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Spatial niche partitioning of coexisting small mammals in sand dunes

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Abstract

Resource partitioning may allow species coexistence. Sand dunes in the typical steppe of Inner Mongolia, China, consist of desert, shrub and grass habitats, providing an appropriate system for studies of spatial niche partitioning among small mammals. We collected data to verify the niche separation hypothesis that coexisting small mammals would separate into spatial niches, and the productivity hypothesis that the highest species richness and overlap were to be expected in the most productive and diverse shrub habitat of the north-facing slopes, in contrast with the less productive grass and desert habitats of sand dunes. We trapped small mammals on 44 sand dunes in the summer of 1984 using snap traps. We captured 12 species of small mammals among three types of habitats. *Cricetulus barabensis* was a habitat generalist, present in all three types of habitats. *Spermophilus dauricus* was present only in the grass habitat, *Allactaga sibirica* and *Dipus sagitta* only in the desert habitat, and *Apodemus peninsulae* primarily in the shrub habitat. The shrub habitat hosted the largest number of small mammal species among the three types of habitats, supporting the productivity hypothesis. Habitat separation is an important mechanism for structuring small mammal communities in Inner Mongolia grasslands.

Keywords: *Habitat, niche breadth, niche overlap, niche separation, species richness*

Introduction

Niche theory is fundamental to understanding species coexistence (Chase & Liebold 2003). Species coexist via mechanisms that avoid competitive exclusion, such as niche separation or resource partitioning (Brown & Lieberman 1973; Schoener 1974; Kotler & Brown 1988). The Hutchinsonian hypervolume niche is defined as the multi-dimensional resource space in which a species lives (Hutchinson 1957). Extant or past interspecific competition (hereafter, competition) may lead to niche separation between coexisting species in one or more dimensions of resource space (Brown & Lieberman 1973; Schoener 1974; Kotler & Brown 1988). Regardless of extant competition or the ghost of competition past as the cause, niche segregation or resource partitioning is necessary for species coexistence in resource-limited systems, and quantification of niche breadth and niche overlap between coexisting species helps to understand the mechanisms

underlying species coexistence (Illoldi-Rangel et al. 2004; Holt 2009).

Space is a critical component of ecological niches (Price 1978; Kotler & Brown 1988). Spatial niche separation may be expressed in the form of habitat separation (Price 1978; Scott & Dunstone 2000). Separation in habitat use may serve as a mechanism for species coexistence, especially when food resources are limited (Price 1978; Shenbrot 1992; Scott & Dunstone 2000). Therefore, quantification of between-species separation or overlap of the spatial niche may provide insight into possible resource partitioning among the co-existing species of animal communities.

Sand dunes in the typical steppe of Inner Mongolia consist of chains of dunes, with nearly bare sand on the south-facing slope, dense shrubs on the north-facing slopes and grassland in the valleys between sand dunes, providing small mammals with diverse types of habitats (Wang et al. 2003). Sand dune ecosystems in the Xilingol grassland

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harbor a total of 12 small mammal species, including desert and grassland species (Wang et al. 1999). Vegetation, soil hardness and soil moisture content are different among three types of habitats, meeting different habitat requirements of the desert and grassland small mammals. Therefore, sand dunes provide an appropriate system for studies of spatial niche separation in small mammals. The niche separation hypothesis predicts that small mammals coexisting in the sand dunes would separate into spatial niches as a possible mechanism of resource partitioning and species coexistence.

Productive habitat would support diverse animal species because abundant resources may allow for ecological similarity or niche overlap between coexisting species (MacArthur 1972). Shrubs on the north-facing slope and grasses in the valley between dunes are denser and have greater standing biomass than desert vegetation on the south-facing slope does (Wang et al. 2003). The productivity hypothesis predicts that the shrub habitats on the north-facing slopes support greater small mammal species richness than the grass and desert habitats of sand dunes because the shrub vegetation on the north-facing slope is more productive than those in the other two habitats. To test this hypothesis, we sampled 44 sand dunes to estimate species richness, spatial niche breadths and spatial niche overlaps of small mammals.

