different spaces and subdivide a common resource. In contrast, the resource heterogeneity formulation explicitly involves variation in the number of resources, which allows the coexistence of more specialists. To this end, two distinct mechanisms potentially drive increases in diversity along heterogeneity gradients.

These two mechanisms are not necessarily mutually exclusive. For example, when prey species respond to the same change in structural heterogeneity as their predators, increases in structural heterogeneity will correspond to like changes in resource heterogeneity for the predator. Similarly, in many systems, diversity of primary producers increases with the structural diversity of edaphic characteristics (Newbery and Proctor 1984, Sollins 1998). Accordingly, consumers respond to increases in both plant diversity (Ganzhorn et al. 1997; Murdoch et al. 1972) and structural diversity of edaphic characteristics (Davis et al. 2008, Shenbrot et al. 1994). In this context an interesting question is what are the relative degrees to which structural and resource heterogeneity affect consumer diversity? If structural heterogeneity is the underlying diversifying mechanism, its effects should be detectable over and beyond that shared with resource heterogeneity, and vice versa. Correlated effects of resource and structural heterogeneity should be accounted for before any one mechanism is implicated as a determinant of species diversity. We examined the effects of environmental heterogeneity on the diversity of Mojave Desert rodent communities and determined the relative degrees to which structural and resource heterogeneity contribute to this diversity.

Materials and Methods

We sampled 31 communities from 8 of the most extensive macrohabitats within the Mojave National Preserve, San Bernardino County, California (35°09′N, 115°23′W): creosote bajada (7 sites), Joshua tree woodland (5), blackbrush scrub (4), Mojave yucca woodland (6), piñon-juniper woodland (3), lava bed (2), sand dune (2), and alkali playa (2). Sampling was conducted between September and November 2005 when all species were active. We sampled rodent species composition using paired 500-m transects separated from each other by approximately 100 m. A Sherman live trap (model number LFAHD; H.B. Sherman Traps, Inc., Tallahassee, Florida) was placed every 5 m for a total of 202 traps sampling each community. Sampling was conducted for 3 nights, and animals were marked and released each morning. Rodent abundance data were based only on unique individuals caught during the 3 nights. All communities received identical sampling effort (606 trap nights). Details regarding sampling, variation among sites in species composition, and habitat affinities of species can be found in Stevens and Tello (2009). We followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007) when handling rodents. To estimate rodent diversity we used species richness, Shannon diversity index (Pielou 1969), Berger–Parker dominance index (Berger and Parker 1970), and Camargo evenness index (Camargo 1993).

Sampling of vegetative characteristics of each community was based on 8 additional transects running perpendicular to each of the mammal transects. Pairs of vegetation transects were spaced evenly 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, maximum length, maximum width, and maximum height of each perennial plant occurring within this transect was determined to estimate the relative volume of each species. Total volume of each plant species at each site was estimated as the sum of the volumes of all individuals of that species.

Soil microprofile was characterized on the basis of 10 samples evenly spaced along the mammal transects. The samples consisted of 1 dm^3 of soil material. Each sample was manually sieved and separated by particle size into 9 categories: <1.4 mm, 1.4 to <3.18 mm, 3.18 to <4.75 mm, 4.75 to <6.3 mm, 6.3 to <12.5 mm, 12.5 to <25 mm, 25 to <50 mm, 50 to <120 mm, and >120 mm. Each portion was weighed, and its percentage in relation to the total sample weight was calculated. Each site was characterized by the mean of each soil category across the 10 samples.

We measured two suites of variables to estimate structural and resource heterogeneity on the basis of edaphic and floral characteristics of communities. The structural role of edaphic characteristics is straightforward. Heterogeneous, rocky habitats are structurally more complex and provide more physical spaces in which to concentrate foraging activities and evade predators. Moreover, substrate particle size affects foraging efficiency of desert rodents (Price and Waser 1985; Wasserberg et al. 2005) and their ability to construct and maintain burrows (Luna et al. 2002; Romanach et al. 2005). Increases in edaphic heterogeneity provide more spaces or substrates for species to specialize their activities. The same 4 diversity measures described above for rodents were calculated on data representing the proportional representation of soil in 9 different soil classes. These diversity measures describe how heterogeneous the substrate is and hence the structural diversity of the habitat.

