

# Habitat heterogeneity, species diversity and null models

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Cramer, M. J. and Willig, M. R. 2005. Habitat heterogeneity, species diversity and null models. – *Oikos* 108: 209–218.

The habitat heterogeneity hypothesis states that an increase in habitat heterogeneity leads to an increase in species diversity. We tested this hypothesis for a community of small mammals in the semiarid, sand-shinnery-oak ecosystem of the southwestern United States. We used indices of differentiation diversity to quantify differences between two habitat types (blowouts in a sand-shinnery-oak matrix) in terms of species diversity. The Wilson-Shmida index ( $\beta_T$ ) considers species composition only, whereas the Morisita-Horn index ( $C_{MH}$ ) also takes species abundances into account. We constructed null models to test the hypothesis that differentiation diversity between habitat types is greater than that produced by stochastic processes. Two models were constructed, one based on the random placement of species and one based on the random placement of individuals. No evidence supported the hypothesis that habitat heterogeneity enhances diversity of a landscape by increasing the number of species in an area. Indeed, paired habitats were more similar than chance alone would dictate in terms of species identities. In contrast, habitat heterogeneity affects diversity by significantly altering the relative proportions of species in contrasting habitat types. Because seeds differentially accumulate at the interface between blowouts and matrix, the high productivity of the edge may actually homogenize habitat types in terms of species richness. Nonetheless, blowouts might best be considered to be microhabitats which enhance or complement the value of the matrix even though the species which use either habitat type are identical.

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The habitat heterogeneity hypothesis proposes that an increase in the number of habitats leads to an increase in species diversity in a landscape (MacArthur and MacArthur 1961) because of an expansion in the number of partitionable niche dimensions. This facilitates specialization and avoidance of competition through spatial segregation. The idea that habitat heterogeneity affects species diversity has been applied to successional (Bollinger 1995) and disturbed environments (Levey 1988, Greenberg et al. 1995), as well as to latitudinal (Willig 2000, Willig et al. 2003), elevational (Finch 1989), and humidity gradients (Daniels et al. 1992). Indeed, maintaining habitat heterogeneity has been proposed as a means of conserving species richness

in habitats threatened by human activities (McGarigal and McComb 1992, Greenberg et al. 1995).

## Mechanisms enhancing diversity

Spatial heterogeneity can increase diversity in one of two ways. First, adaptations to one habitat may result in competitive inferiority in another. To the extent that such tradeoffs exist, distinct habitats within a landscape may differ in species composition and abundance. These differences would lead to increased  $\beta$  diversity, which measures the differences in diversity between habitat types. Increased  $\beta$  diversity among habitats enhances

Accepted 22 June 2004

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the  $\gamma$ , or regional, diversity of the landscape (Whittaker 1972). For habitat heterogeneity to enhance diversity in this way, each habitat type (singly or in combination with other patches of the same type) must be large enough to support viable populations. In landscapes where distinct habitats can support populations of different species, diversity should be enhanced by the presence of specialists that exhibit distinct habitat preferences (sensu Rosenzweig 1981). Alternatively, in landscapes where multiple habitats are nonexistent, highly dispersed, or of low areal extent, diversity may be low because of the absence of specialization and intense competition among generalists. Second, small habitat patches may increase overall quality of a pervasive habitat type (i.e. matrix) in which they occur by supplying predator-free space or complementary resources. Such patches need not be sufficiently large to support distinct populations alone or in combination with other patches, as long as the presence of these alternative habitat types improves the quality of the matrix for some species. In certain circumstances, species that cannot defend such small habitat patches may need to specialize on alternate habitat types to remain in the community. This leads to shared habitat preferences (sensu Rosenzweig 1991), and habitat-specific differences in species abundances.

The sand-shinnery-oak landscape of the southwestern United States is ideal for addressing questions of habitat heterogeneity and species diversity. Blowouts, formed by wind, are areas of open sand with little vegetation (Holland 1994, Deslippe et al. 2001); they are located within a dense shrub-dominated matrix (sand shinnery oak, *Quercus havardii* Rydberg). Due to the small size and the clumped dispersion pattern of blowouts, any effects of this alternative habitat type on diversity would likely be demonstrated via shared habitat preferences by constituent species.

Previous studies of mammals suggest that habitat heterogeneity may be an important structuring agent in this landscape. Total rodent density and species composition differed between areas that had been cleared of shrubs and those that were undisturbed (Colbert 1986, Willig et al. 1993). Moreover, diet overlap was minimal among rodent species in a shinnery oak-mesquite grassland (Best et al. 1993), suggesting exclusive specialization on conditions or resources offered by particular habitats. Finally, habitat preferences of species common to this system have been studied, and the most common species, *Dipodomys ordii*, demonstrates seasonal habitat preferences, whereas other species avoid blowouts (Cramer and Willig 2002). The objective of this study is to assess whether population-level processes (habitat preferences of individual species) translate into community-level effects (species diversity) in a manner consistent with the habitat heterogeneity hypothesis.

## Quantitative approaches

Two approaches have been used to determine the effects of habitat heterogeneity on species diversity. One quantifies the linear relationship between species diversity and habitat diversity (MacArthur and MacArthur 1961, MacArthur 1964, Rosenzweig and Winakur 1969). This approach is problematic because the relationship between habitat and species diversities may be nonlinear. Moreover, other environmental factors, (e.g. climate) simultaneously may affect both species diversity and habitat diversity. A second approach involves  $\beta$ , or differentiation diversity (Whittaker 1960, Harrison 1997, 1999), which quantifies species dissimilarity between habitats in terms of species identities or abundances (Magurran 1988). When the significance of this metric is evaluated using a null model approach (Gotelli and Graves 1996), a series of constraints may be considered so as to isolate the effects of a purported structuring mechanism.

## Methods

The study area was located in Yoakum County, Texas, USA, approximately 19 km southwest from the town of Sundown (33°19'N to 102°37'W). The soil consists of aeolian deposits or cover sands, and has good water retention (Dhillion et al. 1994). The climate is warm-temperate and semiarid, with fluctuating temperatures during winter (Willig et al. 1993). Annual precipitation averages 41 cm, with most rainfall occurring from May through October (Dhillion et al. 1994).

