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## Do desert rodents form metacommunities?

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Numerous model systems have informed classical ideas of the deterministic structure of natural communities. Although a number of important insights have been gained from desert rodents, little is known regarding the relative role of local environmental and spatial processes that embody the emerging metacommunity paradigm in structuring these model systems. We compared patterns of community composition based on environmental characteristics and estimates of spatial isolation by distance to test predictions characterizing contemporary models of metacommunity structure. Analyses were based on rodent community structure at 31 sites within the Mojave Desert. Consistent with previous studies of rodent communities, local environmental characteristics accounted for a significant amount of variation in community structure. Nonetheless, spatial isolation by distance contributed significantly to structure as well, even after accounting for the shared effect between environmental and spatial descriptors. Indeed, regional collections of rodent communities represent metacommunities and a metacommunity perspective promises to complement much that has been learned from primarily local perspectives. Examination of data suggested that the mass effects model of metacommunity structure may best describe regional patterns of species composition, at least for this data set. Moreover, 2 further important insights emerge from analyses. First, important life-history differences among taxa translate into different spatial effects that are likely due to dispersal abilities. Second, despite the spatially uncorrelated nature of environmental variation across our sampling array much of the structure of this metacommunity could be attributed to the shared effects of spatial and environmental characteristics. Typically, empirical analyses of metacommunity structure have attributed this variation to spatial structure generated by environmental spatial autocorrelation, but our analyses suggested that this component of variation may to some degree represent a unique yet underappreciated spatial effect. Moreover, this substantive component of variation suggests that prior analyses of empirical metacommunity structure provide conservative estimates of regional spatial effects and that the role of dispersal in determining metacommunity structure may be greater than is commonly considered.

**Key words:** community ecology, desert rodent community, dispersal, metacommunity, Mojave Desert, variance decomposition

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Understanding the relative effects of local and regional processes on community organization represents a current paradigm in ecological research (Hugueny et al. 2007; Shurin and Allen 2001). Local processes, such as environmental conditions and biotic interactions, have long been used to explain variation in diversity and species composition of communities. More recently, however, consideration of the role of regional spatial processes, such as dispersal, has revolutionized thinking on community organization (Holoak et al. 2005). Although the metacommunity concept of dispersal-mediated variation in species composition of local communities is still in its infancy, it has contributed much to our understanding of community organization. For example,

elevated dispersal can increase alpha diversity and decrease beta diversity within metacommunities (Mouquet and Loreau 2002). Moreover, dispersal can provide sufficient influx of individuals to maintain populations in suboptimal habitats and promote coexistence (i.e., mass effects—Mouquet and Loreau 2002, 2003; Pulliam 1988). Alternatively, dispersal limitation can produce spatial structure of species composition even in the absence of environmental gradients (Hubbell 2001; Rangel and



Diniz-Filho 2005). Although much has been learned from both theoretical and experimental perspectives, empirical surveys of the degree to which metacommunity phenomena actually affect local species composition are relatively few and have focused on a limited subset of the current biota (Cottenie 2005). In particular, few studies have examined vertebrates (Ernest et al. 2008; Guélat et al. 2008; López-González et al. 2012; Manier and Arnold 2006; Meynard and Quinn 2008; Parris 2006; Presley et al. 2009; Presley and Willig 2010; Richter-Boix et al. 2007; Stevens et al. 2007; Werner et al. 2007) despite the prominent role they have played in forming many ideas underlying community ecology over the last century.

Desert rodent communities represent a quintessential system for understanding effects of local biotic interactions and environmental conditions on local diversity. Desert rodents represent ideal model systems because they are abundant and easily sampled, they are quite diverse in terms of species richness and life history, and they play important ecosystem roles because they are abundant consumers (Brown 1973). Much has been learned in terms of effects of environmental variation (Brown 1973, 1975; Kotler and Brown 1988; Krasnov et al. 1996; Rogovin et al. 1994; Rosenzweig and Winakur 1969; Shenbrot 1992), competitive interactions (Abramsky et al. 1990; Brown 1989; Brown et al. 1979; Goheen et al. 2005; Price 1978), and predation (Kotler et al. 1991; Longland and Price 1991) on community organization from research on desert rodents. Although the vast majority of such studies have utilized reductionist approaches and examined single or a few local communities to better understand particular processes that provide structure (Brown and Harney 1993), few have examined numerous communities at the regional level (Brown 1973; Brown et al. 2000; Brown and Kurzius 1987; Fox and Brown 1993; Hafner 1977; Kelt et al. 1996; Patterson and Brown 1991) and none has assumed a metacommunity perspective for understanding structure of regional enclaves of communities. Examination of numerous communities within a regional setting provides a perspective unique to more-focused experimental approaches and allows opportunity to examine generalities in structure (Brown 1973). Indeed, spatial processes are important to the structure of local communities of a number of taxa (Cottenie 2005); however, such a hypothesis has yet to be extended to many model systems in community ecology, in particular desert rodents.