Materials and methods

We conducted our study in a sand dune belt located in the Xilin River Basin, Inner Mongolia, China (N43°38'–43°41', E116°39'–116°43'). The sand dune belt stretched from east to west along the Xilin River for about 10 km and consisted of numerous chains of sand mounts (dunes) taller than 10 m. The dune slopes ranged from 20 to 25 degrees. The vegetation was sparse on the south-facing slope, mainly consisting of *Artemisia intramongolica*, *Agropyron mongolicum*, *Festuca daturica*, *Psammochloa mongolica*, *Polygonum divaricatum* and *Ferula bungeana*. The vegetation was tall and dense on the north-facing slope, mainly consisting of shrubs *Spiraea aquilegifolia*, *Prunus padus*, *Caragana microphylla* and *Salix gordejewii*, elm trees *Ulmus pumila* about 1 m tall, and herbs *Thalictrum squarrosum* and *Veronica incana*. Valleys between sand dunes had dense and short grasslands, mainly consisting of *Leymus chinensis*, *Stipa krylovii*, *Cleistogenes squarrosa*, *Artemisia frigida* and *Potentilla tanacetifolia*. The climate was semi-arid with long, cold winters. Temperatures ranged from –40°C to 30°C with an annual average of

about –0.1°C. Average annual precipitation was about 350 mm, mainly falling in June, July and August. Snow cover lasted from November through March. Most plant growth occurred from April to August (Wang et al. 1999).

We trapped small mammals on 44 sand dunes with a trapping plot of two trap lines per habitat type in a 20-km² (4 km × 5 km) area from June through August 1984. To characterize vegetation and soil in different habitats, we also randomly selected 10 sand dunes from the 44 sand dunes for vegetation and soil sampling in late August 1984. We placed a 1-m² quadrat randomly along each of the two trap lines on each trapping plot (i.e., a total of 60 quadrats over 10 sand dunes). We estimated plant coverage (%) within a quadrat to the nearest 1% and measured plant height (cm) of 10 individuals randomly chosen within a quadrat. We also took three measurements of soil hardness (kg/cm²) in a 3-m interval along the middle line between the two trap lines on each trapping plot (i.e., a total of 90 measurements across 10 sand dunes). The TE-3 penetrometer (Institute of Soil Sciences, Chinese Academy of Sciences, Nanjing, China) penetrated through top 20-cm soil layer to measure average soil hardness. Additionally, we took five soil samples (about 20 g each) at a depth of 35–40 cm at a random location along the middle line of two trap lines on each trapping plot (i.e., a total of 50 soil samples). We stored soil samples in sealed aluminum containers. Soil samples were transported to a laboratory to be dehydrated at 100°C for 72 consecutive hours in ovens. Percent difference in weight before and after dehydration was the estimate of soil water content (%). We calculated average soil water content of five samples for each habitat type of a sampled sand dune.

We set a trapping plot in each of the three habitats of sand dunes, with a total of 132 plots on 44 sand dunes. Each trapping plot had two trap lines at a 5-m inter-line distance. We placed 10 wooden kill or snap traps (16 cm × 6.8 cm) in 2-m inter-trap distances on each trap line. Trapping lasted for three consecutive days (i.e., a total of 60 trap nights per plot). We checked traps three times a day: early in the morning, at noon and late in the afternoon. Traps were reset after each capture was removed. Each captured animal was identified to species. We calculated the number of captures per 100 trap nights as an index of relative abundance for each species in each type of habitat. We tested for differences in small mammal species richness among the three habitat types using the Kruskal-Wallis test with a nominal significance of 0.05. We then used the Wilcoxon test, with Bonferroni correction, for pair-wise comparisons.