The role of floral characteristics is less straightforward, however, because the floral component contributes to both structural heterogeneity and resource heterogeneity. To estimate aspects of vegetative complexity that also contribute to structural diversity we estimated the standard deviation of volumes of perennial plant species and the total volume of all species occurring at each site. Standard deviation of volumes estimates how variable the floral component is in terms of the sizes of its constituents. A large *SD* indicates the presence of both large- and small-stature perennials and thus a structurally diverse habitat. A small *SD* indicates only small- or only large-stature perennials and thus a more uniform habitat. Total volume estimates how much of the floral component occurs in a particular habitat. Structural diversity historically has been measured variously (Tews et al. 2004). Nonetheless, because characteristics we measured were estimated within the same area (i.e., the same area of vegetation transects was measured across all communities), variation in other characteristics of structural diversity, such as the amount of bare ground or foliage height diversity, are captured by our metrics.

Although animal material, in particular insects and other arthropods, are represented in the diets of many desert rodents, the primary energy resources for many desert rodents are the seed component of plants. Moreover, all rodent species addressed herein consume seeds to some degree, if not exclusively. Despite much of seed productivity in desert systems being in the form of annuals, seeds generated by both annual and perennial species represent different contributions to the diets of desert rodents (Reichman 1975). Evidence exists that in our system large perennial seeds are preferred. Price and Joyner (1997) described significant differences in seed distribution between the seed bank and seed traps. The primary difference involved an underrepresentation of large-seeded species in the seed bank, which were absent because of seed predation by rodents. Seventy-five percent of these missing species were perennials, reflecting the energetic importance of desert shrubs and perennial herbs to these vertebrate consumers. Such a difference between seed rain and the seed bank resulting from foraging by consumers compromises the use of seed samples from the seed bank to estimate available resources. This is because what remains in the seed bank is likely what is not consumed by rodents. Nonetheless, advances in our understanding of reproductive allometry suggest that measures of plant size offer a robust estimate of seed production in many species (Niklas 1993; Niklas and Enquist 2003). Seed production is proportional to size of perennial plants (Hendriks and Mulder 2008; Shipley and Dion 1992), even for taxa found in this Mojave Desert system (Cleary et al. 2008; Petersen and Ueckert 2005). Thus, plant size can be used to estimate available resources. To measure resource heterogeneity we estimated the 4 diversity measures described above that describe richness, diversity, dominance, and evenness of perennial species. These were calculated using the volumes of all perennial plant species recorded at a site. Because rodent species in this system are primarily granivorous, these measures estimate how variable sites are in the kinds of resources that are available for consumers.

To characterize pairwise assessments of association between forms of environmental diversity and rodent diversity we calculated Pearson product-moment correlation coefficients (Sokal and Rohlf 1995). These simple correlation analyses were intended to be illustrative, and thus we did not adjust α to diminish experimentwise error rate. We did, however, correct for inflation of degrees of freedom due to spatial autocorrelation by basing significance levels on geographically effective degrees of freedom (Dutilleul 1993) in spatial analysis for macroecology (Rangel et al. 2006). Because rodent diversity, structural heterogeneity, and resource heterogeneity are multivariate data sets, we relied on multivariate analyses to make statistical inference as to the significance of relationships among variables. We used redundancy analyses (Legendre and Legendre 1998) to estimate relationships between rodent diversity and structural heterogeneity and resource heterogeneity separately.