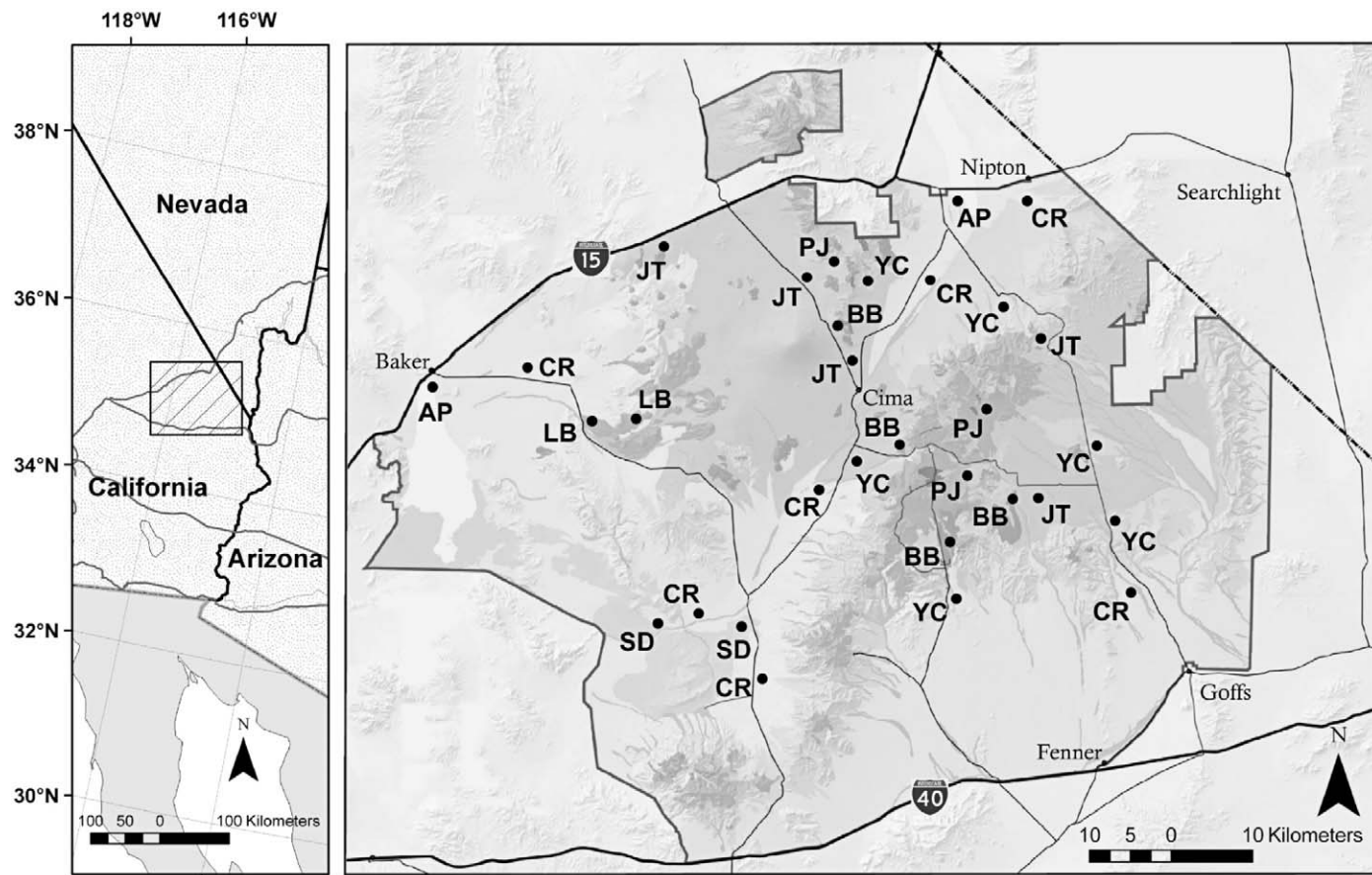
Three phenomena likely contribute to the dearth of metacommunity studies on desert rodents. The 1st is methodological. Simply put, many of the insights from metacommunity approaches are theoretical and such constructs are easier to apply to small-scale mesocosm experiments in which discrete, habitable areas are easily delineated and manipulated. Indeed, analyses of larger-scale, more-continuous landscapes should provide valuable complements to the multitude of metacommunity investigations conducted in more tractable but somewhat contrived study systems. The 2nd reason is the frequently demonstrated strong local control of these simple yet harsh systems (Brown 1973; Brown and Harney 1993) and the resultant assumption that understanding

local processes is sufficient to understand structure of these communities. Third, mammalian communities are spatially expansive and dispersal is often sufficiently cryptic and too far for easy detection. Despite strong local drivers of species composition, rodent communities do not exist in a regional vacuum and dispersal from neighboring communities, especially in heterogeneous regions, may contribute substantively to local species composition.

A number of independent observations suggest that metacommunity processes may be important to the structure of small mammal communities. Guélat et al. (2008) demonstrated that mass effects allowed the rapid recolonization of gardens by shrews of 2 different species. Moreover, species specialized on different habitats but dispersal was sufficiently strong so as to maintain sink populations in unpreferred habitat and facilitate coexistence. Similarly, Ernest et al. (2008) based on a long time series of desert rodent community data suggested that dispersal from the surrounding region facilitated immigration and ultimately recruitment of previously undetected taxa in this system. In particular, species richness remained relatively constant but species went extinct and then were quickly replaced by other taxa repeatedly over a roughly 30-year period. Thus, regional dispersal contributed to species composition and was important in maintenance of diversity. Finally, Milstead et al. (2007) report dispersal from riparian areas (i.e., aguadas) to thornscrub habitats in Chile after substantive precipitation events, indicating that spatial processes integrate different habitats at least under favorable environmental conditions. Taken together, these observations suggest that more spatially extensive studies focusing on numerous communities within heterogeneous regions examined within an explicit metacommunity framework may serve as a valuable springboard to enhance our understanding of not only this valuable model system but also effects of metacommunity processes in general in strongly competitive and climatically harsh environments.

Recently, a number of advances have improved our ability to distinguish communities structured by strong local controls from those determined by broad spatial processes underlying metacommunity dynamics. In particular, there is now a robust conceptual framework for distinguishing among models of metacommunity structure (Leibold et al. 2004), as well as powerful multivariate approaches to distinguish among some of these competing models (Cottenie 2005). Herein we test 2 new predictions regarding desert rodent systems. First, we predict dispersal-mediated metacommunity structure as indicated by significant spatial structure. Second, we predict based on results from other mobile mammalian consumers in heterogeneous environments (Guélat et al. 2008; Milstead et al. 2007) that both local and regional spatial processes influence the structure of a metacommunity of rodents in the Mojave Desert.

Nocturnal desert rodents in North America are primarily composed of members of the Heteromyidae and Cricetidae. These families have very different ecologies, in particular different life-history strategies (Brown 1973). Ecological



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

differences could translate into differences in the relative effects of local and regional processes in determining patterns of species composition. To this end, we make a 3rd prediction that the magnitude and significance of unique and combined environmental and spatial effects will be different for heteromyid and cricetid assemblages.