The study area consisted of two adjacent fields separated by a barbedwire fence. The eastern field (approximately 500 km<sup>2</sup>) was grazed by cattle from September through March. The western field was smaller (approximately 200 km<sup>2</sup>) and ungrazed throughout the study. The plant community in both fields is dominated by sand-shinnery oak, *Quercus havardii* (Dhillion et al. 1994), a low-growing clonal shrub that has a large proportion of its biomass belowground. Other common plant species at the site include sand sagebrush (*Artemisia filifolia* Torrey), little bluestem (*Schizachyrium scoparium* Michaux), sand bluestem (*Andropogon hallii* Hackel), sand dropseed (*Sporobolus cryptandrus* Torrey), and sand paspalum (*Paspalum setaceum* Michaux). Resident rodents (Cramer 1998) include Ord's kangaroo rat (*Dipodomys ordii* Woodhouse), plains pocket mouse (*Perognathus flavescens* Merriam), hispid pocket mouse (*Chaetodipus hispidus* Baird), deer mouse (*Peromyscus maniculatus* Wagner), western harvest mouse (*Reithrodontomys megalotis* Baird), plains harvest mouse (*R. montanus* Baird), northern grasshopper mouse (*Onychomys leucogaster* Baird), hispid cotton rat (*Sigmodon hispidus*

Say and Ord), southern plains woodrat (*Neotoma micropus* Baird), house mouse (*Mus musculus* Linnaeus), and spotted ground squirrel (*Spermophilus spilosoma* Bennett).

We selected ten random sites at the study area; each contained two habitats, a blowout and associated undisturbed sand-shinnery-oak habitat (hereafter referred to as matrix). Blowouts, defined as areas devoid of sand-shinnery-oak (Dhillion et al. 1994), were selected only if they met four criteria. The blowout had to be larger than the trapping configuration (14 × 12 m), be at least 30 m from other selected sites (minimizing the likelihood of rodents traveling among sites), be of recent origin (could not be overgrown with oak), and have been generated by natural forces rather than human activities.

Trapping was conducted in three seasons during 1996–1997: summer (July–September), characterized by maximum plant development and reproduction; winter (November–March), characterized by oak defoliation; and spring (April–June), characterized by oak refoliation (Colbert 1986). Trapping was not conducted for two nights prior to, including, and following a full moon because many nocturnal rodents curtail activity during this period (Carley et al. 1970). A census period characterized each season. We established two pairs of parallel census lines at each site, one pair in the blowout and the other in adjacent undisturbed sand-shinnery-oak habitat. Census lines were 2 m apart and 10 m in length. Each census line contained six trapping stations. One Sherman live trap was located at each station (12 traps in each of two habitats). Length of census lines was constrained by blowout size. This trapping configuration was used to equally sample both habitat types; longer census lines would bias sampling toward matrix habitat. The census trapping period continued at each site until the number of unmarked animals was less than 5% of the number of previously marked animals at that site (Lacher and Alho 1989). Traps were baited with a mixture of sunflower seeds, rolled oats, and peanut butter. All captured rodents were marked by toe-clipping, identified as to species and sex, and weighed before release. To reduce mortality related to hypothermia, trapping was not conducted when the expected overnight minimum temperature was below 2°C. Voucher specimens were collected in a nearby area prior to the initiation of the study, and are deposited at The Museum of Texas Tech University, Lubbock, TX, USA.

### Diversity indices

Two indices of  $\beta$  diversity quantified differences in species composition between habitat types (matrix vs blowout). Both were calculated for each of the 10 replicate sites. The Wilson-Shmida index ( $\beta_T$ ) considers

differences only in terms of the presence or absence of species (Wilson and Shmida 1984):

$$\beta_T = \frac{g(H) + l(H)}{2\alpha} \quad (1)$$

where  $g(H)$  is the number of species present in habitat 2 but not in habitat 1,  $l(H)$  is the number of species present in habitat 1 but not habitat 2, and  $\alpha$  represents the average species richness of paired habitats (Magurran 1988). For binary data, the Wilson-Shmida index is one of the best estimates of  $\beta$  diversity because it is insensitive to sample size and performs well in comparative studies (Wilson and Shmida 1984).

In contrast, the Morisita-Horn index ( $C_{mH}$ ) quantifies differences in terms of the identities and abundances of species (Magurran 1988). We quantified abundances using the minimum number of individuals of each species known alive (MNKA; Krebs, 1999). MNKA has been shown to accurately estimate population sizes (Cameron 1977, Nupp and Swihart 1996, Slade and Blair 2000). The Morisita-Horn index is unbiased with respect to sample size and diversity (Wolda 1981), and is calculated as

$$C_{mH} = \frac{2 \sum_{i=1}^S (n_{ai} \times n_{bi})}{(da + db) \times N_a \times N_b} \quad (2)$$

where  $S$  is the total species richness for paired habitats,  $n_{ai}$  is the number of individuals of the  $i$ th species in habitat a,  $n_{bi}$  is the number of individuals of the  $i$ th species in habitat b,  $N_a$  is the total number of individuals of all species in habitat a, and  $N_b$  is the total number of individuals of all species in habitat b. The terms  $da$  and  $db$  are defined as

$$da = \frac{\sum_{i=1}^S n_{ai}^2}{N_a^2} \quad (3)$$

$$db = \frac{\sum_{i=1}^S n_{bi}^2}{N_b^2} \quad (4)$$

### Null models of differentiation diversity

Directional (one-tailed) hypotheses for each index evaluated if habitat heterogeneity enhanced landscape diversity by increasing  $\beta$  diversity. The hypothesis that the observed index was larger than expected due to chance was assessed for  $\beta_T$ . When habitats contain exactly the same set of species, this index equals zero, whereas it equals unity when no species are shared between habitats. In contrast,  $C_{mH}$  equals one when each habitat comprises the same species in identical proportions;

consequently, the alternate hypothesis was that  $C_{mH}$  equals zero.

Null models assessed hypotheses regarding  $\beta$  diversity. More specifically, reiterative simulations (Manly 1991) were used to represent the probability density functions for the indices under conditions of no differences in species composition and abundances between habitats. In such an approach (Gotelli and Graves 1996), an algorithm is constructed to eliminate the effects of a parameter of interest (i.e. habitat heterogeneity), on the probability density function for a metric (i.e.  $\beta_T$  or  $C_{mH}$ ). The empirical value for the metric can then be compared to this distribution to estimate significance.

