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Physical and biological variables related to habitat preferences of rodents

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Abstract This study determined habitat characteristics related to the presence of species of rodents and possible associations between pairs of these species that may affect their distribution. The study was conducted in the southern half of the Baja California Peninsula, Mexico. We used an environmentally constrained null model with 200 data sites that were sampled from 1999 to 2004 and measurements of different environmental factors obtained from electronic maps, meteorological stations, and measurements in the field. Although most of the isolated factors were not adequate for distinguishing between sites (rodents' habitat), the combination of all the factors gave an acceptable explanation for the presence of rodent species. The low selectivity of the species for the variables used in the model could be related to the selection of variables that were not appropriate for all species and because an artifact of scale of several variables was employed in the analysis. The percentage of rock cover and vegetation types was most closely related to habitat preference for most species. The possible associations between pairs of these species shown by the null model, the negative interaction between two pairs of species (*Peromyscus eva* vs. *P. fraterculus* and *Chaetodipus spinatus* vs. *C. fallax*) have probably affected the distribution of these rodents.

Keywords Baja California Sur · Distribution · Habitat relationships · Habitat model · Null model · Rodents · Species occurrence

Introduction

The presence of species in an area is influenced by the interplay of physical and biotic factors to varying degrees, as well as by historical factors (Anderson et al. 2002; MacArthur 1984; Soberón and Peterson 2005). In the study of species–habitat relationships, the habitat is usually characterized in terms of physical and biotic factors,

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including habitat features that may be relevant to a species at different scales (Mackey and Lindernmayer 2001). There is good evidence that both small-scale and landscape-scale characteristics of the habitat are significant predictors of the presence of vertebrate species (Storch 2002).

In rodents, as in other mammalian species, ecological aspects have become an essential concern for their conservation and importance to their ecosystems (Maccracken et al. 1984). Information about habitat requirements is essential to understand threats to species survival (Schlossberg 2006). This information is also very important in making predictions about species distributions (Martinez-Meyer 2005; Martinez-Meyer et al. 2004).

The State of Baja California Sur has 15 species of rodents among four families: Sciuridae (3), Geomyidae (1), Heteromyidae (6), and Muridae (5). Available information for many of these species does not include habitat preferences and distribution patterns within the state. The only study that included Baja California Sur and dealt with the relationship of small mammals (at subspecies level) with environmental variables is the work of Illoldi et al. (2002), who found that topography, precipitation, and vegetation cover were the best variables to determine the distribution of terrestrial mammals in the area surrounding the Gulf of California.

One of the tools for analyzing distribution patterns has been null models (Beissinger et al. 1996; Peres-Neto et al. 2001). These models are widely used in ecology and biogeography (Gotelli 2001) to evaluate the relationship among different species using different types of algorithms (Gotelli 2000, 2001; Gotelli and Entsminger 2003). The environmentally constrained null model is a type of null model that takes into account habitat characteristics in the analysis of associations of paired species. This allows distinctions among possible true interactions between species of either similarities or differences in environmental requirements of species (Beissinger et al. 1996; Peres-Neto et al. 2001).

In this study, we analyzed the distributional patterns of 13 species of rodents in the State of Baja California Sur. We used an environmentally constrained null model with 200 occurrence data points and recorded different environmental factors. Our objective was to determine habitat preferences of rodents by identifying characteristics of the habitats that are more related to the presence or absence of the rodents, as well as by detecting interactions between species that could have an effect on their distribution.

Materials and methods

We used 200 data points based on records of specimens from the State of Baja California Sur of the order Rodentia, whose range is in the southern half of the Baja California Peninsula. The specimen records were obtained from the database of the mammal collection at Centro de Investigaciones Biológicas del Noroeste (CIB); 79 of the data points were surveyed between 1992 and 2003, and the remaining (121) were surveyed in 2004, specifically for this study. To avoid spatial autocorrelation (Guisan and Zimmermann 2000) that could cause the model to yield misunderstandings of the ecological requirements of the species (Martinez-Meyer 2005), we used data points that had minimal distance intervals of 10 km.

Rodents of the Heteromyidae, Muridae, and Sciuridae families were collected using 2–6 transects containing 40 Sherman live-traps baited with rolled oats (Wilson et al. 1996). Gophers (Geomyidae) were captured with gopher traps. During the sampling in 2004, we also collected information about the presence of squirrels in the localities by direct observation and, in the case of gophers, by the presence of monticules in the entrance of their burrows. When a species was not captured or observed in a locality, it was taken as an "absence". Representative rodents from some of the localities were collected for accurate identification (Animal Care and Use Committee 1998), and were deposited in the mammal collection of CIB. For the nomenclature of species, we followed Alvarez-Castañeda and Patton (1999), Riddle et al. (2000), and Patton et al. (2007).

For each location, different types of environmental variables were recorded. Average annual precipitation (%), average annual temperature (°C), soil permeability, soil texture, soil type, and vegetation type were recorded from electronic maps (1:1000000 scale, CONABIO of Mexico). The slope derivative was taken from a digital elevation model created with topographical electronic maps (scale 1:50000) from Instituto Nacional de Estadistica y Geografia (INEGI). Distances from agricultural areas, altitude, and percentage of rock cover were measured in the field (see Appendix).

In the case of vegetation types that were obtained for each point, one of the following eight classes were assigned: xerophytic scrub, halophytic scrub, halophytic vegetation, sandy desert, coastal dune vegetation, mangrove, deciduous forest (oak and pine-oak forest); for the analysis, each class was taken into account as a different variable using 1 to indicate the presence of a type and 0 to indicate its absence (Appendix), which is commonly known as "dummy variables," the same was done with the variable of soil type, where 1 was used to indicate presence of a type of soil and 0 for its absence.

For the analysis, we also used information from WorldClim climate layers (bioclimatic variables) with a resolution of approximately 1 km (Hijmans et al. 2005) and temperature and precipitation data obtained directly from 115 meteorological stations in Baja California Sur. To choose which bioclimatic variables would be used in the analysis related to autocorrelation between the variables, we performed a principal component analysis (PCA) to extract variables that explain more variability between sites. From these, we retained significant variables based on the correlation matrices that we generated and divided them into categories of temperature and precipitation. At the end of the analysis, we also added some variables that, although they were not significant in the PCA, were minimally correlated with all the bioclimatic variables.