We calculated niche breadth (NB) for each species using the formula:

$$NB = 1 - 0.5 \sum_{i=1}^n |p_i - q_i| \quad (1)$$

where p_i is the proportion of trap nights available in habitat type i , q_i is the proportion of a species in habitat i , and n is the number of habitat types (Feinsinger et al. 1981; Songer et al. 1997). The NB index measures the similarity of the spatial distributions of small mammal's relative recaptures and trap nights among 44 sand dunes. The greater the NB value, the broader the spatial distribution in the 44 sand dunes. Values of NB range from 0 for perfect specialists to 1 for perfect generalists (Songer et al. 1997). We calculated niche overlap (NO) between species i and j using the similarity formula:

$$NO = 1 - 0.5 \sum_{k=1}^n |p_{ki} - q_{kj}| \quad (2)$$

where p_{ki} and q_{kj} are the proportions of species i and j in the habitat type k , respectively, and n is the number of habitat types (Mueller & Altenberg 1985). We bootstrapped the capture data by sand dune with a repetition of 2000 times. At each bootstrapping iteration, we randomly sampled 44 sets of the small mammal captures from the original trap data with replacement. The original capture data by sand dune were sampling units. We then computed NBs and NOs for each of 44 bootstrapped data sets, and repeated this process 2000 times. We used the 2.5% and 97.5% percentiles of 2000 bootstrapped NBs and NOs to estimate empirical 95% confidence intervals (CI) of niche breadth and niche overlap.

We also applied multidimensional scaling (MDS) analysis to data on the relative abundances of small mammal species to demonstrate spatial niche separation among the grass, shrub, and desert habitats. The MDS analysis used a trapping plot of 20 traps in each type of habitat on a sand dune as a sampling unit (Khattree & Naik 2000; Everitt 2004). In MDS analysis, we calculated the Mahalanobis distance between small mammal assemblages of any two habitat types using relative abundance data (Everitt 2004). Small mammal assemblages would separate in multidimensional scale space if the space use or spatial niche of small mammal communities separated among habitat types. We conducted square-root transformation to normalize the multivariate data on the relative abundance of small mammals.

We used a univariate analysis of variance (ANOVA) test to detect differences in soil hardness and water

content and vegetation cover and height among the three habitat types with a nominal significance of 0.05, respectively. If ANOVA was significant, we then used a t test to compare the means of each measured variable between two habitat types. We used the Bonferroni correction for multiple comparisons. Means are reported with \pm standard error (SE).

Results

Vegetation coverage differed among the three habitat types ($F_{2, 27} = 251.43$, $P < 0.001$; Figure 1a). The vegetation coverage ($86.75 \pm 3.53\%$) of the north-facing slopes was greater than that ($29.00 \pm 1.25\%$) of the south-facing slope ($t_{\text{shrub-desert}} = 21.17$, $df = 18$, $P < 0.001$) and that ($69.25 \pm 2.11\%$) of the valley ($t_{\text{shrub-grass}} = 17.19$, $df = 18$, $P < 0.001$). The vegetation of the north-facing slope was denser than that of the valley ($t_{\text{shrub-grass}} = 17.68$, $df = 18$, $P < 0.001$). Additionally, plant height differed among the three habitat types ($F_{2, 27} = 82.51$, $P < 0.001$; Figure 1b). The vegetation (74.70 ± 3.04 cm) of the north-facing slopes was taller than that (33.55 ± 1.77 cm) of the south-facing slope ($t_{\text{shrub-desert}} = 12.17$, $df = 18$, $P < 0.001$) and that (47.50 ± 1.88 cm) of the valley ($t_{\text{shrub-grass}} = 7.68$, $df = 18$, $P < 0.001$). Plants of the valley were taller than those of the south-facing slope ($t_{\text{grass-desert}} = 5.29$, $df = 18$, $P < 0.001$). Average water content was $1.22 \pm 0.05\%$ ($n = 9$), $1.26 \pm 0.04\%$ ($n = 10$) and $1.45 \pm 0.07\%$ ($n = 10$) on the south-facing slope, on the north-facing slope and in the valley, respectively, but did not differ significantly among the three habitat types ($F_{2, 25} = 4.72$, $P = 0.018$ [$> 0.05/4$]; Figure 1c). However, soil hardness differed among the three habitat types ($F_{2, 27} = 14.07$, $P < 0.001$; Figure 1d). The soil of the valley (9.5 ± 0.32 kg/cm²) was harder than that of the south-facing slope (7.52 ± 0.47 kg/cm²; $t_{\text{grass-desert}} = 3.59$, $df = 18$, $P = 0.003$) and that of the north-facing slope (6.3 ± 0.51 kg/cm²; $t_{\text{grass-shrub}} = 5.39$, $df = 18$, $P < 0.001$).