Variation in structural and resource heterogeneity likely are correlated, especially considering that the floral component contributes to both aspects of heterogeneity. To determine shared and unique effects of these two types of heterogeneity on rodent diversity we partitioned variation in rodent diversity according to the procedures defined in Peres-Neto et al. (2006). Significance of partitions was based on permutation. Accounting for spatial autocorrelation is not as straightforward as in aforementioned univariate correlation analyses. Accordingly, we conducted both spatially explicit and nonspatially explicit variation decomposition. For spatially explicit analyses we included geographic coordinates of sites as a third component of variance in the variation decomposition so as to account for spatial and nonspatial contributions of resource and structural diversity to variation in rodent diversity. If variation accounted for by resource or structural diversity is significant, even after accounting for spatial relationships of sites the possibility that spatial autocorrelation affects inference can be eliminated.

Results

On the basis of 18,786 trap nights of effort, we captured 5,641 individual nocturnal rodents from 13 species (Table 1). Species were not distributed uniformly across communities or macrohabitats. The fewest species occurred at playa sites whereas the Joshua tree woodland and black brush macrohabitats possessed the greatest species richness. Much variation among species characterized their incidence across the 31 communities. *Reithrodontomys megalotis* occurred across only about 6% of sites, whereas *Dipodomys merriami* occurred across almost all (97%) sites.

Rodent diversity, resource heterogeneity, and structural heterogeneity exhibit numerous and varying significant correlations (Fig. 1). In particular, three important patterns emerge from these relationships. First, rodent species diversity is related strongly to resource heterogeneity. This relationship is not limited to only richness but also measures sensitive to equitability of items. Second, structural heterogeneity is not related strongly to rodent diversity. Last, resource heterogeneity and structural heterogeneity exhibited numerous significant associations.

Resource heterogeneity accounted for approximately 41% of the variation in rodent diversity. Rodent diversity and resource diversity varied in similar directions along canonical axes (Fig. 2a). Specifically, as richness of perennial species increased, so did richness of rodent species. Diversity and

Table 1.—Environmental characteristics and presence/absence of nocturnal rodents distributed across 8 macrohabitats in the Mojave Desert. Occurrence within a macrohabitat is denoted with •. Incidence represents proportion of 31 communities sampled in which a species was captured.

	Playa	Blackbrush	Creosote	Joshua tree	Lava	Piñyon-Juniper	Dune	Yucca	Incidence
Number of sites	2	4	7	5	2	3	2	6	
Mean rodent species richness	4	7.3	6	7	5.5	6.3	6.5	6.3	
Mean perennial species richess	4	19.5	7.6	20.6	14.5	25	5	21.3	
Mean diversity of soil types	0.48	1.32	1.3	1.18	1.83	1.73	0.03	1.16	
Conspicuous structural component	*Atriplex confertifolia*	*Coleogyne ramosissima*	*Larrea tridentata*	*Yucca brevifolia*	Volcanic rock	*Juniperus osteosperma*	*Hilaria rigida*	*Yucca shidigera*	
Rodent species									
Chaetodipus formosus		•	•	•	•	•	•	•	0.45
C. penicillatus	•		•				•		0.13
Dipodomys deserti	•						•		0.10
D. merriami	•	•	•	•	•	•	•	•	0.97
D. panamintinus		•	•	•		•		•	0.61
Neotoma lepida	•	•	•	•	•	•	•	•	0.97
Onychomys torridus	•	•	•	•	•	•	•	•	0.84
Perognathus longimembris	•	•	•	•			•	•	0.52
Peromyscus crinitus		•			•				0.10
P. eremicus		•	•	•	•	•		•	0.68
P. maniculatus	•	•	•	•		•		•	0.71
P. truei		•		•		•			0.16
Reithrodontomys megalotis				•		•			0.06