The information from meteorological stations was obtained through the Comision Nacional del Agua (CNA). We used temperature and precipitation records from 1950 to 2005, and split the data in two seasons: spring–summer and fall–winter. In the case of precipitation data, these were log transformed ($x = (\log + 1)$) to be normalized. The temperature and precipitation data for each site was interpolated using the ANUSPLIN program developed at the University of Australia (Chapman et al. 2005).

With the species and environmental variable data, we constructed three matrices (A, B, and C), where the sites are represented in rows; the environmental variables in columns, and the species presence with 1 (present) and 0 (absent). The differences in the three matrices were in the climatic variables: in matrix A, we used average annual temperature (°C) and total annual precipitation (%) obtained from electronic maps. In the B matrix, bioclimatic variables were: BIO_1 = annual mean temperature, BIO_4 = temperature seasonality (standard deviation), BIO_5 = max temperature of the warmest month, BIO_8 = mean temperature of the wettest quarter, BIO_12 = annual precipitation, BIO_14 = precipitation of the driest month, and BIO_15 = precipitation seasonality (coefficient of variation). In the C matrix, temperature (fall–winter), temperature (spring–summer), precipitation (fall–winter), and precipitation (spring–summer) were obtained from the meteorological stations.

Statistical analysis

We performed analysis of the species three times, following the protocol described by Peres-Neto et al. (2001) using the matrices A, B, and C each time.

For the first part of the analysis, we constructed a species–habitat single model for each species, using discriminant function analysis to distinguish between 'used' and 'unused' sites (Verner et al. 1986). In this part, we employed the presence–absence data for each species and the environmental variables. From this analysis, we obtained the Wilks' lambda that determines the discriminatory power of the model after each respective variable was included; the partial Wilks' lambda test that shows the unique contribution of the respective variable to discriminate between the sites where the species were present or absent; posterior probabilities that indicate the probability of a species presence at a site; and tolerance that shows redundancy of the factor in relation to other factors, where '1− tolerance' is equivalent to the 'R^2' of the variable.

The agreement between observed and predicted values (posterior probabilities) that were obtained with the discriminant function analysis was assessed with Cohen's Kappa statistics (Titus and Wagner 1984). Kappa values give an indication of the quality of the model fitness, where< 0.20 = poor, 0.21–0.40 = weak, 0.41–0.60 = moderate, 0.61–0.80 = good, and 0.81–1.00 = very good.

In the second part of the analysis, we used the environmentally constrained null program (Peres-Neto et al. 2001) to obtain the possible interactions among species. We initially used the Ct-RA1 algorithm, using presence and absence of the species at each site and the posterior probabilities obtained in the discriminant function analysis. In second run of the program, we used the Ct-RA2 algorithm, which can be applied in models constructed with the discriminant function analysis that result in poor predictions (Peres-Neto et al. 2001). Both protocols maintained fixed species frequencies. The program measures the possible association between species with three indices: the C-score that measures the possible negative associations, counting the sites where species A is present and species B is absent; and the *T* and *S* scores that measure the possible positive associations, where the *T*-score counts the sites where species A and B are jointly present or absent, and the *S*-score measures the number of sites shared by species A and B (Peres-Neto et al. 2001).

For this analysis, we used 1999 random permutations, reporting the associations with $P < 0.05$. To determine habitat-species affinities, we used PCA with the posterior probabilities of the species (Peres-Neto et al. 2001). Statistica v. 6.0 was used to perform the discriminant function analysis and PCA.

Results

By the end of the analysis, we could only provide results for 13 rodent species because (1) data on the California chipmunk (*Neotamias obscurus meridionalis*) that inhabits Baja California Sur is restricted to a very specific habitat covering a few square kilometers in the Sierra de San Francisco in the northeastern part of the State (Alvarez-Castañeda, field obs.) and (2) analyses from the matrices on the woodrat (*Neotoma bryanti, sensus* Patton et al. 2007) were not significant.

At the scale we used, rodents did not show selectivity for a particular type of soil and there were no differences between the sites where the species was present or absent. For this reason, this factor was excluded from the analysis.

Species that were found in a higher number of localities were: white-tailed antelope squirrel (*Ammospermophilus leucurus*), Merriam's kangaroo rat (*Dipodomys merriami*), Baja pocket mouse (*C. rudinoris*), and little desert pocket mouse (*C. arenarius*). Species at a higher percentage of sites that were correctly classified (sites predicted as present/absent) in all the analyses were: pinyon mouse (*P. truei*), Baja California rock squirrel (*Spermophilus atricapillus*), and San Diego pocket mouse (*C. fallax*), as shown in Table 1.

Of the species–habitat single models for each species constructed using different matrices, in general for most of the species, matrix B gave better results, although the differences using the other matrices were not really significant (see Wilks' lambda in Table 2). This result was confirmed with the Cohen's kappa test, where the agreement of observed and predicted values (posterior probabilities) was slightly different in each analysis with variations between 'weak' and 'good' for most of the species (Table 2).

From the discriminant function analysis, we can see that almost all variables alone had a low discriminatory power (partial lambda) in distinguishing between the sites where rodent species are present from those where the species are absent, but they were more useful in combination with the other variables (Wilks' lambda). Between the environmental variables employed, in general, vegetation type and percentage of rock cover were the variables more related to the distribution of several species (Table 3). Of the environmental variables that were significant in the distinction between the 'used' and 'unused' sites, in some cases it was easy to establish if the variable had a negative or positive effect (association) on the presence of the species, as with vegetation types (Table 3).