## MATERIALS AND METHODS

**Sampling.**—Rodent species composition as well as environmental characteristics were estimated in communities distributed throughout the Mojave National Preserve (Fig. 1). Rodent sampling adhered to Louisiana State University Institutional Animal Care and Use Committee protocol 06-033 based on guidelines approved by the American Society of Mammalogists (Sikes et al. 2011). The Mojave National Preserve comprises approximately 0.6 million ha and is located roughly 80 km southwest of Las Vegas in San Bernardino County, California. Thirty-one communities from 8 of the most extensive macrohabitats were sampled: 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). We were interested in whether dispersal-mediated structure may characterize species

composition of rodent communities within this landscape. Thus, number of sites per macrohabitat was proportional to spatial extent of each macrohabitat in the study system. Although this does lead to differences in number of communities sampled from each macrohabitat, it does ensure that rare macrohabitats do not overinfluence and common macrohabitats do not underinfluence our assessment; equal representation across macrohabitats would introduce this bias. Because of heterogeneous and interdigitated macrohabitats, most sites' nearest neighbors were from different macrohabitat types and this minimized 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. Admittedly, this is a short period of time relative to the longer-term temporal dynamics of desert rodent communities. Indeed, a number of systems vary relative to precipitation and productivity and abundances can fluctuate on the scale of a year or more in response to such inputs (Brown and Ernest 2002; Ernest et al. 2000; Shenbrot and Krasnov 2004; Thibault et al. 2004). Our intent here was to demonstrate whether a



metacommunity approach could provide insights in addition to the many that have been gained from single community studies. Moreover, forthcoming manuscripts will explicitly focus on longer-term dynamics and evaluate whether metacommunity structure changes in response to environmental variability across longer time periods than that addressed here.

In each community, rodent species composition was sampled using paired 500 m transects. Sherman live traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) were placed every 5 m for a total of 101 traps on each transect and 202 traps sampling each community. Sampling was conducted for 3 nights and animals were marked with an indelible marker in order to identify recaptures and released every morning. Rodent abundance data were based on the unique number of individuals caught during the 3 nights (i.e., recaptures were not considered in analyses). Rodent abundances were square-root transformed prior to analyses (Legendre and Legendre 1998). More details regarding rodent sampling can be found in Stevens and Tello (2009, 2011) and Stevens et al. (2012).

Currently, it is unclear whether enumeration or statistical estimators provide better approximations of animal density (Hammond and Anthony 2006; Hopkins and Kennedy 2004; McKelvey and Pearson 2001; Nichols 1986; Slade and Blair 2000). Statistical estimators rely on estimations of detection probabilities that require more data than were available here to calculate a robust measure (White and Burnham 1999). We chose the enumeration method of summing the number of unique individuals of a species captured at a particular site as an estimate of its abundance. We did so because in desert rodent systems this is perhaps the most widely used metric of relative abundance. To ensure that this particular estimate of abundance (number of unique individuals) was not driving patterns that we describe, we reran the main analyses underlying this manuscript (variance decomposition, see below) based on 2 other different rodent data sets, each of which characterized less-resolved estimates of abundance: rank abundances, whereby species were ranked at each site based on their abundance; and presence-absence, whereby any species with 1 or more individuals was scored as present and those with no representatives were scored as absent from a particular site. In both of these cases, less-resolved abundance data recapitulated the pattern based on relative abundance. This was true even for the presence-absence data, which suggests that abundance plays a limited role in our results and, thus, even when it was ignored, abundance did not influence the overall conclusions from our analyses.

Environmental characteristics of sites were estimated using volume (length  $\times$  width  $\times$  height) of 81 perennial plant species, representation of soils in 9 microprofile classes, and percent cover of grasses and percent cover of annuals. Sampling of vegetative characteristics of each community was based on a total of 8 additional transects, each 2 m wide and 50 m long, and each running perpendicular to each mammal transect. The positions of these vegetation transects were evenly spaced, located at 0-, 167-, 333-, and 500-m marks along mammal transects. On each transect, length, width, and height of each

perennial plant were determined and summed to estimate aboveground biomass of each species (Cox et al. 2006). A square-root transformation was performed on perennial data so that variances in species with exceedingly large biomass were not the only forms of variance accounted for by analyses (Legendre and Legendre 1998). Within each vegetation transect, we calculated the percent cover of all grasses and all annual plants inside two  $5 \times 2$ -m quadrats set between 15 and 20 m from the center of the vegetation transect. We estimated mean percent values in each quadrat based on independent assessments by 2 observers. Soil microprofile was characterized based on ten 1-dm<sup>3</sup> samples evenly spaced along mammal transects. Each sample was manually sieved and separated based on particle size into 9 categories:  $<1.4$  mm,  $1.4-<3.18$  mm,  $3.18-<4.75$  mm,  $4.75-<6.3$  mm,  $6.3-<12.5$  mm,  $12.5-<25$  mm,  $25-<50$  mm,  $50-<120$  mm, and  $>120$  mm. Each portion was weighed and mean proportional contribution of each particle size class was used for analyses. Principal component analysis based on a covariance matrix was used to reduce the redundancy and hence dimensionality of the perennial and soil microprofile data sets separately. The broken stick method (Jackson 1993) was used to identify principal components that accounted for more variation than would be expected by chance. Details of collection of environmental data and analyses also can be found in Stevens and Tello (2009).

*Effects of environmental characteristics on metacommunity structure.*—To evaluate environmental effects on metacommunity structure, a redundancy analysis was performed whereby perennial principal components, a soil profile principal component, annual percent cover, and grass percent cover were independent variables and rodent abundances at each site were dependent variables. Redundancy analysis selects a combination of independent variables that maximally accounts for variation in dependent variables (Jongman et al. 1995). This analysis also provides amount of variation accounted for by dependent variables and the statistical significance of the result.

*Spatial autocorrelation of environmental characteristics.*—Sites were arranged so as to minimize the relationship between spatial proximity and habitat type. Nonetheless, this does not ensure that spatial autocorrelation of environmental characteristics is not significant. Spatial autocorrelation of environmental characteristics was examined by conducting a redundancy analysis (Jongman et al. 1995) whereby environmental characteristics comprised the dependent matrix and spatial variables (3rd-degree polynomial of  $x$  and  $y$  coordinates, see below) comprised the independent matrix (Legendre and Legendre 1998).

Multivariate correlograms also were used to explore patterns of autocorrelation in rodent species composition and environmental characteristics across space as well as to describe autocorrelation of rodent composition across environmental distances. First, 3 symmetric distance matrices were calculated to separately quantify site-by-site differences in terms of rodent composition, environmental characteristics, and geographic distance. For the rodent dissimilarity matrix, Euclidean distances

were calculated based on abundances. The environmental dissimilarity matrix was based on the original environmental variables (perennial species biomass, soil category weights, and percent cover of grasses and annuals). Because these variables are measured in different units, they were 1st standardized. Then, the environmental dissimilarity matrix was determined using Euclidean distances. Finally, the spatial dissimilarity matrix was calculated as the geographic distance among sites. Three correlograms were produced, one that depicts autocorrelation of rodent composition along spatial distances, a 2nd that depicts a similar spatial autocorrelation for environmental characteristics, and a 3rd that characterizes autocorrelation in rodent composition based on environmental distances. These were multivariate correlograms based on Mantel's test (see Legendre and Legendre [1998] for details). Statistical significance of Mantel's statistic at each distance class was estimated by 1,000 matrix permutations (Legendre and Legendre 1998).