We captured a total 491 individuals of 12 small mammal species from 44 sand dunes (Table I). On average, we captured 1.4 species per plot on the south-facing slope, 2.3 species per plot in grasslands between dunes and 5.5 species per plot on the north-facing plot (Kruskal-Wallis test: $\chi^2 = 55.96$, $df = 2$, $P \leq 0.01$). Species richness per plot on the south facing plot was significantly less than that on the north-facing slope (Wilcoxon test: $w = 115$, $P \leq 0.01$), but not different from that of the grassland habitat (Wilcoxon test: $w = 775$, $P = 0.09$).

Cricetulus barabensis (CRBA) was captured in all three habitats of sand dunes, with spatial niche width being 0.85. *Allactaga sibirica* (ALSI) and the desert

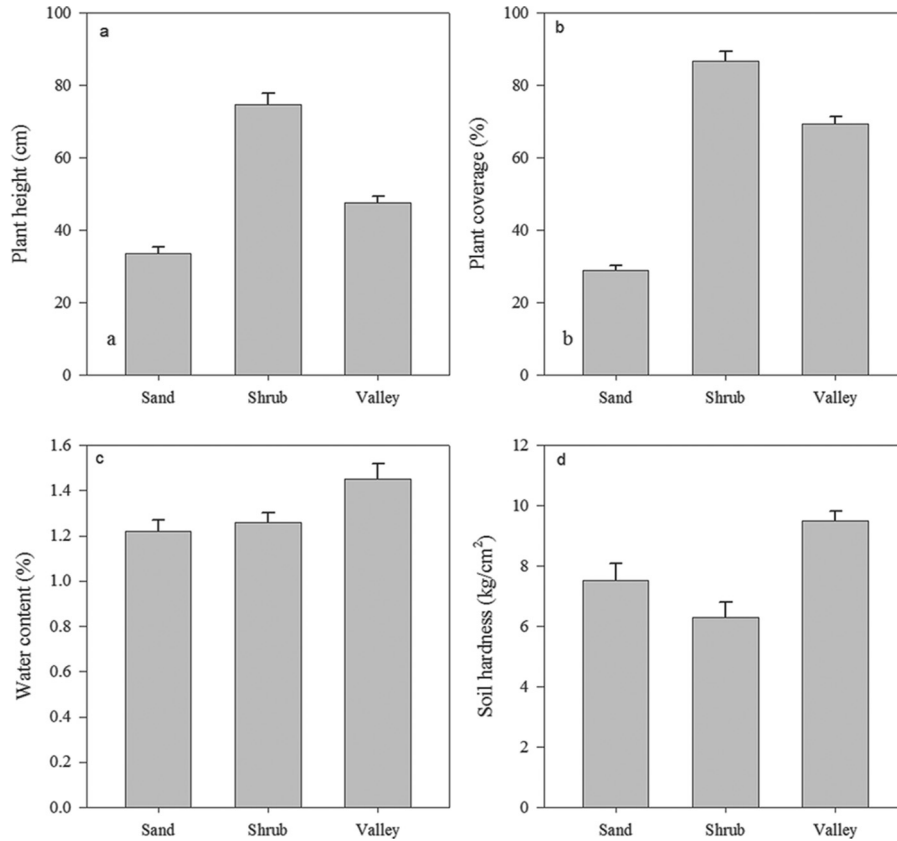


Figure 1. Means of (a) plant height, (b) vegetation coverage, (c) soil water content and (d) soil hardness of the south-facing slope (sand), the north-facing slope (shrub) and the between-dunes valley (valley) in the sand dunes of Baiyingxile, Inner Mongolia, China. Vertical lines are one standard error.