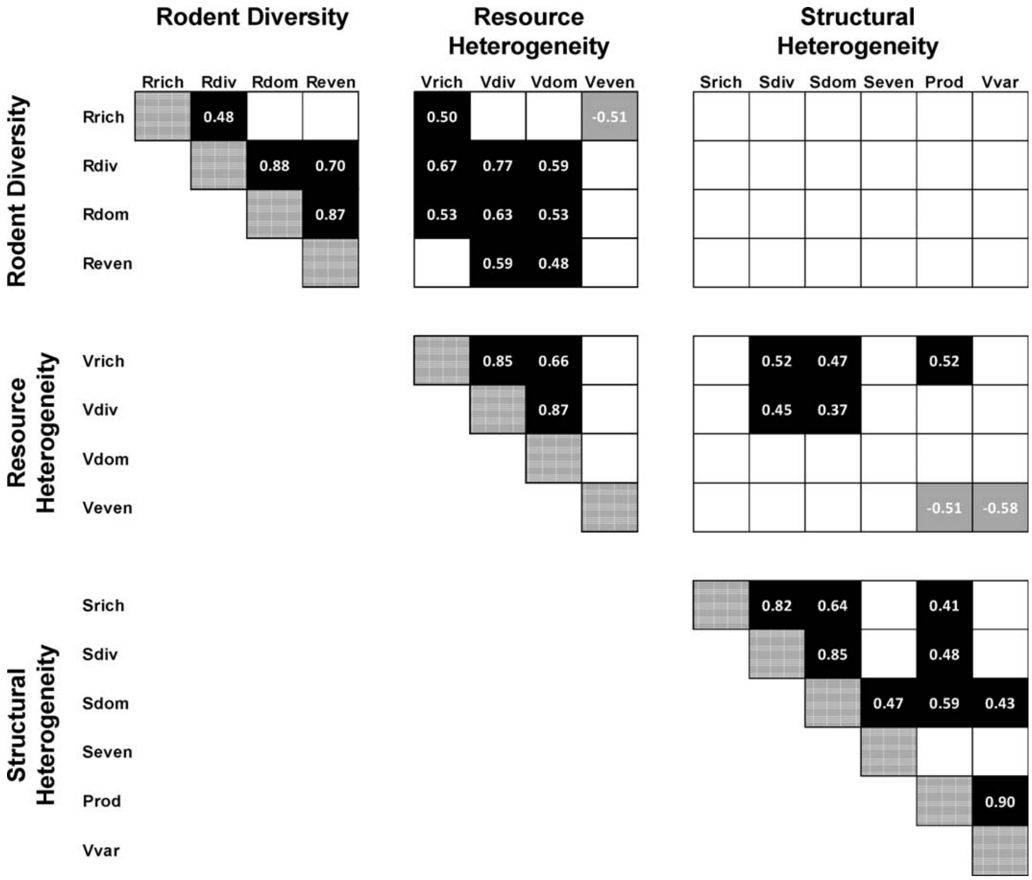
dominance of rodents and perennial species also were positively related. Although evenness of perennial volumes tended to vary orthogonally to most aspects of rodent species diversity, it was associated strongly and negatively with rodent species richness.

Structural heterogeneity accounted for 20% of the variation in rodent diversity. The first canonical axis was most related to the magnitude of diversity and dominance of soil and rodent characteristics, whereas the second canonical axis reflected richness and evenness of these characteristics (Fig 2b). Specifically, high values on the second canonical axis corresponded to high evenness and low richness of soil characteristics and high richness and low evenness of rodent species, whereas low values on this axis corresponded to high richness and low evenness of soil characteristics and low richness and high evenness of rodent species. Total perennial volume was related positively to diversity and dominance of rodent species, whereas the standard deviation of perennial volumes was related positively to rodent species richness.

When analyzed together (Table 2), resource and structural heterogeneity accounted for very different amounts of unique variation in rodent species diversity. Unique variation related to resource heterogeneity was significant, whereas unique variation related to structural heterogeneity was nonsignificant. This was true in both spatially and nonspatially explicit analyses. In both spatially and nonspatially explicit analyses, correlated variation (i.e., that accounted for jointly by all variable suites in the analysis) accounted for between 15.78% and 18.66% of variation in taxonomic diversity of rodents. Variation explained by structural heterogeneity primarily represents a shared effect with resource heterogeneity. Resource heterogeneity is related independently and positively to rodent species diversity, whereas structural heterogeneity is not.