*Estimating spatial effects on metacommunity structure.*—Despite important effects on species composition of local communities, dispersal is difficult to measure for most plant and animal species. One common ecological phenomenon that can be used as a starting point for estimating dispersal is the distance decay of species composition (Soininen et al. 2007). More and more distant sites become more and more different in species composition and this is due to 2 factors, namely environmental characteristics and amount of dispersal. First, because environmental characteristics form gradients, more and more distant sites have more and more different environments and because of niche-based community processes, also possess more and more different species composition. Dispersal also contributes to distance decay of species composition (Soininen et al. 2007). Distance and spatial configuration determine per capita rates of dispersal among sites at short distances and ultimately define the limits of dispersers at long distances. Shurin et al. (2008) made the elegant analogy between such an effect and the “isolation by distance” effect in population genetics. Under a scenario of isolation by distance, sites in close proximity receive relatively more dispersal propagules than sites in distant proximity. As a result of decreased dispersal to more distant sites, increasing genetic differences with distance often is reported (Epperson 2005; Ouborg et al. 1999; Peterson and Denno 1998) and has become a baseline expectation in most population genetic work. “Ecological isolation by distance” (EID) is simply the whole-organism analog of such an effect. EID manifests as more distant sites possessing more disparate species composition, and can be used to estimate dispersal effects, in particular when dispersal is cryptic or occurs at distances beyond those used to characterize species composition of particular communities. For these reasons, EID has become an important estimator of effects of dispersal on metacommunity structure in many studies (Beisner et al. 2006; Brooks et al. 2008; Cottenie 2005; Langenheder and Ragnarsson 2007; McCaughley et al. 2008; Meynard and Quinn 2008; Ng et al. 2009; Stevens et al. 2007; Van der Gucht et al. 2007; Van de Meutter et al. 2007).

It is important to keep in mind when using EID to characterize dispersal that many environmental characteristics form gradients that can exhibit similar spatial signatures. In other words, spatial autocorrelation of environmental conditions can mimic EID and should be accounted for in analyses of metacommunity structure (Cottenie et al. 2003). To this end, demonstration of EID alone is only a weak test of effects of dispersal on metacommunity structure. More-rigorous tests consider effects of dispersal important only when the spatial signature of EID remains after accounting for spatial autocorrelation of environmental characteristics.

Spatial relationships among sites were characterized using all powers of a 3rd-degree polynomial (i.e.,  $x$ ,  $y$ ,  $x^2$ ,  $xy$ ,  $y^2$ ,  $x^3$ ,  $x^2y$ ,  $xy^2$ , and  $y^3$ ) of basic geographic coordinates (Universal Transverse Mercator coordinates) as suggested by Legendre (1989). Such a polynomial characterizes spatial configuration of sites and captures higher-order and nonlinear spatial variation not reflected in basic  $x$  and  $y$  coordinates. Spatial configuration based on this 3rd-degree polynomial was used to estimate EID. To evaluate the degree to which spatial characteristics, and hence EID, accounted for rodent community structure, we conducted a redundancy analysis whereby rodent species composition was the dependent matrix and spatial variables represented the independent matrix.

*Distinguishing unique environmental, spatial, and combined effects.*—Of greatest interest were the relative abilities of both environmental and spatial variables to predict species composition of nocturnal rodent communities. To evaluate this, a suite of full and partial redundancy analyses was used to partition variation in species composition of rodent communities into additive components (Borcard et al. 1992). We were most interested in 3 of these components: a pure environmental component remaining after partialling out that correlated with spatial predictors, a pure spatial component remaining after partialling out that correlated with environmental predictors (EID), and a spatially structured environmental component. We began with 3 matrices of data. The dependent matrix represented species composition of nocturnal rodents at each of the 31 communities. The 9 variables representing the 3rd-degree polynomial of spatial coordinates used to estimate EID constituted the spatial independent matrix. Finally, scores on the 6 perennial principal component axes, scores on the soil principal component axis, grass percent cover, and annual percent cover was used to characterize the environmental independent matrix. Routines written by Peres-Neto et al. (2006) were used to conduct variance partitioning and adjust partitions ( $R^2_{\text{adjusted}}$ ) based on the number of independent variables they incorporated.

## RESULTS

Our sampling of 31 communities from 8 different macrohabitats resulted in 18,786 trap-nights that generated 5,641 unique captures from 13 nocturnal species (Appendix I). *Dipodomys merriami* was by far the most-abundant species,

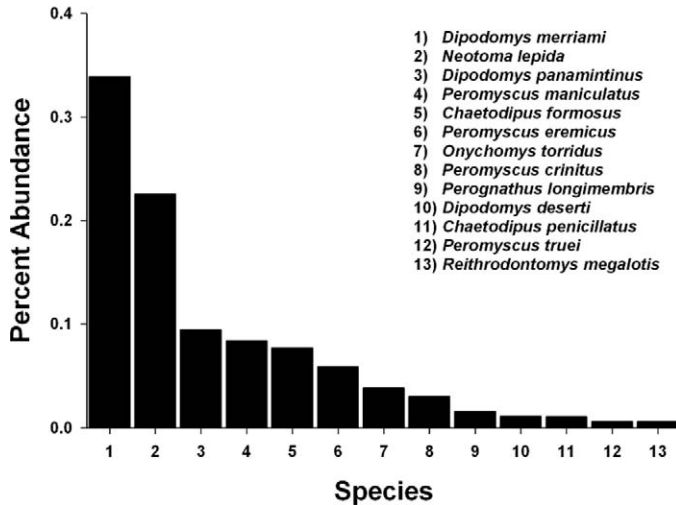


FIG. 2.—Rank abundance distribution of rodent species involved in this study.

representing approximately 37% of all captures. *Reithrodontomys megalotis* was the least-abundant taxon, representing less than 1% of all captures (Fig. 2).