Table 1 Results of discriminant function analysis

Species	%SP[d]	Total %CC[a]			%CCP[b]			%CCA[c]		
		A	B	C	A	B	C	A	B	C
Ammospermophilus leucurus	64.00	79.50	82.00	78.00	87.50	88.28	86.72	65.28	70.83	62.50
Spermophilus atricapillus	4.00	98.00	98.50	98.50	75.00	62.50	62.50	98.96	100.00	100.00
Thomomys bottae	14.00	87.50	87.00	87.50	42.86	39.29	39.29	94.77	94.77	95.35
Chaetodipus arenarius	34.50	82.50	82.50	84.00	79.71	76.81	84.06	83.97	85.50	83.97
Chaetodipus fallax	8.50	94.00	96.50	97.00	58.82	82.35	88.24	97.27	97.81	97.81
Chaetodipus rudinoris	40.00	75.00	78.00	77.00	63.75	72.50	68.75	82.50	81.67	82.50
Chaetodipus spinatus	29.50	91.00	91.50	91.50	89.83	89.83	91.53	91.49	92.20	91.49
Dipodomys merriami	41.50	84.00	85.50	84.00	90.36	92.77	91.57	79.49	80.34	78.63
Dipodomys simulans	19.50	82.00	84.00	86.00	33.33	35.90	41.03	93.79	95.65	96.89
Peromyscus eva	25.00	79.50	80.50	77.50	46.00	46.00	42.00	90.67	92.00	89.33
Peromyscus fraterculus	9.00	93.50	94.50	93.00	55.56	61.11	55.56	97.25	97.80	96.70
Peromyscus maniculatus	26.00	81.50	81.00	84.00	46.15	48.08	57.69	93.92	92.57	93.24
Peromyscus truei	3.50	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00	100.00

[a] Total percentages of correctly classified sites

[b] Percentage of correctly classified sites where a species was present

[c] Percentage of correctly classified sites where a species was absent

[d] Percentages of sites where a species was present

Table 2 Results of the models produced with discriminant function analysis and Cohen's kappa statistics

Species	Wilks' lambda			*P*-level	Kappa		
	A	B	C		A	B	C
A. leucurus	0.60	0.57	0.60	0.00	0.54	0.60	0.51
S. atricapillus	0.76	0.74	0.70	0.00	0.74	0.76	0.76
T. bottae	0.78	0.76	0.75	0.00	0.42	0.39	0.40
C. arenarius	0.52	0.49	0.51	0.00	0.62	0.62	0.66
C. fallax	0.68	0.62	0.50	0.00	0.59	0.78	0.82
C. rudinoris	0.69	0.62	0.67	0.00	0.47	0.54	0.52
C. spinatus	0.36	0.34	0.36	0.00	0.79	0.80	0.80
D. merriami	0.47	0.45	0.46	0.00	0.68	0.71	0.68
D. simulans	0.78	0.77	0.76	0.00	0.32	0.38	0.46
P. eva	0.72	0.70	0.71	0.00	0.40	0.42	0.34
P. fraterculus	0.73	0.65	0.69	0.00	0.57	0.64	0.55
P. maniculatus	0.63	0.61	0.61	0.00	0.45	0.45	0.55
P. truei	0.03	0.02	0.03	0.00	1.00	1.00	1.00

However, with other variables, even though they were significant in the construction of the models, it was not possible to establish the type of association by using 'presence' or 'absence' of the species because they show intermediate values. In other words, their relationship type is weak, which makes these same variables significant or insignificant depending on the number of localities or on the type of variables employed in the construction of the models.

The PCA reflect a general pattern of spatial relationships among species based on preferences for some habitat characteristics and different responses to environmental gradients (Figs. 1, 2, 3). In the three analyses, PCA resulted in the retention of three components that explained 65.7% of the variance (CP-I = 37.5%, CP-II = 15.6%, and CP-III = 12.53%), 60.46% (CP-I = 34.14%, CP-II = 14.82%, and CP-III = 11.47%), 61.62% (CP-I = 33.75%, CP-II = 16.21%, and CP-III = 11.66%), respectively. In the three cases, the variable with the highest correlation for PC-I was the percentage of rock cover (0.86, −0.84 and −0.870, respectively), xerophytic scrub for PC-II in Analyses A and B (−0.69 and 0.54), temperature spring–summer in Analysis C (0.59); and forest for PC-III in Analyses A, B, and C (−0.56, 0.64, −0.59).

In the analyses with the environmentally constrained null model, the positive association measurement using *S* and *T* indices gave the same results with the Ct-RA1 and CT-RA2 algorithms. None of the analyses with the null model using the results of Analyses A, B, and C gave exactly the same results, and the same happened between the results of each analysis using algorithms Ct-RA1 and CT-RA2 (Figs. 4, 5, 6). The possible association between species that remained in Analyses A, B, and C with the C-score using Ct-RA1 were: *C. spinatus* and *C. fallax*, *P. eva* and *C. arenarius*, *P. eva* and *P. fraterculus*; of associations using Ct-RA2, all remained with the exception of the association *P. eva* and *P. fraterculus* in Analysis C. In the case of the analysis with *S* and *T* scores using Ct-RA1, the associations that coincided in Analyses A, B, and C were *C. arenarius* with *Dipodomys merriami* and *D. simulans* with *P. maniculatus*, with Ct-RA2 the results were the same as with Ct-RA1, but with the only difference that Ct-RA2 included an association of *C. spinatus* with *A. leucurus*.

Table 3 Summary of the variables that were more important for distinguishing between the sites where the species where present from those where they were absent