Discussion

As with several other studies on a variety of taxa (Tews et al. 2004), our results indicate that environmental heterogeneity is an important determinant of species diversity of communities. Increases in environmental heterogeneity translate into increases in species diversity. Nonetheless, the distinction made here between two very different types of heterogeneity indicates that this effect is not generic. Resource heterogeneity accounts for more variation in rodent diversity than does structural heterogeneity. Structural and resource heterogeneity differentially affect species diversity, and this distinction can improve our understanding of underlying mechanisms. Our study reflects only a single snapshot in time, and rodent populations and ultimately the communities they form are highly variable both within and among years (Brown and Heske 1990; Brown and Zeng 1989). Future study should examine more long-term patterns to evaluate variability in the strength of the relationship between environmental heterogeneity and rodent species diversity and variation in the relative contributions of structural and resource heterogeneity to such patterns.



	Rrich	Rdiv	Rdom	Reven	Vrich	Vdiv	Vdom	Veven	Srich	Sdiv	Sdom	Seven	Prod	Vvar
Rrich	▨	0.48			0.50			-0.51						
Rdiv		▨	0.88	0.70	0.67	0.77	0.59							
Rdom			▨	0.87	0.53	0.63	0.53							
Reven				▨		0.59	0.48							
Vrich					▨	0.85	0.66			0.52	0.47		0.52	
Vdiv						▨	0.87			0.45	0.37			
Vdom							▨							
Veven								▨					-0.51	-0.58
Srich									▨	0.82	0.64		0.41	
Sdiv										▨	0.85		0.48	
Sdom											▨	0.47	0.59	0.43
Seven												▨		
Prod													▨	0.90
Vvar														▨

FIG. 1.—Correlogram describing univariate associations of rodent species diversity, resource heterogeneity, and structural heterogeneity. Rrich, Rdiv, Rdom, and Reven correspond to rodent species richness, diversity, dominance, and evenness, respectively. Vrich, Vdiv, Vdom, and Veven correspond to resource richness, diversity, dominance, and evenness, respectively. Srich, Sdiv, Sdom, Seven, Prod, and Vvar correspond to structural richness, structural diversity, structural dominance, structural evenness, total perennial volume, and standard deviation of perennial biomasses, respectively. Black cells correspond to significantly positive associations, gray cells to significantly negative correlations, and white cells to no significant correlation on the basis of $\alpha = 0.05$.

For mammalian communities in particular, environmental heterogeneity often is implicated as a diversifying mechanism (Rosenzweig and Winakur 1969). Nonetheless, results are not consistent (Tews et al. 2004), and this could be due in part to whether resource or structural heterogeneity was used in analyses. Often investigators use characteristics that confound resource and structural heterogeneity. For example, the seminal investigation of this question for mammals demonstrated that structural diversity was related strongly and positively to desert rodent diversity (Rosenzweig and Winakur 1969). This study measured structural diversity using a composite variable representing amount of vegetation and soil characteristics. This caused Bond et al. (1980) to question conclusions of Rosenzweig and Winakur (1969) because of the difficult interpretation underlying such composite variables. In particular, patterns described by Rosenzweig and Winakur (1969) were influenced strongly by the floral component and not the soil component of this index. If a strong component of floral heterogeneity represents variation in the number of plant species, such a metric potentially could confound both structural and resource heterogeneity. Often when the importance of structural diversity is implicated, it might be more a reflection of the effects of resource heterogeneity rather than structural heterogeneity. When true structural diversity has been measured it often fails to account for species richness in rodent systems. For example, when structural characteristics such as canopy height, canopy density, and tree diameter at breast height are used to predict the diversity of tropical rodent communities, no significant relationships emerge (August 1983; Williams and Marsh 1998). Such patterns are consistent in systems of both tall stature (August 1983; Williams and Marsh 1998) and low stature (Bond et al. 1980) and mirror those in this Mojave Desert rodent system.