Separate suites of null models were constructed for hypotheses concerning presence–absence (Wilson-Shmida) versus abundance of species (Morisita-Horn). All models were executed via Matlab v4.2 (MathWorks Inc. 1995); the code appears in Cramer (1998). Two different kinds of models were constructed – one based on the random placement of species and the other based on the random placement of individuals. The significance of  $\beta_T$  and  $C_{mH}$  can be assessed using models based on the random placement of individuals. Models based on the random placement of species cannot be applied to  $C_{mH}$ , because the metric requires knowledge of the allocation of individuals into species for both simulated and empirical habitats.

The first model was constrained by empirical species richness for each habitat at each site. For each season, the pool from which species were selected was set equal to the species list for the combined sites regardless of habitat type. Species were selected without replacement from this species pool until observed richness was obtained for each habitat at each site.  $\beta_T$  was then calculated for each of the 10 sites. These 10 values were then averaged, producing a metric (mean  $\beta_T$ ) for the null model. The model was iterated 1000 times, producing a probability density function for random values of mean  $\beta_T$ , assuming habitat heterogeneity has no effect on differences in species composition. The empirical metric was compared to the probability density function to test the hypothesis that  $\beta$  diversity was significantly larger than expected by chance alone.

The second model was constrained by empirical abundances (number of individuals regardless of species) for each habitat at each site. For each season, the pool from which individuals were selected was determined by combining abundance data for all species at all sites regardless of habitat. In essence, the species pool was set equal to the empirical species abundance distribution for the entire study area (sum of both habitats at the 10 sites). The model then selected individuals at random and with replacement for each habitat at each site, until the simulated abundances in each habitat were the same as those in the actual habitats.  $C_{mH}$  was calculated for each of the 10 sites. These 10 values were averaged,

producing a metric (mean  $C_{mH}$ ). In addition, the abundances of each species for each habitat at each site were converted to presences ( $n \geq 1$ ) or absences ( $n = 0$ );  $\beta_T$  was calculated for each of the 10 sites and then averaged, producing a metric (mean  $\beta_T$ ). This was iterated 1000 times, producing a probability density function for each metric (mean  $C_{mH}$  and mean  $\beta_T$ ). To assess the hypotheses that  $C_{mH}$  is smaller or  $\beta_T$  is larger than expected due to chance alone, the empirical metric was compared to corresponding probability density function for simulated metrics.

### Seasonal variation in diversity

A repeated-measures analysis of variance (Wilkinson et al. 1996) was used to assess temporal variation in  $\beta$  diversity based on MNKA for each species. Repeated measures were necessary because the assumption of independence was violated (i.e. measurements were taken at the same paired sites in different seasons). Post-hoc hypothesis testing was used to determine where differences occurred for significant factors. For significant seasonal effects, two hypotheses were evaluated: the first tested the difference between summer and winter and the second tested the difference between winter and spring. Although separate analyses were conducted for each diversity index, probabilities were modified using Bonferroni's sequential adjustment (Rice 1989) to avoid spurious rejection of the null hypothesis, thereby maintaining experiment-wise error rate at 0.05.

### Results

Nine taxa of nocturnal rodent were captured from the sand-shinnery-oak ecosystem (Table 1). Although both *Peromyscus leucopus* Rafinesque and *P. maniculatus* occur in the sand-shinnery-oak ecosystem, these species are difficult to identify in the field (Hall 2001). Consequently, they are not distinguished from each other and are designated as *Peromyscus* spp. in all analyses. Because even combined as a single taxon *Peromyscus* spp. are rare components of the community, it is unlikely that this approach biased estimates of diversity in an appreciable fashion. Three species dominated the community (*Dipodomys ordii*, *Onychomys leucogaster* and *Perognathus flavescens*) in terms of abundance as well as frequency of occurrence, and did so in both habitat types. Nonetheless, the degree of dominance by *D. ordii* was greater in blowout habitats than in matrix habitats (Fig. 1), resulting in a more diverse rodent assemblage in the matrix (mean Shannon Index,  $H' = 0.53393$ ) than in the blowout ( $H' = 0.39279$ ) habitat (paired t-test:  $t = -3.99$ ,  $p < 0.001$ ).

Table 1. Species composition of blowout and matrix habitats in each of three phenological seasons in the sand-shinnery-oak ecosystem of the southwestern USA. Frequency of occurrence was equal to the number of replicates at which a particular species was captured during each season (maximum equals 10).

Species	Summer		Winter		Spring		Total	
	Blowout	Matrix	Blowout	Matrix	Blowout	Matrix	Blowout	Matrix
Minimum number known alive (MNKA)								
<i>Dipodomys ordii</i>	29	24	87	113	92	116	208	253
<i>Onychomys leucogaster</i>	13	13	16	38	41	59	70	110
<i>Perognathus flavescens</i>	3	18	1	4	5	28	9	50
<i>Peromyscus spp.</i>	0	0	0	4	8	8	8	12
<i>Reithrodontomys montanus</i>	0	2	1	4	0	4	1	10
<i>Reithrodontomys megalotis</i>	0	0	2	0	0	1	2	1
<i>Chaetodipus hispidus</i>	0	3	0	0	0	0	0	3
<i>Sigmodon hispidus</i>	0	1	0	0	0	1	0	2
<i>Neotoma micropus</i>	1	0	0	0	1	0	2	0
<i>Mus musculus</i>	0	0	0	1	0	0	0	1
Total	46	61	107	164	147	217	300	442
Frequency of occurrence								
<i>Dipodomys ordii</i>	10	10	10	10	10	10	30	30
<i>Onychomys leucogaster</i>	6	7	9	9	10	10	25	26
<i>Perognathus flavescens</i>	4	9	1	3	4	10	9	22
<i>Peromyscus spp.</i>	0	0	0	4	4	4	4	8
<i>Reithrodontomys montanus</i>	0	2	1	3	0	3	1	8
<i>Reithrodontomys megalotis</i>	0	0	2	0	0	1	2	1
<i>Chaetodipus hispidus</i>	0	3	0	0	0	0	0	3
<i>Sigmodon hispidus</i>	0	2	0	0	0	1	0	3
<i>Neotoma micropus</i>	1	0	0	0	1	0	2	0
<i>Mus musculus</i>	0	0	0	1	0	0	0	1
Total	21	33	23	30	29	39	73	102

## Species diversity

### Presence-absence

Analyses of the Wilson-Shmida index do not support the habitat heterogeneity hypothesis. The model constrained by the number of species in each habitat at each site

indicated that the existence of two habitat types did not enhance diversity in any season (Fig. 2;  $p > 0.99$ ). In fact, each habitat type contributed less to overall diversity than expected by chance alone for each season. The model constrained by the number of individuals in each habitat at each site also indicated that the habitat types were no more different than expected by chance, although the results for summer approached significance ( $p = 0.065$ ; Fig. 3A). Results for winter ( $p = 0.694$ ; Fig. 3B) and spring ( $p = 0.901$ ; Fig. 3C) indicated no significant effect of habitat heterogeneity on diversity measured by the Wilson-Shmida index.