	Analysis A				Analysis B				Analysis C				
	Wilks' lambda	Partial lambda	*P*-level	R^2	Wilks' lambda	Partial lambda	*P*-level	R^2	Wilks' lambda	Partial lambda	*P*-level	R^2	Associate
A. leucurus													
% Rocks	0.62	0.97	0.02	0.35	0.60	0.95	0.00	0.39	0.63	0.96	0.00	0.36	
Halophytic vegetation	0.62	0.98	0.04	0.38	0.59	0.97	0.02	0.38	0.62	0.98	0.05	0.37	Negative
Mangrove swamp	0.62	0.96	0.01	0.83	0.59	0.97	0.01	0.84	0.63	0.97	0.01	0.83	Negative
Forest	0.62	0.97	0.02	0.77	0.59								Negative
Precipitation	0.63	0.95	0.00	0.55	0.59								
Crop distance					0.58	0.98	0.04	0.23					
BIO_1					0.59	0.97	0.02	0.91					
BIO_5					0.59	0.96	0.01	0.92					
S. atricapillus													
Slope	0.79	0.97	0.01	0.34	0.78	0.97	0.03	0.38	0.73	0.98	0.04	0.34	
Altitude	0.79	0.97	0.01	0.70	0.78	0.98	0.04	0.90	0.73	0.98	0.03	0.89	
% Rocks	0.79	0.97	0.01	0.41	0.81	0.95	0.00	0.44	0.75	0.95	0.00	0.42	
Permeability	0.81	0.94	0.00	0.31	0.80	0.95	0.00	0.50	0.76	0.94	0.00	0.49	
Crop distance	0.81	0.94	0.00	0.16	0.81	0.95	0.00	0.21	0.76	0.93	0.00	0.16	Positive
Temperature	0.78	0.98	0.05	0.53									
Temperature (fall–winter)									0.74	0.96	0.01	0.90	
Precipitation (fall–winter)									0.74	0.95	0.00	0.77	
Precipitation (spring–summer)									0.73	0.98	0.04	0.93	
T. bottae													
Permeability	0.81	0.97	0.03	0.33									
Crop distance	0.87	0.91	0.00	0.11	0.83	0.92	0.00	0.16	0.85	0.89	0.00	0.12	Positive
Total annual precipitation (%)	0.80	0.98	0.04	0.59									

Table 3 continued

	Analysis A				Analysis B				Analysis C				
	Wilks' lambda	Partial lambda	*P*-level	R^2	Wilks' lambda	Partial lambda	*P*-level	R^2	Wilks' lambda	Partial lambda	*P*-level	R^2	Associate
Temperature (spring–summer)									0.77	0.97	0.03	0.86	
Precipitation (spring–summer)									0.79	0.96	0.01	0.93	
C. arenarius													
% Rocks	0.64	0.82	0.00	0.32	0.59	0.83	0.00	0.35	0.636	0.81	0	0.332	Negative
Halophytic scrub	0.56	0.94	0.00	0.81	0.51	0.95	0.00	0.81	0.547	0.94	0	0.81	Positive
Sandy desert vegetation	0.58	0.90	0.00	0.79	0.55	0.89	0.00	0.79	0.577	0.9	0	0.79	Positive
Coastal dune vegetation	0.57	0.93	0.00	0.48	0.52	0.93	0.00	0.50	0.558	0.93	0	0.474	Positive
Xerophytic scrub	0.55	0.95	0.00	0.92	0.52	0.95	0.00	0.92	0.547	0.94	0	0.921	Positive
Forest	0.55	0.97	0.01	0.77	0.51	0.96	0.01	0.91	0.532	0.97	0.02	0.846	Negative
BIO_8					0.50	0.98	0.04	0.65					
Tropical deciduous forest									0.53	0.97	0.03	0.737	
C. fallax													
% Rocks	0.75	0.92	0.00	0.47	0.67	0.93	0.00	0.48	0.56	0.91	0.00	0.48	Positive
Soil texture	0.70	0.98	0.05	0.11	0.64	0.98	0.04	0.14					
Permeability	0.77	0.90	0.00	0.37	0.64	0.98	0.04	0.51					
Precipitation	0.75	0.92	0.00	0.58									
BIO_1					0.65	0.96	0.01	0.91					
BIO_8					0.65	0.96	0.01	0.62					
Altitude	0.52	0.98	0.04	0.90									
Temperature (spring–summer)									0.58	0.87	0.00	0.81	
C. rudinoris													
% Rocks	0.75	0.92	0.00	0.44	0.69	0.90	0.00	0.47	0.739	0.92	0	0.438	Positive
Crop distance	0.71	0.97	0.01	0.17	0.65	0.97	0.01	0.23	0.705	0.96	0.01	0.168	

Table 3 continued

	Analysis A				Analysis B				Analysis C				
	Wilks' lambda	Partial lambda	*P*-level	R^2	Wilks' lambda	Partial lambda	*P*-level	R^2	Wilks' lambda	Partial lambda	*P*-level	R^2	Associate
Xerophytic scrub	0.72	0.96	0.01	0.92	0.64	0.97	0.02	0.92	0.702	0.97	0.01	0.914	Positive
Slope					0.64	0.97	0.02	0.36					
Tropical deciduous forest					0.64	0.97	0.02	0.76					Positive
Forest					0.64	0.98	0.05	0.90	0.692	0.98	0.05	0.844	Negative
BIO_4					0.64	0.97	0.03	0.83					
BIO_12					0.65	0.97	0.01	0.94					
C. spinatus													
% Rocks	0.56	0.64	0.00	0.30	0.56	0.61	0.00	0.36	0.60	0.61	0.00	0.34	Positive
Permeability	0.37	0.96	0.01	0.30									
Tropical deciduous forest	0.37	0.98	0.03	0.73									Positive
Temperature	0.38	0.94	0.00	0.50									
BIO_1					0.36	0.95	0.00	0.92					
D. merriami													
% Rocks	0.62	0.77	0.00	0.32	0.59	0.77	0.00	0.34	0.62	0.76	0.00	0.33	Negative
Halophytic scrub	0.50	0.96	0.00	0.80	0.48	0.96	0.01	0.81	0.49	0.96	0.01	0.80	Positive
Sandy desert vegetation	0.50	0.94	0.00	0.79	0.49	0.94	0.00	0.79	0.50	0.94	0.00	0.79	Positive
Coastal dune vegetation	0.49	0.97	0.01	0.46	0.48	0.96	0.01	0.49	0.49	0.96	0.01	0.46	Positive
Xerophytic scrub	0.49	0.97	0.03	0.92	0.47	0.97	0.02	0.92	0.48	0.97	0.02	0.92	Positive
D. simulans													
% Rocks	0.84	0.95	0.00	0.39	0.84	0.93	0.00	0.43	0.83	0.92	0.00	0.41	Negative
Xerophytic scrub	0.81	0.98	0.05	0.92									Positive
Precipitation	0.82	0.96	0.01	0.56									
Temperature (spring–summer)									0.80	0.95	0.00	0.86	