Resource and structural heterogeneity commonly can be confounded in nature. For example, the relationship between environmental heterogeneity and animal diversity has been examined frequently in successional systems (Frauke et al. 2002; Horvath et al. 2001; Sullivan et al. 2000). In these studies structural heterogeneity and animal species diversity typically vary together and peak at mid-successional stages. Nevertheless, such temporal patterns also likely correspond to a similar pattern of plant species richness, which often peaks at mid-succesional stages with subsequent decreases due to

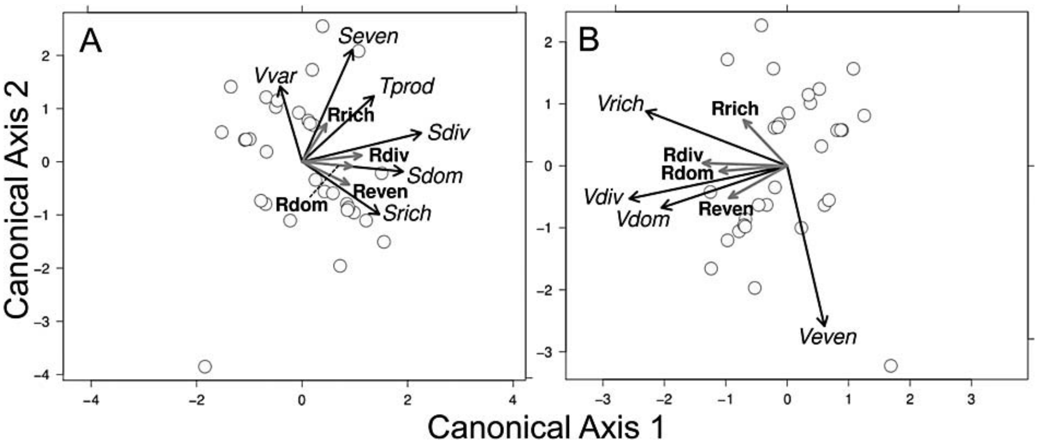


Fig. 2.—Independent redundancy analyses between rodent diversity and A) resource heterogeneity and B) structural heterogeneity. Circles represent the position of particular communities in the 2-dimensional space represented by derived axes. Arrows represent the importance of particular variables in defining a particular axis. Acronyms follow those in Fig. 1.

inhibition by dominant late-succession competitors. In these situations it remains unclear whether changes in resources or structure are driving patterns of consumer diversity. A similar problem occurs when patterns are examined at broad spatial extents, as has been done commonly in macroecological studies. Patterns can result at least partially from changes in numerous confounding factors along extensive environmental gradients (Jetz et al. 2009). Moreover, environmental heterogeneity often is characterized by crude measures, such as number of habitats or elevational relief, and strong positive relationships exist with animal species richness (Atauri and de Lucio 2001; Fox and Fox 2000; Kerr and Packer 1997). However, such metrics undoubtedly mirror variation in plant species richness, in particular beta diversity among sampling units, and thus likely reflect variation more in resource heterogeneity than in structural heterogeneity.

In our analyses structural heterogeneity did not account for a significant amount of unique variation in rodent diversity. Even so, the interaction term was large, indicating that correlated variation between structural and resource heterogeneity accounted for substantive variation in rodent diversity. Such an outcome could result from confounded variation because vegetation characteristics are aspects of both structural and resource heterogeneity, or this could result from an indirect effect of structural diversity acting through its effect on resource diversity. Correlations between soil characteristics and perennial diversity are strong and positive. The primary role of structural diversity could be to act indirectly on the diversity of consumers by enhancing plant species diversity and thus increasing resource heterogeneity. To this end, the most important effect of structural diversity could be indirect through its effects on resource heterogeneity.

