Research article

Bat and rodent diversity in a fragmented landscape on the Isthmus of Tehuantepec, Oaxaca, Mexico

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Resumen

Estimamos los patrones de diversidad (riqueza y abundancia) y disimilitud en comunidades de roedores y murciélagos en cuatro sitios (unidades de paisaje) en el Istmo de Tehuantepec en Oaxaca, México, una región muy importante debido a la gran cantidad de especies endémicas neotropicales. El objetivo principal fue relacionar los parámetros de la comunidad de roedores y murciélagos con la diversidad de hábitats y disturbio humano en un paisaje fragmentado. Capturamos 1,133 individuos de 13 especies de roedores y 26 especies de murciélagos de enero a agosto de 2006. En la unidad de paisaje con mayor diversidad de hábitats se registró la más alta diversidad de roedores. La disimilitud de especies fue baja entre las unidades de paisaje con mayor similitud en grado de disturbio humano. En roedores, el valor de disimilitud de especies entre diferentes hábitats del paisaje fue generalmente alto; por lo tanto, las especies no se distribuyen completamente por todo el paisaje. En murciélagos, el grado de disimilitud de especies entre los diferentes hábitats en el paisaje fue bajo. La distribución de las especies de murciélagos en el paisaje depende de su alta vagilidad y de la estructura espacial del paisaje. Los resultados muestran la importancia de la diversidad de hábitats en los patrones de la riqueza, abundancia y disimilitud de mamíferos en el área de estudio.

Palabras claves: Biodiversidad; Istmo de Tehuantepec; unidades de paisaje; mamíferos; Oaxaca, México.

Abstract

We assessed the patterns of diversity, richness, abundance, and dissimilarity in rodent and bat communities for four sites on the Isthmus of Tehuantepec in Oaxaca, Mexico, an important region given the enormous number of endemic Neotropical species. The main objective was to examine rodent and bat community parameters relative to habitat diversity and human habitat disturbance in a fragmented landscape. We captured 1,133 individuals of 13 rodent species and 26 bat species from January to August 2006. The site (landscape unit) with greatest habitat diversity also had the highest diversity of rodents. Species dissimilarity was low between sites that had similar degrees of human disturbance. For rodents, species dissimilarity between habitats on the Isthmus of Tehuantepec landscape was generally high; therefore, the species are not distributed evenly across the entire landscape. For bats, the degree of species dissimilarity between the different habitats of the landscape was low. The distribution of bat species across the landscape is a reflection of their high vagility and the spatial structure of the landscape. The results show the importance of a diversity of habitats to the patterns of richness, abundance, and dissimilarity of mammals in the study area.

Key-words: Biodiversity; Isthmus of Tehuantepec; landscape; mammals; Oaxaca, Mexico

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Introduction

Mammals exhibit different adaptations to the environment which allow them to occupy different ecological niches (from terrestrial to arboreal), and these adaptations play an important role in the patterns of biodiversity and in the ecosystem's processes [1,2]. In particular, bats and rodents are good indicators of ecosystems that have been disturbed by human activities: both groups occur in different environments and they are diverse and abundant [3,4]. They can be found at various trophic levels, as seed, pollen, or root eaters. Some bat species even consume small vertebrates and fish and can be found in specific habitats [3,5].

This highlights the importance of carrying out studies in landscapes with differing degrees of disturbance, given that tropical landscapes are currently fragmented to varying degrees and have gaps or have had their natural vegetation replaced [6-9]. Thus, in these landscapes there are different sizes of habitat fragments of natural or anthropogenically modified vegetation (i.e., crops, pastures, human settlements, and secondary vegetation) to which the movement of many species of both plants and animals is restricted. These changes do not affect all species equally since some are favored by these modifications [10]. Some authors have found that a greater diversity of habitats is associated with higher mammal diversity [11, 12]. This positive relationship has also been found in other groups such as beetles [13], butterflies [14], raptors [15], herbaceous plants [16], and soil fauna [17].

In Mexico, one region worthy of this kind of study is the Isthmus of Tehuantepec in Oaxaca, owing to its geographic location and, particularly, the fact that it shares several floristic elements with the southern Sierra Madre Mountain Range and the Central Valley of Oaxaca, which makes the transition between these areas almost undetectable [18]. The Isthmus represents a significant barrier for highland species and an important corridor between the Atlantic and Pacific coastal plains, and also favors a high degree of endemicity [19-21]. It is currently subject to different types of disturbance, so it is possible to find fragmented landscapes for which it is important to detect how the diversity patterns of animal species are modified by disturbance and landscape fragmentation [22].

Diversity can be analyzed at different scales within a landscape [10], and the study of the components of diversity can be useful for measuring and monitoring the effects of human activities on biodiversity [23]. The purpose of this paper was to examine the relationship between Neotropical rodent and bat community parameters (diversity, species dissimilarity) with habitat diversity and human habitat disturbance. According to the hypothesis proposed by Rosenzweig [12], species richness increases with landscape heterogeneity, so we would expect a more heterogeneous landscape to have greater mammal diversity. Also, we propose that for a landscape with a greater degree of human disturbance, mammal diversity should be lower. Finally, species composition is expected to be more similar between habitats with similar degrees of human disturbance. The results of this study can be applied to conservation strategies for small mammals at the local level and on highly fragmented landscapes.