Table 3 continued

	Analysis A				Analysis B				Analysis C				
	Wilks' lambda	Partial lambda	*P*-level	R^2	Wilks' lambda	Partial lambda	*P*-level	R^2	Wilks' lambda	Partial lambda	*P*-level	R^2	Associate
Precipitation (fall–winter)									0.79	0.98	0.03	0.77	
P. eva													
Permeability	0.80	0.90	0.00	0.33	0.74	0.96	0.01	0.49	0.76	0.95	0.00	0.48	
Tropical deciduous forest	0.75	0.97	0.02	0.74	0.74	0.96	0.00	0.76	0.75	0.96	0.01	0.74	Positive
Slope					0.72	0.98	0.04	0.38					
% Rocks									0.74	0.98	0.05	0.40	
P. fraterculus													
Altitude	0.76	0.96	0.01	0.69									
% Rocks	0.81	0.90	0.00	0.43	0.73	0.89	0.00	0.46	0.75	0.92	0.00	0.42	Positive
Permeability	0.75	0.97	0.03	0.35									
Forest	0.76	0.96	0.01	0.78					0.71	0.97	0.02	0.85	Negative
P. maniculatus													
Permeability	0.66	0.96	0.01	0.33									
Halophytic vegetation	0.66	0.96	0.01	0.40					0.639	0.96	0.01	0.388	Positive
Mangrove swamp	0.67	0.95	0.00	0.83	0.64	0.96	0.00	0.40	0.651	0.94	0	0.833	Positive
Precipitation	0.65	0.98	0.04	0.54	0.64	0.96	0.01	0.84					
Crop distance					0.63	0.97	0.02	0.23	0.628	0.98	0.05	0.154	
Sandy desert vegetation					0.64	0.96	0.00	0.79	0.639	0.96	0.01	0.787	Positive
BIO_8					0.64	0.96	0.01	0.63					
Temperature (spring–summer)									0.628	0.98	0.05	0.827	
P. truei													
Halophytic scrub	0.03	0.95	0.00	0.81	0.03	0.95	0.00	0.82	0.03	0.96	0.00	0.81	Negative
Sandy desert vegetation	0.03	0.95	0.00	0.80	0.03	0.95	0.00	0.80	0.03	0.95	0.00	0.81	Negative

Table 3 continued

	Analysis A				Analysis B				Analysis C				
	Wilks' lambda	Partial lambda	P-level	R^2	Wilks' lambda	Partial lambda	P-level	R^2	Wilks' lambda	Partial lambda	P-level	R^2	Associate
Coastal dune vegetation	0.03	0.97	0.02	0.47	0.03	0.98	0.04	0.49	0.03	0.98	0.04	0.46	Negative
Halophytic vegetation	0.03	0.97	0.02	0.41	0.03	0.98	0.04	0.40	0.03	0.97	0.03	0.40	Negative
Mangrove swamp	0.03	0.97	0.01	0.84	0.03	0.97	0.03	0.84	0.03	0.98	0.04	0.84	Negative
Tropical deciduous forest	0.03	0.92	0.00	0.76	0.03	0.92	0.00	0.77	0.03	0.92	0.00	0.76	Negative
Halophytic scrub	0.03	0.92	0.00	0.92	0.03	0.93	0.00	0.92	0.03	0.93	0.00	0.92	Negative
Forest	0.20	0.15	0.00	0.02	0.09	0.32	0.00	0.14	0.14	0.22	0.00	0.04	Positive
Slope					0.03	0.97	0.02	0.37	0.03	0.97	0.03	0.33	
BIO_14					0.03	0.97	0.02	0.50					
Precipitation (spring–summer)									0.03	0.97	0.03	0.88	

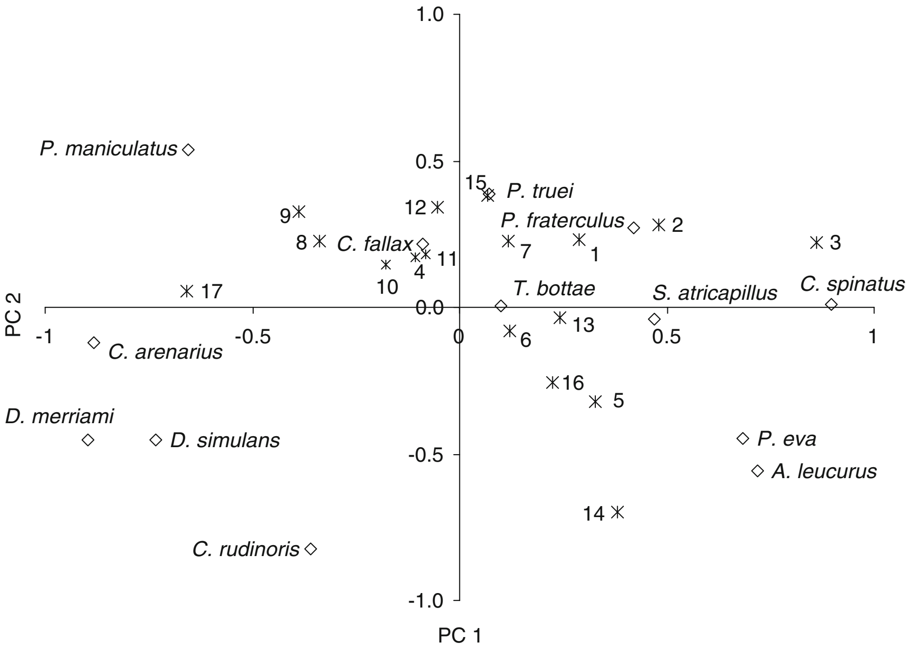


Fig. 1 Habitat affinities between species from the first analysis. Numbers represent correlation between environmental variables and principal components: Slope (1), altitude (2), % of rocks (3), soil texture (4), permeability (5), culture areas (6), vegetation cover (7), halophytic scrub (8), sandy desert vegetation (9), coastal dune vegetation (10), halophytic vegetation (11), mangrove swamp (12), tropical deciduous forest (13), xerophytic scrub (14), forest (15), temperature (16), precipitation (16)

Discussion

Although most of the isolated factors were not adequate for distinguishing between the sites (the species' habitat), the combination of all the factors gave an acceptable explanation for the presence of rodent species. This result agrees with those found by Illoldi et al. (2002) who indicated that their results point to a complex interplay of abiotic and biotic factors that define the geography of mammalian species in the states adjacent to the Gulf of California.