Table I. Number of captures per 100 trap nights and mean spatial niche width with 95% confidence intervals (CI) of 12 small mammal species in the sand dunes, Inner Mongolia, China.

	SPDA	ALSI	CRBA	PHCA	PHRO	APPE	DISA	MIMA	MIGR	MYSH	OCDA	RANO
South-facing slope	0.00	0.04	2.05	0.27	3.14	0.00	0.11	0.00	0.00	0.04	0.00	0.00
North-facing slope	0.00	0.00	7.92	0.15	0.00	0.41	0.00	0.04	0.08	0.34	0.15	0.04
Between-dunes valley	0.42	0.00	2.65	0.00	0.30	0.04	0.00	0.00	0.04	0.00	0.30	0.00
Mean niche breadth	0.20	0.19	0.85	0.59	0.39	0.57	0.29	0.32	0.44	0.59	0.53	0.32
95% CI lower limit	0.15	0.00	0.81	0.27	0.32	0.45	0.00	0.00	0.00	0.45	0.29	0.00
95% CI upper limit	0.26	0.36	0.90	0.82	0.47	0.71	0.36	0.55	0.73	0.80	0.72	0.54

Note: SPDA: *Spermophilus dauricus*; ALSI: *Allactaga sibirica*; CRBA: *Cricetulus barabensis*; PHCA: *Phodopus campbelli*; PHRO: *Phodopus roborovskii*; APPE: *Apodemus peninsulae*; DISA: *Dipus sagitta*; MIMA: *Microtus maximowiczii*; MIGR: *Microtus gregalis*; MYSH: *Myodes shanensis*; OCDA: *Ochotona dauurica*; RANO: *Rattus norvegicus*.

species *Dipus sagitta* (DISA) were captured only on the south-facing slope, with mean spatial niche width being 0.19 and 0.29, respectively. The grassland species *Spermophilus dauricus* (SPDA) was captured only in grasslands, with mean spatial niche width being 0.22 (Table I). *Microtus maximowiczii* (MIMA) and *Rattus norvegicus* (RANO) were only captured in the shrub habitat. The remainder of the species were captured in two different types of habitats (Table I).

Cricetulus barabensis had significant spatial niche overlap with all other species (Table II). *Allactaga sibirica*, DISA, *Phodopus roborovskii* (PHRO) and *Phodopus campbelli* (PHCA) had significant spatial niche overlap with each other, with the 95% CI of niche overlap excluding zero (Table II). *Ochotona dauurica* (OCDA), *Microtus gregalis* (MIGR) and SPDA had significant spatial niche overlap with each other and with PHRO (Table II). Forest species

Table II. Bootstrap means and variances of interspecific spatial niche overlap of 12 small mammal species in the sand dunes, Inner Mongolia, China.