Principal component analysis reduced the 81 perennial shrub variables to 6 derived variables that accounted for 83.6% of the variation among sites regarding vegetative characteristics (Table 1). Correlations of the original shrub species with the principal components were used to interpret the identity of derived variables (Stevens and Tello 2009). Environmental principal components had straightforward interpretations reflecting transitions from one macrohabitat to another (Table 1). A 2nd principal component analysis reduced the 9 soil particle sizes to a single derived variable that accounted for 77% of the variation among sites regarding soil texture. Correlations of the original soil variables with this soil principal component indicated it represented an axis ranging from sandy soils at low values to rocky soils at high values (Stevens and Tello 2009).

The arrangement of sites among macrohabitats was such that there was little spatial autocorrelation in environmental characteristics. Spatial variables accounted for little variation in environmental variables and this relationship was nonsignificant ( $R^2_{\text{adjusted}} = 0.05$ ,  $P = 0.67$ ). Fig. 3 illustrates spatial autocorrelation in rodent species composition and environmental characteristics and the autocorrelation of rodent species composition along environmental gradients. Correlograms demonstrated spatial structure of rodent species composition, with significant positive autocorrelations primarily at the shortest distances (Fig. 3A). There was a notable decline in spatial structure from short to intermediate distances and no pattern to structure at the largest distances. Spatial structure in environmental characteristics was much weaker and no significant autocorrelation values were found at any distance (Fig. 3B). Nevertheless, there was a significant relationship between rodent species composition and environmental gradients. Sites that were similar in their environmental characteristics (short environmental distances) were more

TABLE 1.—Results from principal component (PC) analysis on 81 perennial plant variables.

PC	Variance explained	Identity of gradient
1	33.8	Creosote to Joshua tree
2	17.6	Joshua tree–yucca to piñon–juniper
3	11	Amount of Joshua tree
4	9	Sage to piñon–juniper
5	7.5	Saltbush to piñon–juniper
6	4.7	Yucca to saltbush
Total	83.6	

similar to each other in terms of rodent species composition (significant positive autocorrelation; Fig. 3C), whereas sites that were dissimilar environmentally also were dissimilar in rodent composition (significant negative autocorrelation at high environmental distances; Fig. 3C).

Environmental redundancy analysis indicated that environmental principal components accounted for 55% of the variation among sites regarding rodent species composition (Fig. 4). The 1st environmental redundancy axis was primarily associated with the 1st perennial principal component, whereas the 2nd environmental redundancy axis was primarily associated with the 1st soil principal component and percent cover of annuals. *D. merriami*, *Chaetodipus formosus*, *Neotoma lepida*, *Peromyscus maniculatus*, and *Dipodomys panamintinus* exhibited strong correlations with environmental redundancy axes. In contrast, spatial variables accounted for only about 35% of the variation among sites in terms of rodent species composition (Fig. 4). *D. merriami*, *C. formosus*, *N. lepida*, *P. maniculatus*, and *D. panamintinus* exhibited the strongest relationships with spatial redundancy axes. Relationships of individual species were weaker (i.e., shorter arrows) for spatial than for environmental canonical axes.

When both environmental and spatial variables were combined into the same independent matrix they accounted for approximately 66% of the variation among sites in terms of rodent species composition. Variation in rodent species composition that was uniquely accounted for by the environment (i.e., that remaining after removing environmental variation shared with spatial variation) was 31% ( $P < 0.005$ ), whereas that uniquely accounted for by spatial variables was 11% ( $P = 0.025$ ). Variation in rodent species composition accounted for by the combined effect of space and environmental variables was 24%. Cricetid and heteromyid assemblages evinced similar patterns (Table 2). In particular, environmental effects always were greater than spatial effects. Pure environmental effects always were strong and significant; spatial effects were typically weak and significant only for the heteromyid assemblage. Shared variation always was intermediate in magnitude (Table 2).

## DISCUSSION

*Spatial perspective on rodent community structure.*—Desert rodents have been a quintessential model system for understanding the effects of local processes on community

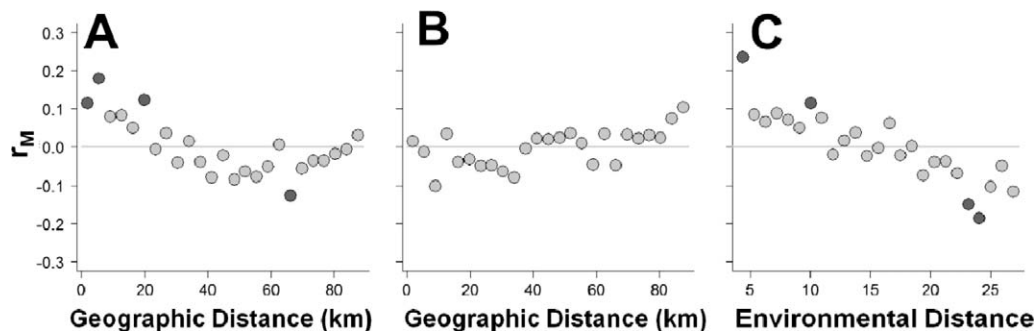


FIG. 3.—Correlograms depicting the autocorrelation of A and B) rodent composition and environmental characteristics along geographic distances, and C) rodent composition along environmental gradients. Dark gray dots represent statistically significant autocorrelation based on a 95% confidence interval produced by 1,000 matrix permutations.

structure such as climatic controls (Coppeto et al. 2006; Ernest et al. 2000; Holmgren et al. 2006; Krasnov et al. 1996; Meserve et al. 1996; Rogovin et al. 1994; Shenbrot 1992; Shenbrot and Rogovin 1995), edaphic characteristics (Hardy 1945; Root et al. 2000), and biotic interactions (Abramsky et

al. 1990; Brown 1989; Brown et al. 1979; Brown and Munger 1985; Kelt et al. 2004; Kotler et al. 1991; Longland and Price 1991; Meserve et al. 2003; Price 1978; Stevens and Willig 2000). Strong local processes determine not only species diversity, but also the combinations of taxa that can coexist