Most of the species showed low selectivity for the characteristics of the habitat used in the three analyses. This result could be related to the similarity between some sites, where species were present or absent (Johnson 2000), which mainly causes two situations. The first is a low discriminatory power of the variables in the prediction of 'presence' or 'absence' of the species; and the second is a hard determination in the type of association or preference of the species with some of the environmental variables (characteristics of habitat).

On the other hand, in some cases the lack of relationships between 'presence' or 'absence' of the species with variables that have been previously reported or noticed can be an artifact of scale in the analysis because causal factors may operate at different scales (Macpherson et al. 2006). For example, this situation happens with vegetation cover, where the classification was overly general and therefore did not show an influence. Nevertheless, fieldwork shows that most species of the genus *Chaetodipus* prefer areas with relatively

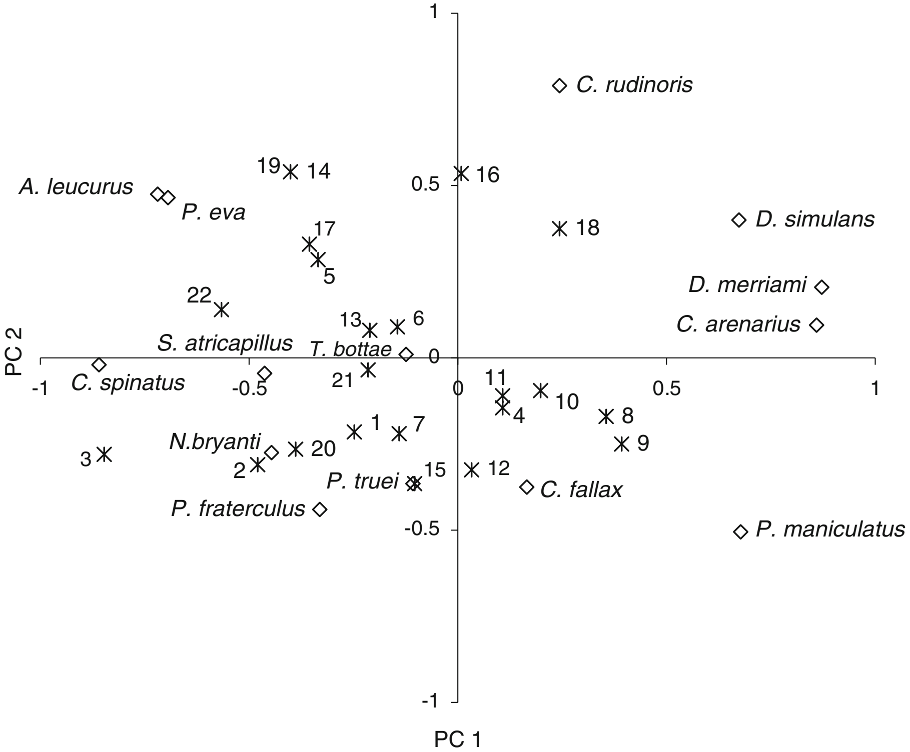


Fig. 2 Habitat affinities between species from the second analysis. Numbers represent correlation between environmental variables and principal components: Slope (1), altitude (2), % of rocks (3), soil texture (4), permeability (5), culture areas (6), vegetation cover (7), halophytic scrub (8), sandy desert vegetation (9), coastal dune vegetation (10), halophytic vegetation (11), mangrove swamp (12), tropical deciduous forest (13), xerophytic scrub (14), forest (15), bio_1 (16), bio_4 (17), bio_5 (18), bio_8 (19), bio_12 (20), bio_14 (21), bio 15 (22)

closed vegetation, in contrast to the genus *Dipodomys* that prefers open areas (Falkenber and Clarke 1998; Soltz and Valone 2000; Sullivan and Best 1997). Another example of lack of discrimination involves general soil texture, which was not linked with *C. arenarius*, whose presence is usually related to areas with sandy soils (Lackey 1991).

Lack of discrimination power of the models for some species could have resulted because the analysis did not include the most critical variables for the species, as in the case of *S. atricapillus*, that have a preference for sites with running water (Alvarez-Castañeda et al. 1996) and *D. simulans* that have a preference for habitats with deep soils, which, in turn, apparently leads to a mosaic pattern of distribution in the Magdalena Plains (25°N, 111.63°W). In other cases, as with *Thomomys bottae*, the result can be related to the fact that the species is not correctly represented in the data points because, under natural conditions, their presence or absence is difficult to determine since their distribution is discontinuous and at low density, as opposed to agricultural areas, where distribution is uniform and density increases (Alvarez-Castañeda and Patton 2004; Trujano-Alvarez and Alvarez-Castañeda 2007). For this reason, we suspect that this species shows 'absence' at some data points where they are probably present. These geographical matters affect the functionality of the analysis and resulted in a weak model for this species.