	SPDA	ALSI	CRBA	PHCA	PHRO	APPE	DISA	MIMA	MIGR	MYSH	OCDA	RANO
SPDA	1.0 (0.0)											
ALSI	0.0 (0.0)	1.0 (0.0)										
CRBA	0.24* (0.0008)	0.16* (0.0008)	1.0 (0.0)									
PHCA	0.0 (0.0)	0.62* (0.07)	0.49* (0.04)	1.0 (0.0)								
PHRO	0.09* (0.001)	0.91* (0.001)	0.25* (0.002)	0.61* (0.06)	1.0 (0.0)							
APPE	0.09 (0.007)	0.0 (0.0)	0.69* (0.008)	0.37 (0.07)	0.05 (0.002)	1.0 (0.0)						
DISA	0.0 (0.0)	1.0* (0.0)	0.16* (0.0008)	0.62* (0.07)	0.91* (0.001)	0.0 (0.0)	1.0 (0.0)					
MIMA	0.0 (0.0)	0.0 (0.0)	0.60* (0.001)	0.38 (0.07)	0.0 (0.0)	0.91* (0.007)	0.0 (0.0)	1.0 (0.0)				
MIGR	1.0* (0.0)	0.0 (0.0)	0.23* (0.0008)	0.0 (0.0)	0.09* (0.001)	0.09 (0.007)	0.0 (0.0)	0.0 (0.0)	1.0 (0.0)			
MYSH	0.0 (0.0)	0.12 (0.01)	0.69* (0.006)	0.48 (0.07)	0.12 (0.01)	0.84* (0.01)	0.12 (0.01)	0.88* (0.01)	0.0 (0.0)	1.0 (0.0)		
OCDA	0.64* (0.04)	0.0 (0.0)	0.59* (0.02)	0.24 (0.03)	0.09* (0.001)	0.45* (0.03)	0.0 (0.0)	0.36* (0.02)	0.64* (0.02)	0.38* (0.02)	1.0 (0.0)	
RANO	0.0 (0.0)	0.0 (0.0)	0.60* (0.09)	0.38 (0.09)	0.0 (0.0)	0.91* (0.007)	0.0 (0.0)	1.0* (0.0)	0.0 (0.0)	0.88* (0.01)	0.36* (0.02)	1.0 (0.0)

Note: SPDA: *Spermophilus dauricus*; ALSI: *Allactaga sibirica*; CRBA: *Cricetulus barabensis*; PHCA: *Phodopus campbelli*; PHRO: *Phodopus roborovskii*; APPE: *Apodemus peninsulae*; DISA: *Dipus sagitta*; MIMA: *Microtus maximowiczii*; MIGR: *Miconus gregalis*; MYSH: *Myodes shansuis*; OCDA: *Ochotona dauurica*; RANO: *Rattus norvegicus*.

* indicates that the empirical 95% confidence interval excludes zero.

Apodemus peninsulae (APPE) and *Myodes shanseius* (MYSH) had significant spatial niche overlap with each other and with MIMA and OCDA (Table II). Small mammal assemblages were separated in the space defined by first two MDS coordinates (Figure 2).

Discussion

Habitat structure and primary productivity influence the diversity of animal communities (MacArthur 1964; Rosenzweig 1995). Our data support the productivity hypothesis that the shrub habitats of sand dunes would harbor more small mammal species probably due to greater plant standing biomass in the shrub habitat than in the grass and desert habitats (Figure 1a). Differences in habitat use among the small mammals on the sand dunes may lead to niche space separation among the small mammals, supporting the niche separation hypothesis (Table I; Figure 2). Differences in habitat use or selection may be an important mechanism for the coexistence of desert rodents (Scott & Dunstone 2000).

The shrub habitat had the tallest, most dense vegetation and the greatest small mammal species richness in the sand dunes (Figure 1; Table I). Plant coverage and plant height may suggest plant standing biomass levels. Brown and Lieberman (1973) showed that more productive habitats support more seed-eating rodents in the sand dunes of North America. Plant productivity influences the species diversity patterns of small mammals, with a unimodal pattern between plant productivity and small mammal species richness in the desert and

grassland ecosystems (Abramsky & Rosenzweig 1984; Wang et al. 1999; Reed et al. 2006). More plant resources as indexed by plant coverage and height in the shrub habitat may alleviate competition for food resources among small mammals and thus support more small mammal species, compared to the grass and desert habitats. Alternatively, the greatest plant coverage and plant height of the north-facing slopes may suggest the highest complexity of habitat structure in the sand dunes. Complex habitat structure may support diverse small mammal species (MacArthur 1964).