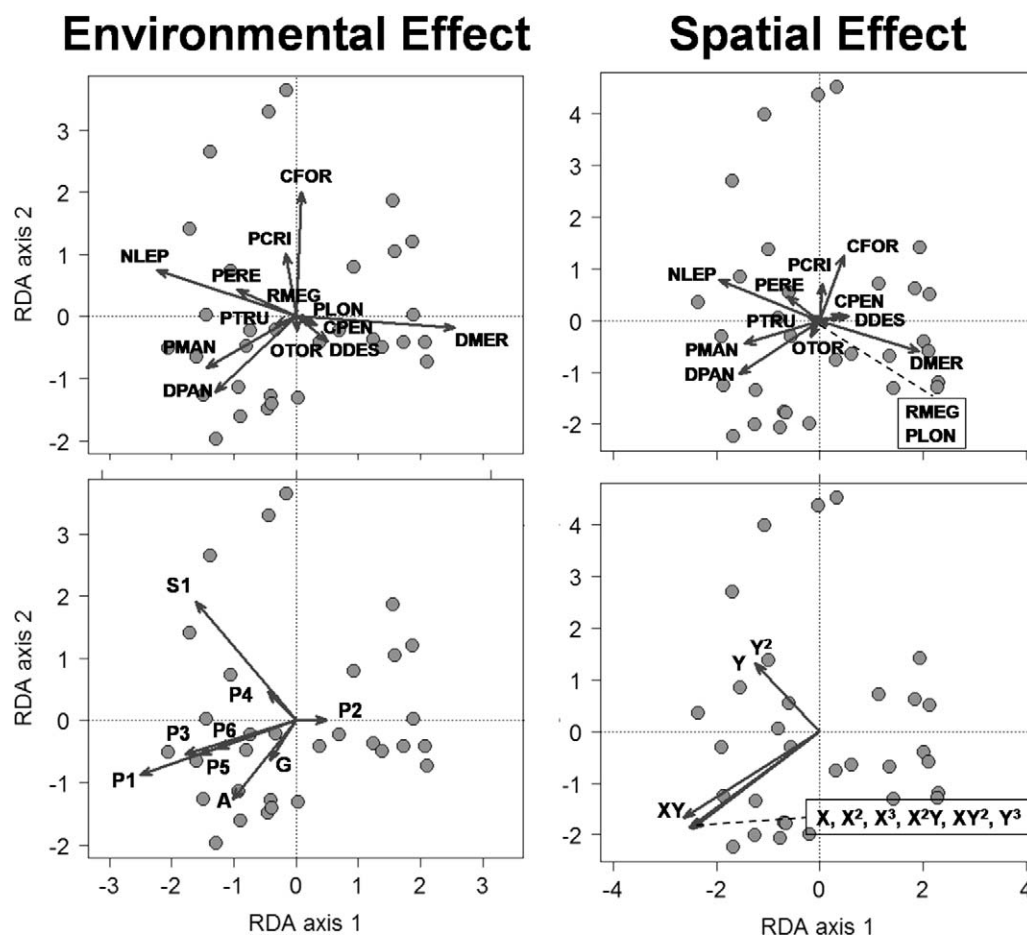


FIG. 4.—Results from redundancy analyses using environmental (left column) and spatial (right column) predictors to account for rodent species composition across the metacommunity. Rodent species acronyms are: CFOR, *Chaetodipus formosus*; CPEN, *C. penicillatus*; DDES, *Dipodomys deserti*; DMER, *D. merriami*; DPAN, *D. panamintinus*; NLEP, *Neotoma lepida*; OTOR, *Onychomys torridus*; PLON, *Perognathus longimembris*; PCRI, *Peromyscus crinitus*; PERE, *Peromyscus eremicus*; PMAN, *Peromyscus maniculatus*; PTRU, *Peromyscus truei*; RMEG, *Reithrodontomys megalotis*. Environmental and spatial acronyms are: P1–P6, 6 perennial principal components; S1, soil principal component; G, grass percent cover; A, annual percent cover.



**TABLE 2.**—Variance decomposition examining combined and unique effects of spatial and environmental processes on metacommunity structure. Values in the pure environment, interaction, pure space, and unaccounted variation columns correspond to variation accountable by that additive component.

Focus	Pure environment		Interaction	Pure space		Unaccounted variation
	Value	<i>P</i>		Value	<i>P</i>	
Entire assemblage	0.31	<0.005	0.24	0.11	0.025	0.34
Cricetid assemblage	0.31	<0.005	0.21	0.09	0.10	0.38
Heteromyid assemblage	0.32	<0.005	0.26	0.12	0.010	0.30

(Brown and Lieberman 1973). Typically, these model systems have been examined in isolation (see Brown et al. [1979], Brown and Munger [1985], Price [1978], and Rosenzweig [1973] for model systems) and from the perspective of local interactions. Indeed, local environmental conditions account for a greater amount of variation in rodent species composition than does spatial configuration in the Mojave Desert. Nonetheless, significant spatial structure not only exists, but remains significant even after controlling for that related to environmental gradients. Such spatial effects are not just apparent at the level of the entire metacommunity, but for the heteromyid assemblage as well.

Our results suggest that exploring spatial processes may improve our understanding of well-known desert rodent systems. For example, these results demonstrate that desert rodents represent metacommunities and complement those based on species turnover, in particular replacements of locally extinct species from the regional fauna that has been reported from the Portal, Arizona, rodent system (Ernest et al. 2008; Goheen et al. 2005) and dispersal from neighboring but different habitats reported at Fray-Jorje, Chile (Milstead et al. 2007). These sites represent 2 important systems for understanding maintenance of diversity of desert mammalian consumers. Strong local interactions among taxa as well as between species and their environment are major determinants of coexistence in these 2 systems. Nonetheless, replacement of locally extinct species by new taxa can only result from dispersal from other communities in the region. These results combined with ours on the significance of EID suggest that spatial processes such as dispersal need to be considered when trying to more fully understand determinants of species composition and in particular maintenance of diversity. Nonetheless, in the Portal system, replacements by new taxa corresponded to local extinction of others, suggesting strong local controls on the particular combination of species that can coexist (Goheen et al. 2005). Thus, dispersal is important for providing the opportunity for vacancies to be invaded by new species, but only particular species are able to invade depending on the particular vacancies in the community.