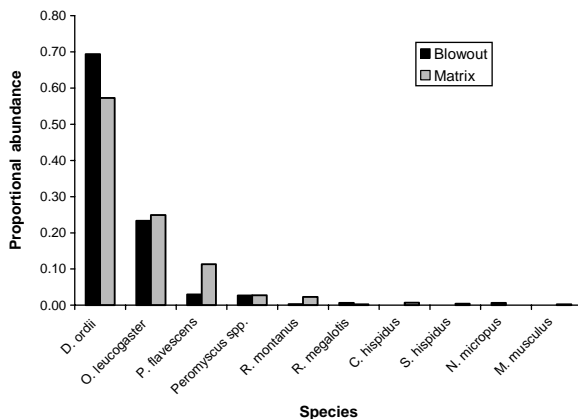


Fig. 1. Species abundance distributions for the rodent assemblages in each of two habitats (blowouts versus matrix) in a sand-shinnery-oak community. Relative proportions were based on combined data for all three seasons (Table 1). Species composition differed significantly between the two habitat types (contingency  $\chi^2$  test:  $X^2 = 25.41$ , d.f. = 6,  $p < 0.001$ ) after pooling rare taxa (*R. megalotis* and *C. hispidus* into a group; *S. hispidus*, *N. micropus* and *M. musculus* into a group) to fulfill assumptions of the test.

### Species abundance

Differences between habitat types significantly contributed to diversity in the summer based on analyses of Morisita-Horn index ( $p = 0.022$ ; Fig. 4A). However, differences between habitat types were no larger than expected by chance in the other seasons (winter:  $p = 0.912$ ; Fig. 4B; spring:  $p = 0.484$ ; Fig. 4C).

### Seasonal comparisons

No differences occurred among seasons for the Wilson-Shmida index ( $F_{2,18} = 1.02$ ,  $p = 0.378$ ). The Morisita-Horn index demonstrated significant seasonal effects ( $F_{2,18} = 17.55$ ,  $p < 0.001$ ): higher in the winter than in the summer ( $F_{1,9} = 15.67$ ,  $p = 0.003$ ), but equivalent in winter and spring ( $F_{1,9} = 0.002$ ,  $p = 0.969$ ).

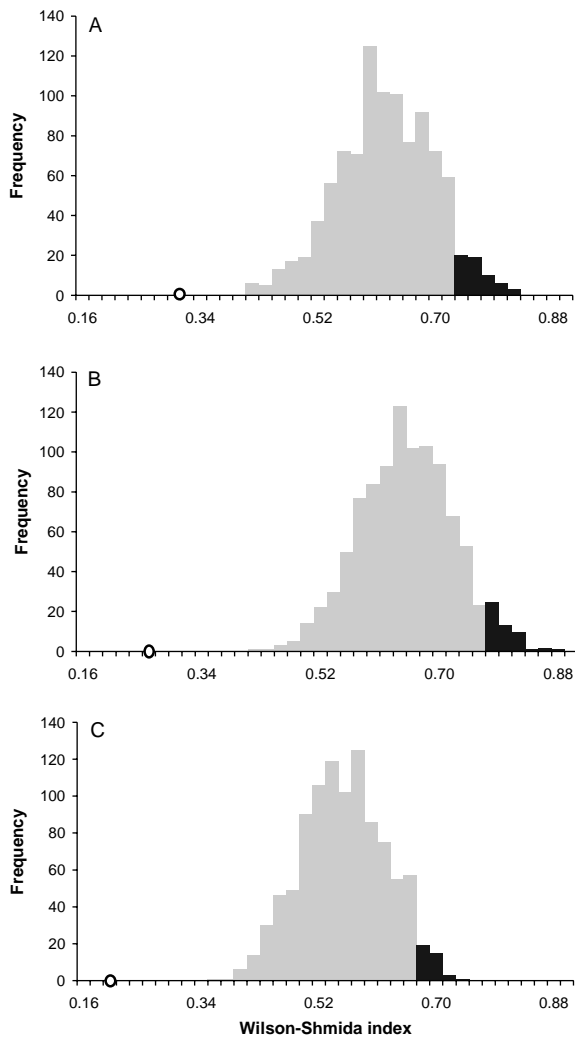


Fig. 2. Results of null model analyses based on the random placement of species. The simulated probability density function for the Wilson-Shmida index is constrained by empirical species richness on each grid for each season. Critical regions are shaded and define the area of the distribution consistent with the habitat heterogeneity hypothesis. The open circles on the x-axis represent empirical values of the Wilson-Shmida index. Results for summer (A, mean  $\beta_T = 0.310$ ,  $P > 0.999$ ), winter (B, mean  $\beta_T = 0.261$ ,  $P > 0.999$ ), and spring (C, mean  $\beta_T = 0.198$ ,  $P > 0.999$ ) are nonsignificant.

## Discussion

We explored the effect of spatial heterogeneity and temporal variation on species diversity by considering differentiation diversity between habitat types at replicated sites in different seasons. The presence of blowouts affected species abundances, but not the presence or absence of species in each habitat type. In addition, there was a significant seasonal effect on diversity. Considerations of scale and edge effects facilitate an interpretation of these results.