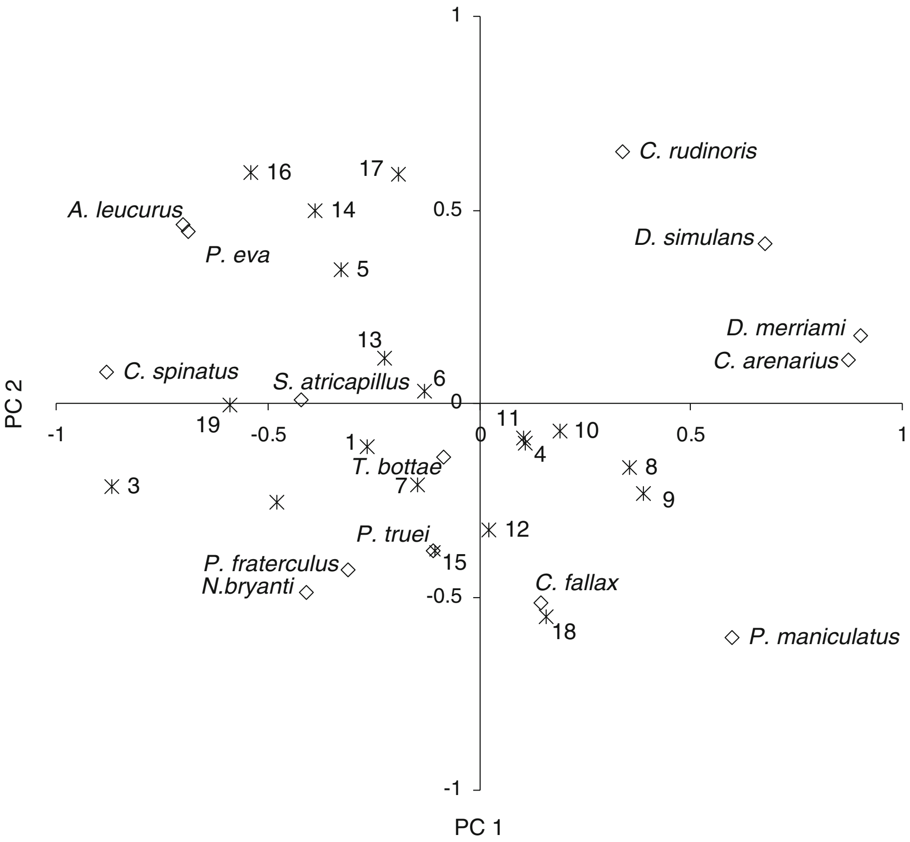


Fig. 3 Habitat affinities between species from the third analysis. Numbers represent correlation between environmental variables and principal components: Slope, (1), altitude (2), % of rocks (3), soil texture (4), permeability (5), culture areas (6), vegetation cover (7), halophytic scrub (8), sandy desert vegetation (9), coastal dune vegetation (10), halophytic vegetation (11), mangrove swamp (12), tropical deciduous forest (13), xerophytic scrub (14), forest (15), temperature spring–summer (16), temperature fall–winter (17), precipitation fall–winter (18), precipitation spring–summer (19)

The classification between the ‘used’ and ‘unused’ sites by a species was better for species that have a specific area of distribution, specific habitat requirements, or both. This is the case for: *P. truei*, which is restricted to rocky areas with pine-oak and oak forest at higher elevations in the Sierra de La Laguna in the southern part of the State (Alvarez-Castañeda and Patton 1999); and *C. fallax*, which is the species within the genus *Chaetodipus* with the narrowest distribution in State and is restricted to the northwestern part of the Desierto de Vizcaíno (Alvarez-Castañeda and Patton 1999).

Only *Neotoma bryanti* showed no relationship to the variables in the analysis. At this scale of analysis, *N. bryanti* seems to occur in several habitats and does not show a preference for a specific habitat characteristic. According to Verts and Carraway (2002), the critical habitat feature related to this species is the presence of features that offer protection from predators. We noticed that *N. bryanti* was present on sites with many rocks or where the vegetation was dense or clustered, but this was not reflected in the analyses. Another explanation is that *N. bryanti* prospers with a specific plant diet (Sorensen et al.

	C-score							S and T-score				
	A. leucurus	*C. arenarius*	*C. fallax*	*C. rudinoris*	*C. spinatus*	*P. eva*	*P. fraterculus*	*A. leucurus*	*C. arenarius*	*D. merriami*	*D. simulans*	*P. maniculatus*
A. leucurus												
S. atricapillus												
T. bottae												0.033
C. arenarius				0.030		0.002				0.003	0.001	0.022
C. fallax					0.006							
C. rudinoris												
C. spinatus			0.021					0.019				
D. merriami									0.001			
D. simulans									0.009			0.028
P. eva		0.002					0.003					
P. fraterculus						0.009						
P. maniculatus	0.036								0.010			
P. truei												

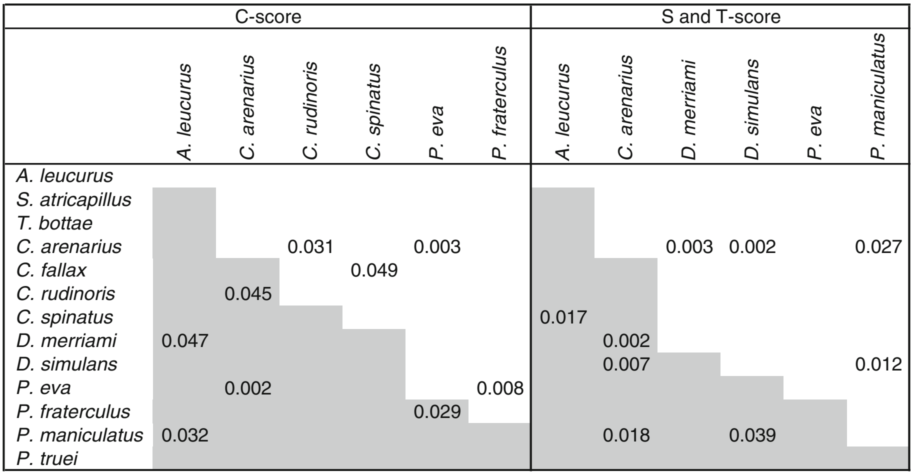
Fig. 4 Results of the first analysis with the environmentally constrained null model. The upper part shows the results from the Ct-RA1 algorithm. The shaded area contains the results from the Ct-RA2 algorithm

	C-score					S and T-score					
	C. arenarius	*C. fallax*	*C. spinatus*	*P. eva*	*P. fraterculus*	*A. leucurus*	*T. bottae*	*C. arenarius*	*D. merriami*	*D. simulans*	*P. maniculatus*
A. leucurus											
S. atricapillus											
T. bottae								0.046			0.017
C. arenarius				0.003					0.005	0.004	
C. fallax			0.020								
C. rudinoris	0.043										
C. spinatus		0.038				0.030					
D. merriami								0.001			
D. simulans								0.008			0.026
P. eva	0.002				0.009						
P. fraterculus				0.025							
P. maniculatus							0.050	0.028			
P. truei											

Fig. 5 Results of the second analysis with the environmentally constrained null model. The upper part shows the results from the Ct-RA1 algorithm. The shaded area contains the results from the Ct-RA2 algorithm

2005). In general, we found that the amount of rock cover is one of the most important habitat features for rodents in the State. This factor is important because rocks are refuges for some species (Rogovin et al. 1992).