Recently, a theoretical framework has been established to characterize the structure of metacommunities and to distinguish relative effects of local and regional processes on structure. In particular, 4 different types of metacommunities result from different degrees of control by local environmental conditions or regional dispersal (Neutral [Bell 2000; Caswell 1976; Hubbell 2001], Patch Dynamics [Holt 2002; Levins and

Culver 1971], Species Sorting [Chase and Leibold 2003; Tilman 1982; Whitaker 1962], and Mass Effects [Amarasekare and Nisbet 2001; Holt 1993; Mouquet and Loreau 2003] models). Moreover, Cottenie (2005) presented a formal logical construct to distinguish niche-based from neutral-type models as well as between the 2 niche-based models based on observational data. The 1st characteristic distinguishing among metacommunity models is environmental heterogeneity. The Neutral and Patch Dynamics models assume either that patches are homogeneous or at least that focal species do not respond to heterogeneity inherent to different communities. Alternatively, Species Sorting and Mass Effects models assume strong environmental preferences of species that affect their distribution among communities. Accordingly, demonstration that environmental characteristics account for significant variation in species composition among communities is sufficient to eliminate the possibility of Neutral and Patch Dynamics models, whereas a lack of environmental signal justifies elimination of Species Sorting and Mass Effects models from consideration. Amount of spatial structure can further help to distinguish between Species Sorting and Mass Effects models. Specifically, significant spatial structure after accounting for environmental spatial autocorrelation characterizes Mass Effects, whereas a lack of spatial structure provides support for Species Sorting. The combined significance of both environmental and spatial characteristics seen here most closely matches predictions of the Mass Effects model. Specifically, rodents exhibit species sorting indicated by the strong environmental component to metacommunity structure. Nonetheless, the weaker but still significant spatial structure of EID suggests that dispersal promotes the occurrence of species in more suboptimal habitats that are not characteristic of the environmental correlates of species abundances. Mass effects have been reported in other small mammal systems. For example, mass effects can be inferred by the pattern of migration at Fray-Jorje (Milstead et al. 2007). Moreover, direct determination of mass effects was demonstrated in a system of spatially structured high-elevation habitats in Switzerland (Guélat et al. 2008). Regional coexistence was mediated by strong habitat differences yet local coexistence was mediated by rescue effects of inferior competitors from productive habitats. Studies from Portal (Ernest et al. 2008; Goheen et al. 2005), Fray-Jorje (Milstead et al. 2007), and Switzerland (Guélat et al. 2008) and our results provide phenomenological support for the important role of dispersal in integrating communities and provide a productive working hypothesis in

terms of future study to better understand systems that have been previously assumed to be structured primarily by local interactions. Indeed, differences in results characterizing these 3 studies suggest phylogenetic, environmental, or geographic differences that may be important in determining which metacommunity model fits regional patterns of structure best. Indeed, use of more mechanistic approaches will likely clarify the particular contexts in which different models best describe structure.

*Short-distance spatial effects further support a metacommunity perspective.*—Herein we demonstrated significant spatial integration across sites, suggesting that rodents form a metacommunity in the central Mojave Desert. Nonetheless, effects of dispersal of individuals across a metacommunity could manifest from 2 quite different spatial processes depending on spatial scale, only 1 of which is a mass effect. By preventing membership in distant communities, dispersal limitation can limit coexistence and create spatial pattern (Shurin 2000). Dispersal also can enhance coexistence by facilitating movement among sites of relatively close proximity (spatial structuring or mass effects—Cottenie et al. 2003). Our sampling regime includes both sites in close proximity as well as sites that are very distant from each other; such a sampling regime can distinguish between these 2 different processes. Mantel's analyses (Fig. 3) indicated that significant spatial integration of rodent species composition occurred primarily at the smallest spatial scales with larger spatial scales exhibiting no significant spatial autocorrelation. Such a result suggests spatial effects of close proximity that are more indicative of mass effects than dispersal limitation.

*Underappreciated spatial effects.*—The interdigitating macrohabitats found in our study system offer a unique opportunity to disentangle unappreciated spatial effects from spatial autocorrelation of environmental characteristics. The interaction term from the variance decomposition between environmental and spatial characteristics was relatively high (i.e., always greater than the pure spatial component) in terms of accounting for rodent species composition. Such large interactions as those found in our analyses can result from 1 of 2 mechanisms: spatially structured environmental descriptors (i.e., spatial autocorrelation), or separate relationships of environmental variables and species composition with some other external space-structuring process (Borcard et al. 1992). Typically this interaction is considered to represent spatial autocorrelation of species composition due to spatial autocorrelation of environmental characteristics. Nonetheless, our sites exhibited a very low, nonsignificant relationship between spatial arrangement of sites and their underlying environmental characteristics (i.e., no spatial autocorrelation), which rules out the possibility that this interaction term characterizes spatial autocorrelation of environmental variables. Moreover, multivariate correlograms and Mantel's tests (Fig. 2) indicated no significant spatial autocorrelation in environmental variables. Taken together, these results suggest an additional spatial effect not appreciated by prior studies utilizing EID and variance decomposition to understand

metacommunity structure. Variation in species composition related to the pure spatial effect likely represents mass effects promoting the existence of species in nearby suboptimal habitats. This is because source–sink phenomena represent spatial movements that are decoupled from environmental preferences. In contrast, variation in species composition related to correlated environmental and spatial variables is likely due to dispersal occurring along environmental gradients. To this end, an environmental gradient provides the corridor and the movement of individuals along that gradient creates spatial structure of species composition. Indeed, in other studies, even where significantly spatially autocorrelated environmental variables contribute to the environment–space interaction, spatial processes along environmental gradients are likely underappreciated. To this end, spatial processes likely have an even greater effect on metacommunity structure than is currently appreciated.

*Life-history differences.*—North American desert rodents can be organized into 3 large groups based on ecology and life history, although this corresponds to systematic differences as well: Sciuridae, Heteromyidae, and Cricetidae. Sciurids are primarily diurnal and not considered here. Heteromyids and cricetids have quite different ecologies and life histories that likely have ramifications to metacommunity structure. Heteromyids are composed primarily of granivores and considered to be more specialized, whereas cricetids are considered much more behaviorally and ecologically diverse, being folivorous, carnivorous, insectivorous, and granivorous (Brown and Zeng 1989). Cricetids tend to produce litters more rapidly under favorable conditions, whereas heteromyids have less-explosive reproduction but can reproduce even under adverse situations (Whitford 1976). Finally, potential differences in dispersal capacities exist that could differentially contribute to spatial effects. For example, at Portal, Arizona, cricetid species have some of the largest lifetime dispersal distances and for the assemblage as a whole the average median lifetime dispersal distance is larger for cricetids than for heteromyids (Brown and Zeng 1989). Heteromyids can be philopatric and often demonstrate limited dispersal on the order of only hundreds of meters (Price et al. 1994; Skvarla et al. 2004; Waser et al. 2006; Waser and Elliott 1991; Winters and Waser 2003). In contrast, very large movements are commonly reported for cricetids in the literature (*P. maniculatus*—1.7 km [Bowman et al. 1999], 3 km [Jung et al. 2005], and 3.2 km [Murie and Murie 1931]; *Peromyscus leucopus*—14.7 km and 6.8 km [Maier 2002]; *Neotoma cinerea*—3.2 km [Escherich 1981]; and *R. megalotis*—3.2 km [Clark 1988]). Moreover, the frequency of such movements is likely grossly underestimated due to low probability of detection because far dispersers are more diffusely distributed across a landscape and less likely to be recaptured (Rehmeier et al. 2004).