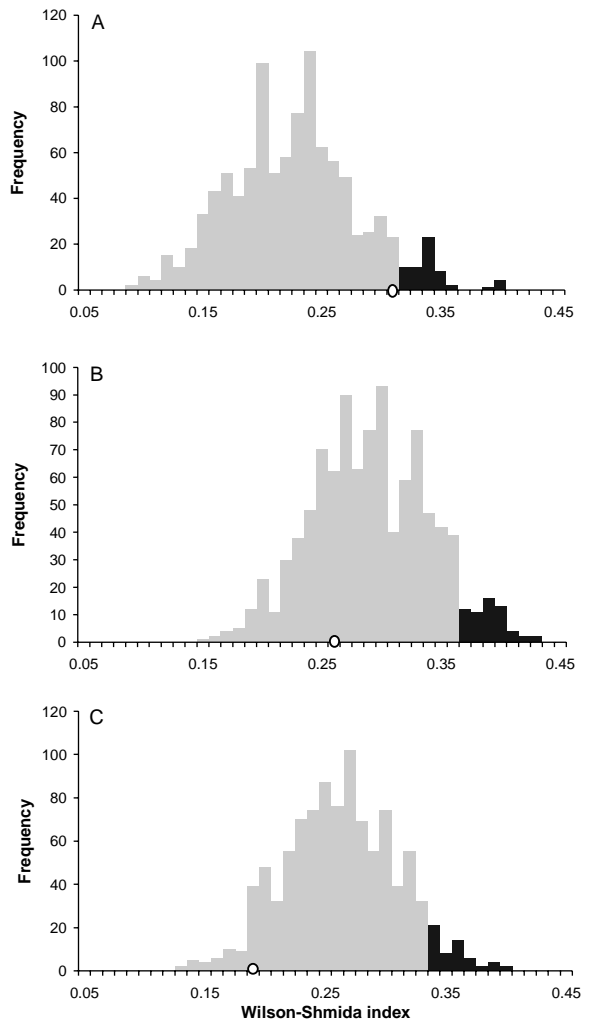


Fig. 3. Results of null model analyses based on the random placement of individuals. The simulated probability density function for the Wilson-Shmida index is constrained by empirical total abundances on each grid for each season. Critical regions are shaded and define the area of the distribution consistent with the habitat heterogeneity hypothesis. The open circles on the x-axis represent empirical values of the Wilson-Shmida index. Results for summer (A, mean  $\beta_T = 0.310$ ,  $P = 0.065$ ) approach significance; results for winter (B, mean  $\beta_T = 0.261$ ,  $P = 0.694$ ), and spring (C, mean  $\beta_T = 0.198$ ,  $P = 0.901$ ) are nonsignificant.

## Seasonal effects

Diversity has a strong seasonal component. For the model constrained by observed species abundances, the presence of blowouts affected diversity only during the summer. Habitat associations of common species could explain this observation. Cramer and Willig (2002) found that *D. ordii*, the numerically dominant species in the community, was associated with blowouts during the summer only, and switched preference to the matrix in other seasons. Only the model constrained by the

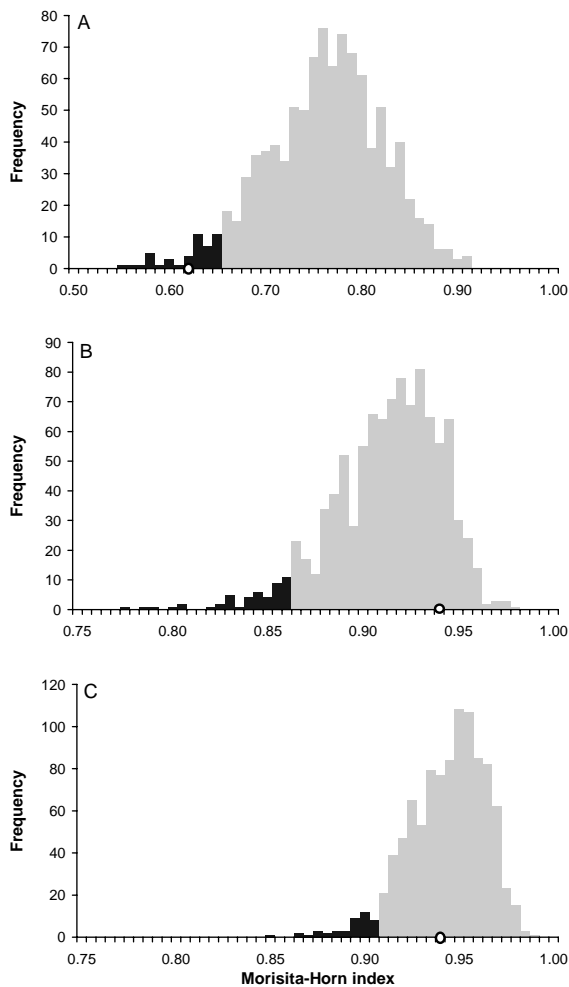


Fig. 4. Results of the null model analyses based on the random placement of individuals. The simulated probability density function for the Morisita-Horn index is constrained by empirical total abundance on each grid for each season. Critical regions are shaded and define the area of the distribution consistent with the habitat heterogeneity hypothesis. The open circles on the x-axis represent empirical values of the Morisita-Horn index. Results for summer (A, mean  $C_{mH} = 0.626$ ,  $P = 0.022$ ) are significant; results for winter (B, mean  $C_{mH} = 0.944$ ,  $P = 0.912$ ) and spring (C, mean  $C_{mH} = 0.943$ ,  $P = 0.484$ ) are nonsignificant.

random placement of individuals detected this switch in habitat association.

$\beta$  diversity was not significant in winter, probably due to lower resource levels and higher physiological stress on individuals. Seasonal changes in vegetation supports this contention (Cramer 1998). Significant differences among seasons existed for grass cover, litter cover, and vegetation height. Both grasses and vegetation height consistently decreased in both habitats in winter. Grass seed forms a large proportion of the diet of *D. ordii* (Garrison and Best 1990). In contrast, the percent cover of litter increased in the winter (Cramer 1998),

which may have made it more difficult for rodents, especially *D. ordii*, to locate seeds. Both laboratory and field studies demonstrate that heteromyid rodents respond to differences in soil texture during foraging (Reichman and Price 1993). Differences between habitats were observed for soil characteristics: blowouts had a higher percentage of coarse soil (0.25–2.00 mm), and the matrix had a higher percentage of debris (>2.00 mm) and fine (<0.25 mm) soil (Cramer 1998). *D. ordii* preferentially gathered small seeds (thistle and millet) over large seeds in the laboratory (Mares and Williams 1977). Small seeds would be difficult to find in the matrix, because of the high amount of debris. Additionally, the diet of *O. leucogaster* switches from primarily insects in the summer to seeds in the winter (McCarty 1978). This dietary shift further effectively reduces food resources for granivores. Consequently, individual granivores may need more space to gather resources, which should result in an increase in home-range size. O'Farrell (1978) observed an increase in the home-range sizes of *D. ordii* in the spring and late fall that persisted into early winter in Nevada. Population estimates of *D. ordii* and *O. leucogaster* significantly increased from summer to winter in the sand-shinnery-oak habitat (Cramer and Willig 2002). These species use both types of habitat in times of physiological stress or resource shortage. Resting metabolic rate for *D. ordii* remains relatively constant throughout the winter (Garrison and Best 1990). Given a decrease in ambient temperature during this period, individuals would have to compensate by increasing caloric intake, which would necessitate use of the matrix in addition to blowouts. This would lead to a homogenization of species composition between the habitats, consequently leading to rejection of the habitat-heterogeneity hypothesis.