In our study site, spatial niche separation mainly occurred between the habitat specialists, which only utilized the desert (ALSI and DISA), shrub (RANO and MIMA) or grass (SPDA) habitats (Tables I–II). Voles MIMA and MIGR selected productive and dense vegetation (Wang et al. 2003). The relative abundance of the two voles was greater in the shrub habitat than in the other two habitats (Table I). Differences in habitat utilization between habitat specialists differentiated small mammal assemblages among the three types of habitats (Figure 2). *Allactaga sibirica* is generally distributed in the grasslands in our geographical area (Zhong et al. 1981). Although values of spatial niche overlap between the species captured in the shrub habitat (i.e., APPE, MYSH, MIMA, OCDA and RANO) were greater than 0.8 (Table II), these small mammals have different diets. For example, MIMA and OCDA eat plant foliage, MYSH and APPE feed on plant foliage and seeds, and RANO is an omnivore (Zhong et al. 1981). Therefore, differences in diets among small mammal species in the shrub habitat may allow for the coexistence of the species with high spatial niche overlaps.

Our findings also have conservation implications for small mammal diversity in the Inner Mongolia grassland. *Spermophilus dauricus* is a characteristic rodent species and habitat specialist of the typical steppe. *Spermophilus dauricus*, MIMA and MIGR were found only in the grassland habitat (Table I). *Spermophilus dauricus*, MIMA and MIGR are associated with the moist grassland and are less abundant in the grasslands overgrazed by livestock in our study area (Zhong et al. 1981). Livestock grazing may change small mammal communities through habitat alteration (Valone & Sauter 2005; Torre et al. 2007; Wallgren et al. 2009). Therefore, SPDA, OCDA, MIMA and MIGR may be vulnerable to the loss of grasslands due to livestock overgrazing in central eastern Inner Mongolia.

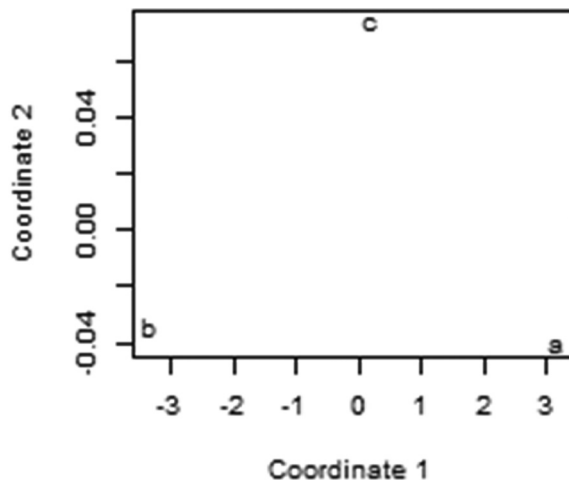


Figure 2. Multidimensional scaling analysis of small mammal assemblages in the habitats (a) on the south-facing slope, (b) on the north-facing slope and (c) in the between-dunes valley of sand dunes, Inner Mongolia, China.