According to Peres-Neto et al. (2001), associations between species remain, even when taking into account species–environmental relationships, are related to three specific situations: (a) species associations are truly related to biotic interactions; (b) interactions



	C-score						S and T-score					
	A. leucurus	*C. arenarius*	*C. rudinoris*	*C. spinatus*	*P. eva*	*P. fraterculus*	*A. leucurus*	*C. arenarius*	*D. merriami*	*D. simulans*	*P. eva*	*P. maniculatus*
A. leucurus												
S. atricapillus												
T. bottae												
C. arenarius			0.031		0.003				0.003	0.002		0.027
C. fallax				0.049								
C. rudinoris		0.045										
C. spinatus							0.017					
D. merriami	0.047							0.002				
D. simulans								0.007				0.012
P. eva		0.002				0.008						
P. fraterculus					0.029							
P. maniculatus	0.032							0.018		0.039		
P. truei												

Fig. 6 Results of the third analysis with the environmentally constrained null model. The upper part shows the results from the Ct-RA1 algorithm. The shaded area contains the results from the Ct-RA2 algorithm

between environmental variables at particular sites might facilitate coexistence; and (c) some important environmental variables are not used in the species–environmental models. Any of these situations may contribute to their contiguous or disjunctive distribution. In the three analyses of associations between species, we obtained slightly different results between the analyses and Ct-RA1 and Ct-RA2 algorithms. This was expected for some of the species because we obtained weak prediction models. Most of the positive relationships were between species that are usually present in the same habitat (Figs. 1, 2, 3), while the negative relationships in the three analyses were between species that were morphologically similar. Of the total possible negative interactions shown by the environmental model, we think that the negative association of *P. eva* with *P. fraterculus* and *C. spinatus* with *C. fallax* could be truly related to biotic interactions, a case of competitive exclusion (Gotelli 2001) that affects the distributional pattern of the species. The first case could be supported by the results of PCA that suggest that the distribution of *P. eva* with *P. fraterculus* do not overlap and each one is excluded from the other's area and by the fact that the two species were not actually collected in the same habitat or locality in this study. In the second case, although localities in the northern part of the Baja California Peninsula have been reported where *C. spinatus* and *C. fallax* have been found together (Hall 1981; Lackey 1996), we never found both species in the same place during our field work. Nevertheless, *C. fallax* was found in habitats with similar characteristics to those where *C. spinatus* was found. In the case of other types of negative relationships shown by the null model (with Ct-RA1), these are probably related to some important environmental variables that were not used in the species– environmental models or to a dissimilarity in habitat preferences of the species where Ct-RA2 was used. An example is the negative association between *A. leucurus* and *D. merriami* determined with Analysis C, where we know that *A. leucurus* is essentially absent in places where the other species is more frequently found, such as coastal dunes.

In the positive association shown by the null model (with Ct-RA2), we can see that we are focusing on species that share preferences for similar habitats or characteristics that cause these species to inhabit a similar area together; in these cases we believe that these positive associations are just co-occurrence.

The protocol we followed was useful for detecting possible associations between rodent species, where the variables may have an effect on their actual distribution. However, it did not provide really useful conclusion in the establishment of habitat preferences of the rodent species there is a lack of strong relationships of species with the selected environmental variables, that some of the important variables were not used in the analysis for particular species, or that the scale of some of the variables employed was not sensitive to providing distinct relationships between species.

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Appendix

See Table 4.

Table 4 Values given to the factors measured in this study

Name	Values
1. Precipitation of total annual (%)[a]	1 = 5–10.2, 2 = more than 18%, 3 = > 36%
2. Average annual temperature (°C)[a]	1 = 12–18, 2 = 18–22 and 3 = > 22
3. Permeability[a]	1 = Low, 2 = medium to high, 3 = medium to high generalized
4. Soil texture[a]	1 = Clayey, 2 = loamy, 3 = sandy
5. Soil type[a]	0 to indicate the absence of a type of soil and 1 to indicate its presence
6. Vegetation type[a]	0 = absence 1 = presence. For forests, 1 for oak forest; 2 for pine-oak forest
7. Distances from agricultural areas (m)[b]	0 = > 300, 1 = 201–300, 2 = 101–200, 3 = 0–100
8. Altitude (m)[b]	1 = 0–199, 2 = 200–399, 3 = 400–599, 4 = 600–799, 5 = 800–999, 6 = 1,000–1,199, 7 = 1,200–1,399, 8 = 1,400–1,599, 9 = 1,600–1,799, 10 = 1,800–1,900
9. Vegetation cover (%)[b]	0 = 0–9, 1 = 10–19, 2 = 20–29, 3 = 30–39, 4 = 40–49, 5 = 50–59, 6 = 60–69, 7 = 70–79, 8 = 80–89, 9 = 90–99, and 10 = 100
10. Percentage of land covered by rocks[b]	0 = 0–9, 1 = 10–19, 2 = 20–29, 3 = 30–39, 4 = 40–49, 5 = 50–59, 6 = 60–69%, 7 = 70–79, 8 = 80–89, 9 = 90–99, and 10 = 100
11. Slope (%)[b]	1 = < 1, 2 = 1–5, 3 = 6–10, 4 = 11–20, 5 = 21–30, 6 = 31–40, 7 = 41–50, and 8 = 51–60

[a] Data derived from electronic maps

[b] Data collected in the field

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