The Morisita-Horn index increased seasonally, coincident with seasonal increases in abundance. This might indicate that species abundance distributions converged between habitats with an increase in abundance. Although many sources indicate that the Morisita-Horn index is preferable to other indices of  $\beta$  diversity (Wolda 1981, Magurran 1988), it is sensitive to abundance of rare species. Therefore, this result should be interpreted with caution. The values of  $C_{mH}$  increased seasonally, not because of ecological reasons, but instead because of an artifact inherent in the index of diversity. In cases where a species was captured in a blowout, but not the matrix, the term  $n_{ai} \times n_{bi}$  (Eq. 2) would be zero; that particular species would not contribute to the index. However, if the number of individuals in both habitats for a given species were small, then they would be represented by the index, although the contribution of that species would be small compared to more common species. The magnitude of this effect is dependent on both the number of rare species and the total number of individuals in the community. Therefore,

increases in abundance, especially for rare species, differentially affect the values of the Morisita-Horn index, and may not necessarily represent species responses to ecological factors. For this reason, interpretation of diversity indices using parametric statistics may be misleading, and approaches using null model techniques may yield more meaningful information about patterns in species diversity.

## Scale

Recognizing the scale at which animals perceive environmental heterogeneity is essential for understanding community structure. Perception of spatial heterogeneity can be understood in terms of micro- or macrohabitat selection. Habitats which are sufficiently small so as to occur within an individual's home range might best be considered microhabitats, whereas habitats which are sufficiently large so as to contain the home ranges of one or more individuals would best be considered macrohabitats (Morris 1987a). Dispersal and emigration reflect macrohabitat selection, whereas daily movements within a home range such as those during foraging reflect microhabitat selection (Morris 1987b). The perception of habitat is dependent on the size and mobility of the organism of interest (Kolasa and Rollo 1991), making distinctions between macro- and microhabitat a species-specific characterization of spatial heterogeneity. For the purposes of this study, macrohabitat corresponds to a section of sand-shinnery-oak that contains several blowouts, whereas microhabitat corresponds to matrix or blowout.

Two approaches provide answers to questions concerning the effects of habitat heterogeneity on species diversity. Each approach deals with heterogeneity at a different scale. First, areas of sand-shinnery-oak that do not contain blowouts could be compared to areas where blowouts are present. This approach directly tests the hypothesis that the presence of blowouts contributes to diversity, and considers heterogeneity at the macrohabitat scale. However, a sand-shinnery-oak landscape without blowouts is rare. Also, if differences occur at the macrohabitat scale, it would not be clear how blowouts affect diversity. A second approach considers heterogeneity at the microhabitat scale, using indices of differentiation diversity to provide an assessment of the effects of habitat heterogeneity on diversity. By investigating heterogeneity at a small scale, space utilization can be investigated for particular species. Documenting where particular species forage, for example, may aid in understanding how species respond to spatial heterogeneity. These species-specific responses may contribute to variation in diversity. Rodents in the sand-shinnery-oak ecosystem generally do not display distinct preferences for either microhabitat, because blowouts are too

small to support viable populations (Cramer 1998, Cramer and Willig, 2002). Consequently, the effect of microhabitat on species diversity primarily concerns changes in abundance in the sand-shinnery-oak ecosystem.

Our results could imply that in the absence of blowouts, species richness would be the same as when blowouts are present. This interpretation should be scrutinized with caution because of considerations of scale. The implication that blowouts do not affect species richness of the landscape is made at the macrohabitat scale. Emergent properties (Kolasa and Rollo 1991) of blowouts may affect rodent perception of macrohabitat, even though rodents cannot persist by exclusively using the blowout microhabitat. Consequently, the absence of this microhabitat type could exclude some species from the sand-shinnery-oak landscape, or modify their ecological densities.

Like any disturbance, blowouts can affect animals at population or community levels (Wiens 1985, Willig and McGinley 1999). Community effects are reflected in indices of diversity, and effects at the population level are evident in habitat associations and density. Differences between habitats at the community level were not detected by the Wilson-Shmida index, presumably because changes in species identity occur at larger scales (Rahel 1990). Nonetheless, the presence of blowouts affects abundances of species, and hence community structure. Although the particular mechanism whereby abundance is affected is unclear (e.g. resource-mediation, predator-mediation), particular species (i.e. *Perognathus flavescens*, *O. leucogaster*, *R. montanus* and *Peromyscus* spp.) avoid blowouts (Cramer 1998, Cramer and Willig 2002).

Regardless of their size, blowouts may influence rodent demography. Blowouts are too small and widely dispersed to support viable populations of rodents. In particular, blowouts generally were smaller than home range sizes of *D. ordii* (Garner 1974) and *O. leucogaster* (McCarty 1978). Moreover, species that require continuous open space may not be able to colonize the sand-shinnery-oak ecosystem because blowouts are small and dispersed. Although blowouts may be too small to be considered macrohabitats from the perspective of rodents, their presence within an individual's home range may increase overall habitat quality by contributing resources necessary for persistence, such as unique food types or space for behavioral activities, such as dustbathing (Eisenberg 1963).

## Edge effects

The presence of blowouts may affect species composition and abundance because of the edge between blowouts and sand-shinnery-oak habitat. Edges may contain more

resources because seeds collect under shrubs along the perimeter of blowouts. Diversity and frequency of seed resources are greater near shrubs than in open spaces (Reichman and Price 1993). As a result, the edge may attract more individuals of granivorous species, and these individuals may wander into both blowouts and sand-shinnery-oak habitats. This would homogenize the distribution of species in each habitat, masking the effects of habitat heterogeneity (i.e. blowout vs sand-shinnery-oak) on species richness. This is supported by the observation that blowouts and sand-shinnery-oak patches were much more similar in terms of species compositions than expected by chance alone. At the population level, species may avoid blowouts, but still use the edge. Thus, the presence of blowouts may be important, not because of the open area, per se, but because of the edge it creates.