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References

- Abramsky Z, Rosenzweig ML. 1984. Tilman's predicted productivity-diversity relationship shown by desert rodents. *Nature* 309:150–151. doi:10.1038/309150a0.
- Brown JH, Lieberman G. 1973. Resource utilization and coexistence of seed-eating desert rodents in sand dune habitats. *Ecology* 54:788–797. doi:10.2307/1935673.
- Chase JM, Liebold MA. 2003. *Ecological niches: Linking classical and contemporary approaches*. Chicago, IL: University of Chicago Press.
- Everitt B. 2004. *An R and S-PLUS companion to multivariate analysis*. London, UK: Springer.
- Feinsinger P, Spears EE, Poole RW. 1981. A simple measure of niche breadth. *Ecology* 62:27–32. doi:10.2307/1936664.
- Holt RD. 2009. Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences of the United States of America* 106:19659–19665. doi:10.1073/pnas.0905137106.
- Hutchinson GE. 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology* 22:415–427. doi:10.1101/SQB.1957.022.01.039.
- Illoldi-Rangel P, Sánchez-Cordero V, Peterson AT. 2004. Predicting distributions of Mexican mammals using ecological niche modeling. *Journal of Mammalogy* 85:658–662. doi:10.1644/BER-024.
- Khattree R, Naik RN. 2000. *Multivariate data reduction and discrimination with SAS software*. Cary, NC: SAS Institute.
- Kotler BP, Brown JS. 1988. Environmental heterogeneity and the coexistence of desert rodents. *Annual Review of Ecology and Systematics* 19:281–307. doi:10.1146/annurev.es.19.110188.001433.
- MacArthur RH. 1964. Environmental factors affecting bird species diversity. *The American Naturalist* 98:387–397. doi:10.1086/an.1964.98.issue-903.
- MacArthur RH. 1972. *Geographic ecology*. New York, NY: Harper and Row.
- Mueller LD, Altenberg L. 1985. Statistical inference on measures of niche overlap. *Ecology* 66:1204–1210. doi:10.2307/1939173.
- Price MV. 1978. The role of microhabitat in structuring desert rodent communities. *Ecology* 59:910–921. doi:10.2307/1938543.
- Reed AW, Kaufman GA, Kaufman DW. 2006. Species richness-productivity relationship for small mammals along a desert-grassland continuum: Differential responses of functional groups. *Journal of Mammalogy* 87:777–783. doi:10.1644/05-MAMM-A-253R2.1.
- Rosenzweig ML. 1995. *Species diversity in space and time*. Cambridge, UK: Cambridge University Press.
- Schoener TW. 1974. Resource partitioning in ecological communities. *Science* 185:27–39. doi:10.1126/science.185.4145.27.
- Scott DM, Dunstone N. 2000. Environmental determinants of the composition of desert-living rodent communities in the north-east Badia region of Jordan. *Journal of Zoology* 251:481–494. doi:10.1111/jzo.2000.251.issue-4.
- Shenbrot G. 1992. Spatial structure and niche patterns of a rodent community in the south Bukhara desert (Middle Asia). *Ecography* 15:347–357. doi:10.1111/eco.1992.15.issue-4.
- Songer MA, Lomolino MV, Perault DR. 1997. Niche dynamics of deer mice in a fragmented, old-growth-forest landscape. *Journal of Mammalogy* 78:1027–1039. doi:10.2307/1383046.
- Torre I, Díaz M, Martínez-Padilla J, Bonal R, Viñuela J, Fargallo JA. 2007. Cattle grazing, raptor abundance and small mammal communities in Mediterranean grasslands. *Basic and Applied Ecology* 8:565–575. doi:10.1016/j.baec.2006.09.016.
- Valone TJ, Sauter P. 2005. Effects of long-term cattle enclosure on vegetation and rodents at a desertified arid grassland site. *Journal of Arid Environments* 61:161–170. doi:10.1016/j.jaridenv.2004.07.011.
- Wallgren M, Skarpe C, Bergström R, Danell K, Bergström A, Jakobsson T, Karlsson K, Strand T. 2009. Influence of land use on the abundance of wildlife and livestock in the Kalahari, Botswana. *Journal of Arid Environments* 73:314–321. doi:10.1016/j.jaridenv.2008.09.019.
- Wang GM, Wang ZW, Zhou QQ, Zhong WQ. 1999. Relationship between species richness of small mammals and primary productivity of arid and semi-arid grasslands in north China. *Journal of Arid Environments* 43:467–475. doi:10.1006/jare.1999.0572.
- Wang GM, Zhong WQ, Zhou QQ, Wang ZW. 2003. Soil water condition and small mammal spatial distribution in Inner Mongolian steppes, China. *Journal of Arid Environments* 54:729–737. doi:10.1006/jare.2002.1083.
- Zhong WQ, Zhou QQ, Sun CL. 1981. Study on structure and spatial pattern of rodent communities in Baiyinxile typical steppe, Inner Mongolia. *Acta Ecologica Sinica* 1:12–21.