Different dispersal strategies could give rise to differences in the relative contributions of environmental and spatial determinants of metacommunity structure. Differences between cricetid and heteromyid assemblages suggest this. Spatial

effects in general were substantively larger for heteromyids (38%) than for cricetids (30%). Moreover, pure spatial structure not related to environmental gradients was significant for heteromyids but not for cricetids. Such an effect may be due to dispersal abilities. If heteromyids are limited in their dispersal abilities they may have limited options in terms of where to disperse. Given the heterogeneous, interdigitating habitats found at our study site, the only option for many heteromyids may be to disperse into a neighboring less-preferred habitat; the embodiment of source-sink dynamics. Such a scenario would enhance spatial effects, in particular the pure spatial component, because close, environmentally different habitats would have similar rodent species composition due to these dispersal dynamics.

In contrast, in our heterogeneous system, more-mobile dispersers may be able to cross less-suitable areas and colonize like habitats but by traveling longer distances. Such a scenario would minimize spatial effects because distant but similar habitat types would have similar species composition due to ability of dispersers to colonize them readily, whereas neighboring different habitats would be less colonized. Natal habitat preference induction (Mabry and Stamps 2008) is a phenomenon whereby individuals pass over other suitable habitats to colonize familiar habitats and has been reported to occur in rodents. For example, in patchy habitat of contrasting chaparral and oak woodlands of California, dispersing brush mice (*Peromyscus boylii*) prefer to settle in the same habitat type they were raised in as opposed to the other yet neighboring habitat types (Mabry and Stamps 2008). To this end, spatial effects resulting from dispersal of nonphilopatric and mobile organisms may be quite different from spatial effects of less-mobile organisms. Specifically, mass effects may be more prominent in the latter group, whereas the spatial signature of the former group may be less detectable.

Indeed, a vast amount has been learned about the structure of desert rodent communities from local investigations conducted over the last 35 years. Nonetheless, regional perspectives involving collections of numerous communities examined from a spatial perspective, in particular the metacommunity paradigm, may have much to contribute to this body of information.

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## APPENDIX I

Community structure of rodents across 31 sites in the Mojave National Preserve. Species acronyms are: CFOR, *Chaetodipus formosus*; CPEN, *C. penicillatus*; DDES, *Dipodomys deserti*; DMER, *D. merriami*; DPAN, *D. panamintinus*; NLEP, *Neotoma lepida*; OTOR, *Onychomys torridus*; PLON, *Perognathus longimembris*; PCRI, *Peromyscus crinitus*; PERE, *Peromyscus eremicus*; PMAN, *Peromyscus maniculatus*; PTRU, *Peromyscus truei*; RMEG, *Reithrodontomys megalotis*. Sites 10, 11, 15, and 28 are intentionally missing because they were dropped after the initial scouting of study sites.

Site	Macrohabitat	Species												
		CFOR	CPEN	DDES	DMER	DPAN	NLEP	OTOR	PLON	PCRI	PERE	PMAN	PTRU	RMEG
1	Pinion-Juniper woodland	1	0	0	0	1	6	0	0	0	2	18	15	0
2	Pinion-Juniper woodland	0	0	0	10	96	21	4	0	0	0	43	1	4
3	Blackbrush scrub	48	0	0	5	3	98	2	0	6	45	1	0	0
4	Blackbrush scrub	4	0	0	9	9	79	1	4	0	4	40	8	0
5	Joshua Tree woodland	0	0	0	104	42	11	7	0	0	33	27	0	0
6	Mojave yucca woodland	11	0	0	8	0	175	14	2	0	13	22	0	0
7	Creosote bajada	29	0	0	113	0	5	3	16	0	0	0	0	0
8	Mojave yucca woodland	0	0	0	64	13	33	8	1	0	0	0	0	0
9	Joshua Tree woodland	18	0	0	17	9	56	3	0	0	18	21	1	1
12	Mojave yucca woodland	0	0	0	25	52	115	2	1	0	12	20	0	0
13	Joshua Tree woodland	0	0	0	20	64	76	8	0	0	1	37	0	0
14	Blackbrush scrub	0	0	0	44	47	59	15	0	0	4	28	0	0
16	Mojave yucca woodland	0	0	0	107	15	116	14	4	0	8	7	0	0
17	Creosote bajada	0	0	0	155	3	50	4	3	0	5	6	0	0
18	Joshua Tree woodland	0	0	0	11	14	132	4	12	0	14	80	0	0
19	Creosote bajada	10	0	0	71	0	19	1	2	0	0	0	0	0
20	Sand dune	1	13	34	85	0	1	4	1	0	0	0	0	0
21	Creosote bajada	4	7	0	145	0	1	0	2	0	0	1	0	0
22	Creosote bajada	31	0	0	198	0	8	6	1	0	5	0	0	0
23	Sand dune	0	2	32	145	0	1	14	1	0	0	0	0	0
24	Lava bed	85	0	0	34	0	54	7	0	50	16	0	0	0
25	Lava bed	52	0	0	38	0	95	0	0	33	19	0	0	0
26	Alkali playa	0	1	0	152	0	0	0	0	0	0	0	0	0
27	Creosote bajada	82	0	0	124	0	3	5	0	0	1	1	0	0
29	Mojave yucca woodland	0	0	0	57	62	26	11	0	0	3	23	0	0
30	Alkali playa	0	0	1	77	0	4	2	13	0	0	1	0	0
31	Mojave yucca woodland	0	0	0	69	47	32	11	0	0	7	25	0	0
32	Creosote bajada	1	0	0	113	5	2	4	1	0	0	1	0	0
33	Joshua Tree woodland	0	0	0	47	25	11	27	5	0	15	51	0	0
34	Blackbrush scrub	0	0	0	39	67	36	8	0	0	1	41	0	0
35	Pinion-Juniper woodland	0	0	0	12	10	27	0	0	0	9	13	21	0