The importance of disturbance in structuring communities and affecting ecosystem processes has become a paradigm in contemporary ecology (Pickett and White 1985, Platt and Strong 1989, Willig and Walker 1999). Nonetheless, the effects of disturbance on animal communities are both less well-documented and less dramatic than that described for plant communities. This is especially true when the spatial extent of the disturbance is relatively small (e.g. treefalls versus hurricanes) compared to the home range or cruising distance of individuals (Schemske and Brokaw 1981, Schowalter 1985, Wunderle et al. 1987, Feinsinger et al. 1988, Levey 1988, Alvarez and Willig 1993, Willig et al. 1998). Our results corroborate those perceptions, and suggest that a more likely mechanism whereby relatively small disturbances affect animal communities is through attributes of diversity that are sensitive to relative abundance of species. This has important management implications. If human activities create disturbances that are perceived as microhabitats rather than macrohabitats by species of concern, then it may be difficult to document positive or negative consequences by comparing disturbed and undisturbed areas directly, especially if the metric of response primarily reflects species richness. Moreover, the consequences of microhabitat modification may require more time to manifest because they represent alterations in the value of a macrohabitat rather than the addition of macrohabitat, per se.

*Acknowledgements* – This study could not have been completed without the help of many people, especially A. Acrey and D. Hall. Additionally, S. Cox, J. Dever, D. Hart, J. Homan, C. López-González, E. Richards, J. Roberts, R. Stevens, M. Stringer, and D. Yee assisted in the field. Some traps were provided by M. Rylander, and F. Yancey helped with taxonomic identification of rodents. R. Bradley provided advice concerning field techniques, and C. Jones and M. McGinley were instrumental in developing the project. We also thank J. Fitzgerald, C. Caswell, and J. Grey for allowing access to their land. Comments on earlier versions of this manuscript were provided by C. Bloch, G. Cameron, C. Christopher, S. Cox, M. Hopton, S. Presley, J. Roberts, and R. Stevens. M. Cramer was supported by the Department of Biological

Sciences at Texas Tech University through various teaching assistantships and a summer mini-grant.

## References

- Alvarez, J. and Willig, M. R. 1993. Effects of treefall gaps on the density of land-snails in the Luquillo Experimental forest of Puerto Rico. – *Biotropica* 25: 100–110.
- Best, T. L., Skupski, M. P. and Smartt, R. A. 1993. Food habits of sympatric rodents in the shinnery oak-mesquite grasslands of southeastern New Mexico. – *Southw. Nat.* 38: 224–235.
- Bollinger, E. K. 1995. Successional changes and habitat selection in hayfield bird communities. – *Auk* 112: 720–730.
- Cameron, G. N. 1977. Validation of temporary removal trapping and extension to a two-species system. – *J. Mammal.* 58: 78–83.
- Carley, C. J., Fleharty, E. D. and Mares, M. A. 1970. Occurrence and activity of *Reithrodontomys megalotis*, *Microtus ochrogaster* and *Peromyscus maniculatus* as recorded by a photographic device. – *Southwest. Nat.* 15: 209–216.
- Colbert, R. L. 1986. The effect of the shrub component on small mammal populations in a sand shinnery oak ecosystem. – MS thesis, Texas Tech Univ., Lubbock, TX.
- Cramer, M. J. 1998. Effects of spatial and temporal heterogeneity on rodent diversity in a semi-arid environment. – MS Thesis, Texas Tech Univ., Lubbock, TX.
- Cramer, M. J. and Willig, M. R. 2002. Habitat heterogeneity, habitat associations, and rodent species diversity in a sand shinnery oak landscape. – *J. Mammal.* 83: 743–753.
- Daniels, R. J. R., Joshi, N. V. and Gadgil, M. 1992. On the relationship between bird and woody plant species diversity in the Uttara Kannada district of south India. – *Proc. Natl. Acad. Sci., USA* 89: 5311–5315.
- Deslippe, R. J., Salazar, J. R. and Guo, Y-J. 2001. A darkling beetle population in west Texas during the 1997–1998 El Niño. – *J. Arid Environ.* 49: 711–721.
- Dhillion, S. S., McGinley, M. A., Friese, C. F. et al. 1994. Construction of sand shinnery oak communities of the Llano Estacado: animal disturbances, plant community structure, and restoration. – *Restor. Ecol.* 2: 51–60.
- Eisenberg, J. F. 1963. The behavior of heteromyid rodents. – *Univ. of California Publ. Zool.* 69: 1–100.
- Feinsinger, P., Busby, W. H., Murray, K. G. et al. 1988. Mixed support for spatial heterogeneity in species interactions: hummingbirds in a tropical disturbance mosaic. – *Am. Nat.* 131: 33–57.
- Finch, D. M. 1989. Habitat use and habitat overlap of riparian birds in three elevational zones. – *Ecology* 70: 866–880.
- Garrison, T. E. and Best, T. L. 1990. *Dipodomys ordii*. – *Mammal. Sp.* 353: 1–10.
- Garner, H. W. 1974. Population dynamics, reproduction, and activities of the kangaroo rat, *Dipodomys ordii*, in western Texas. – *Grad. Studies Texas Tech Univ.* 7: 1–28.
- Gotelli, N. J. and Graves, G. R. 1996. Null models in ecology. – Smithsonian Institution Press.
- Greenberg, C. H., Harris, L. D. and Neary, D. G. 1995. A comparison of bird communities in burned and salvage-logged, clearcut, and forested Florida sand pine scrub. – *Wilson. Bull.* 107: 40–54.
- Hall, E. R. 2001. The mammals of North America, 2nd ed. – Blackburn Press, Caldwell, NJ.
- Harrison, S. 1997. How natural habitat patchiness affects the distribution of diversity in Californian serpentine chaparral. – *Ecology* 78: 1898–1906.
- Harrison, S. 1999. Local and regional diversity in a patchy landscape: native, alien, and endemic herbs on serpentine. – *Ecology* 80: 70–80.