Another explanation for the lack of a unique effect of structural diversity on species diversity here and in several other systems could simply be a lack of structural diversity in general. Deserts are structurally simple systems. The Mojave Desert is the least productive of the American deserts (MacMahon 1979) and could be considered structurally simple. Moreover, in many desert systems rodent movements are typically 2-dimensional despite measurable 3-dimensional structure. Few desert rodent species take advantage of vertical structure beyond obtaining shelter from predators (Kotler and Brown 1988). It is possible that resource heterogeneity is a more important diversifying mechanism in structurally simple systems because more diversity exists in resources to facilitate specialization.

In contrast, structural heterogeneity can be a more important diversifying mechanism in structurally diverse systems, especially for taxa that forage in 3 dimensions (Pianka 1967). The best support for structural diversity acting as a diversifying mechanism comes from birds, especially those living in coniferous and deciduous forest systems. On the basis

Table 2.—Results from variation-partitioning analyses. Total variation refers to variation explained by a particular variable suite, not accounting for variation shared with the other 2 variable suites. Unique variation refers to variation explained by a particular variable suite after removing variation shared with other variable suites. Nonspatially explicit analyses did not account for spatial structure among sites, whereas spatially explicit analyses did.

			Nonspatially explicit		Spatially explicit	
Variable suite	Total variation	Total *P*	Unique variation	Unique *P*	Unique variation	Unique *P*
Resource heterogeneity	0.41	0.005	0.22	0.017	0.22	0.022
Structural heterogeneity	0.20	0.017	0.01	0.360	<0.01	0.530
Spatial structure	0.02	0.22			<0.01	0.790

of a recent review by Tews et al. (2004), 24 of the 28 (86%) studies finding a positive relationship between bird diversity and environmental heterogeneity were conducted in systems containing forest. Moreover, 20 (71%) of these studies were in temperate systems of low tree species richness such as coniferous, deciduous, or riparian forests that are dominated by a few tree taxa. This suggests that the greatest amount of diversity might be represented by structure and not resources.

Community structure is complex, in part because it often is determined by numerous influences reflecting both biotic and abiotic processes and contemporary and historical mechanisms. For example, rodent community structure often is determined by competitive interactions (Brown and Harney 1993; Stevens and Willig 2000), and this varies biogeographically (Kelt et al. 1996). In addition, in this same type of system predation has been demonstrated to mediate competitive interactions and enhance coexistence (Brown et al. 1994). In addition, processes such as dispersal have received much attention recently because of the large impact it can have on regional metacommunities (Ernest et al. 2008; Holyoak et al. 2005, Stevens et al. 2007). Multiple determinants of structure likely decrease the influence of any one process. We have identified environmental heterogeneity as one of those important processes. Structural and resource heterogeneity represent 2 complementary mechanisms driving patterns of species diversity, but the relative effects of these 2 different types of heterogeneity might be taxon and system specific, depending on the dimensionality of foraging by consumers and relative variation in structure and resources found in an area. Future studies should distinguish between the type of heterogeneity examined so that a richer understanding of the relative effects of structural and resource heterogeneity on diversity can emerge. Also, much variation in species diversity across our study system remains unexplained. Effects of other biotic processes such as competition, and abiotic influences such as primary gradients of precipitation and temperature on diversity, should be examined, in particular to evaluate the degree to which they potentially modulate effects due to environmental heterogeneity.

Acknowledgments

This research was funded by grants from the National Science Foundation (DEB-0535939) and the Louisiana Board of Regents (LEQSF-2006-09). A. Gates provided invaluable field assistance. We also thank the National Park Service, especially D. Hughson, for permission to work in the Mojave National Preserve and for logistical support. We thank J. Andre and R. Fulton for verifying plant identifications.

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Submitted 8 April 2010. Accepted 30 September 2010.

Associate Editor was Victor Sánchez-Cordero.