- Holland, M. 1994. Disturbance, environmental heterogeneity, and plant community structure in a sand shinnery oak community. – MS Thesis, Texas Tech Univ., Lubbock, TX.
- Kolasa, J. and Rollo, C. D. 1991. Introduction: the heterogeneity of heterogeneity: a glossary. – In: Kolasa, J. and Pickett, S. T. A. (eds), Ecological heterogeneity. Springer-Verlag, pp. 1–23.
- Krebs, J. C. 1999. Ecological methodology, 2nd ed. – Benjamin-Cummings, Menlo Park, CA.
- Lacher, T. E., Jr. and Alho, C. J. R. 1989. Microhabitat use among small mammals in the Brazilian Pantanal. – *J. Mammal.* 70: 396–401.
- Levey, D. J. 1988. Tropical wet forest treefall gaps and distributions of understory birds and plants. – *Ecology* 69: 1076–1089.
- MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. – *Am. Nat.* 98: 387–397.
- MacArthur, R. H. and MacArthur, J. W. 1961. On bird species diversity. – *Ecology* 42: 594–598.
- Magurran, A. E. 1988. Ecological diversity and its measurement. – Princeton Univ. Press.
- Manly, B. F. J. 1991. Randomization and Monte Carlo methods in biology. – Chapman and Hall.
- Mares, M. A. and Williams, D. F. 1977. Experimental support for food particle size resource allocation in heteromyid rodents. – *Ecology* 58: 1186–1190.
- Mathworks Inc. 1995. The student edition of Matlab for the Macintosh/Power Mac, Version 4 manual. – Prentice Hall.
- McCarty, R. 1978. *Onychomys leucogaster*. – *Mammal. Spec.* 87: 1–6.
- McGarigal, K. and McComb, W. C. 1992. Streamside versus upslope breeding bird communities in the central Oregon coast range. – *J. Wildlife. Manage.* 56: 10–23.
- Morris, D. W. 1987a. Ecological scale and habitat use. – *Ecology* 68: 362–369.
- Morris, D. W. 1987b. Spatial scale and the cost of density-dependent habitat selection. – *Evol. Ecol.* 1: 379–388.
- Nupp, T. E. and Swihart, R. K. 1996. Effect of forest patch area on population attributes of white-footed mice (*Peromyscus leucopus*) in fragmented landscapes. – *Can. J. Zool.* 74: 467–472.
- O'Farrell, M. J. 1978. Home range dynamics of rodents in a sagebrush community. – *J. Mammal* 59: 657–668.
- Pickett, S. T. A. and White, P. S. 1985. The ecology of natural disturbance and patch dynamics. – Academic Press.
- Platt, W. J. and Strong, D. R. 1989. Special feature: treefall gaps and forest dynamics. – *Ecology* 70: 535–576.
- Rahel, F. J. 1990. The hierarchical nature of community persistence: a problem of scale. – *Am. Nat.* 136: 328–344.
- Reichman, O. J., Price, M. V. 1993. Ecological aspects of heteromyid foraging. – In: Genoways, H. H. and Brown, J. H. (eds), Biology of the Heteromyidae. *Spec. Publ. Am. Soc. Mammal.* 10: 539–574.
- Rice, W. R. 1989. Analyzing tables of statistical tests. – *Evolution* 43: 223–225.
- Rosenzweig, M. L. 1981. A theory of habitat selection. – *Ecology* 62: 327–335.
- Rosenzweig, M. L. 1991. Habitat selection and population interactions: the search for mechanism. – *Am. Nat.* 137: S5–S28.
- Rosenzweig, M. L. and Winakur, J. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. – *Ecology* 50: 558–572.
- Schemske, D. W. and Brokaw, N. L. V. 1981. Treefalls and the disturbance of understory birds in a tropical forest. – *Ecology* 62: 938–945.
- Schowalter, T. D. 1985. Adaptations of insects to disturbance. – In: Pickett, S. T. A. and White, P. S. (eds), Ecology of natural disturbance and patch dynamics. Academic Press, pp. 235–252.
- Slade, N. A. and Blair, S. M. 2000. An empirical test of using counts of individuals captured as indices of population size. – *J. Mammal.* 81: 1035–1045.
- Wiens, J. A. 1985. Vertebrate responses to environmental patchiness in arid and semiarid ecosystems. – In: Pickett, S. T. A. and White, P. S. (eds), The ecology of natural disturbance and patch dynamics. Academic Press, pp. 169–193.
- Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. – *Ecol. Monogr.* 30: 279–338.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. – *Taxon* 21: 213–251.
- Wilkinson, L., Blank, G. and Gruber, C. 1996. Desktop analysis with Systat. – Prentice Hall.
- Willig, M. R. 2000. Latitude, trends with. – In: Levin, S. (ed.), Encyclopaedia of biodiversity. Academic Press, pp. 701–714.
- Willig, M. R. and McGinley, M. A. 1999. The response of animals to disturbance and their roles as agents of disturbance. – In: Walker, L. A. (ed.), Ecosystems of disturbed ground. Elsevier Science, pp. 651–675.
- Willig, M. R. and Walker, L. R. 1999. Disturbance in terrestrial ecosystems: salient themes, synthesis, and future directions. – In: Walker, L. A. (ed.), Ecosystems of disturbed ground. Elsevier Science, pp. 747–767.
- Willig, M. R., Colbert, R. L., Petit, R. D. et al. 1993. Response of small mammals to conversion of a sand shinnery oak woodland into a mixed mid-grass prairie. – *Texas J. Sci.* 45: 29–43.
- Willig, M. R., Secrest, M. F., Cox, S. B. et al. 1998. Long-term monitoring of snails in the Luquillo Experimental Forest of Puerto Rico: heterogeneity, scale, disturbance, and recovery. – In: Dallmeier, F. and Comisky, J. (eds), Forest biodiversity in North, Central, and South America and the Caribbean: research and monitoring. Parthenon Group, New York, NY, pp. 293–322.
- Willig, M. R., Kaufman, D. M. and Stevens, R. D. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. – *Annu. Rev. Ecol. Evol. Syst.* 34: 273–309.
- Wilson, M. V. and Shmida, A. 1984. Measuring beta diversity with presence-absence data. – *J. Ecol.* 72: 1055–1064.
- Wolda, H. 1981. Similarity indices, sample size and diversity. – *Oecologia* 50: 296–302.
- Wunderle, J. M., Diaz, A., Velasquez, J. et al. 1987. Forest openings and the distribution of understory birds in a Puerto Rican rainforest. – *Wilson Bull.* 99: 22–37.