Methods

Study site

The study region is located in the southern part of the Isthmus of Tehuantepec, Oaxaca, Mexico, and extends over approximately 200 km^2. Mean annual temperature is 27.6°C, average annual precipitation is 932.2 mm, and altitude is 50 to 150 m a.s.l. The climate is warm, subhumid, with rainfall between June and October, and a dry season from March through May [24].

In the region, four landscape units were set up in the northern part of the Laguna Inferior. In this study, a set of habitat patches (diversity of habitats) within a certain radius was defined as a landscape unit: (1) El Rancho, (2) El Puente, (3) Las Palmas, and (4) Huamuchil (Figure 1). A vegetation map of the study area was prepared from a 2003 Landsat ETM-7 satellite image.

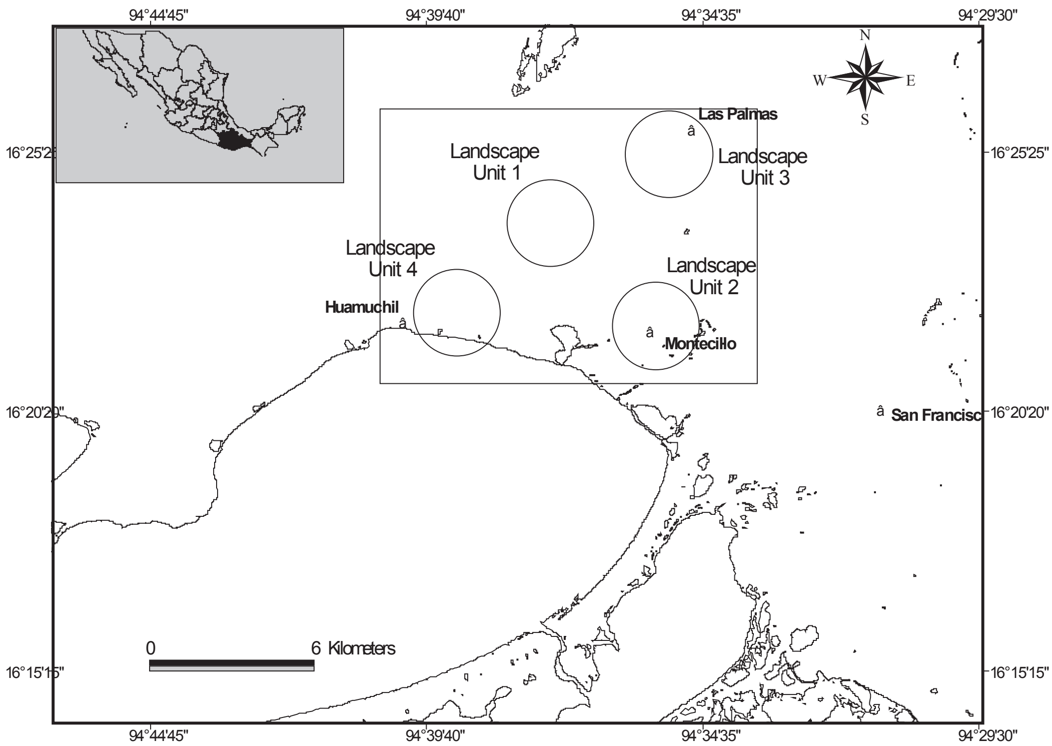

Fig. 1. Location of the study area on the Isthmus of Tehuantepec, Oaxaca, Mexico.
Landscape Unit ◯ Study Area ▭

For each landscape unit, we drew a circumference of 12.5 km² using the program ArcView 3.2™, in order to determine rodent and bat diversity. Rodent species move over relatively short distances and their home ranges are small (less than 1 km) [25], while some species of bats can fly up to 8 km daily [26, 27]. Inside each landscape unit, we recorded the number and percentage of habitats present (habitat heterogeneity). For each landscape unit**,** habitat types were verified in the field and their altitude and geographic coordinates determined with a Garmin 12XL™ GPS personal navigator.

To analyze the effect of the degree of human disturbance, three types of habitat resulting from human activities were used: croplands, pastures, and towns. The percentage occupied by each was obtained for each landscape unit. We used Shannon's index to calculate landscape heterogeneity values for each landscape unit, as suggested by Anderson [15].

Sampling survey

Between January and August 2006, eight surveys were conducted in the field (four in the dry season and four in the wet season). The capture-recapture method was used to keep individual records of rodent and bat specimens [28, 29]. During each survey, rodents were captured with 100 Sherman™ live traps placed in a radial formation starting at the center of each landscape unit and left in the field for three consecutive nights (Figure 2). At the same time, bats were captured with three 12-m-long mist nets placed in the center of each unit for the same three consecutive nights. Mist nets were set 1.50 m above the ground, and left open from 1800 h to 2400 h every night with a routine check every 45 minutes.

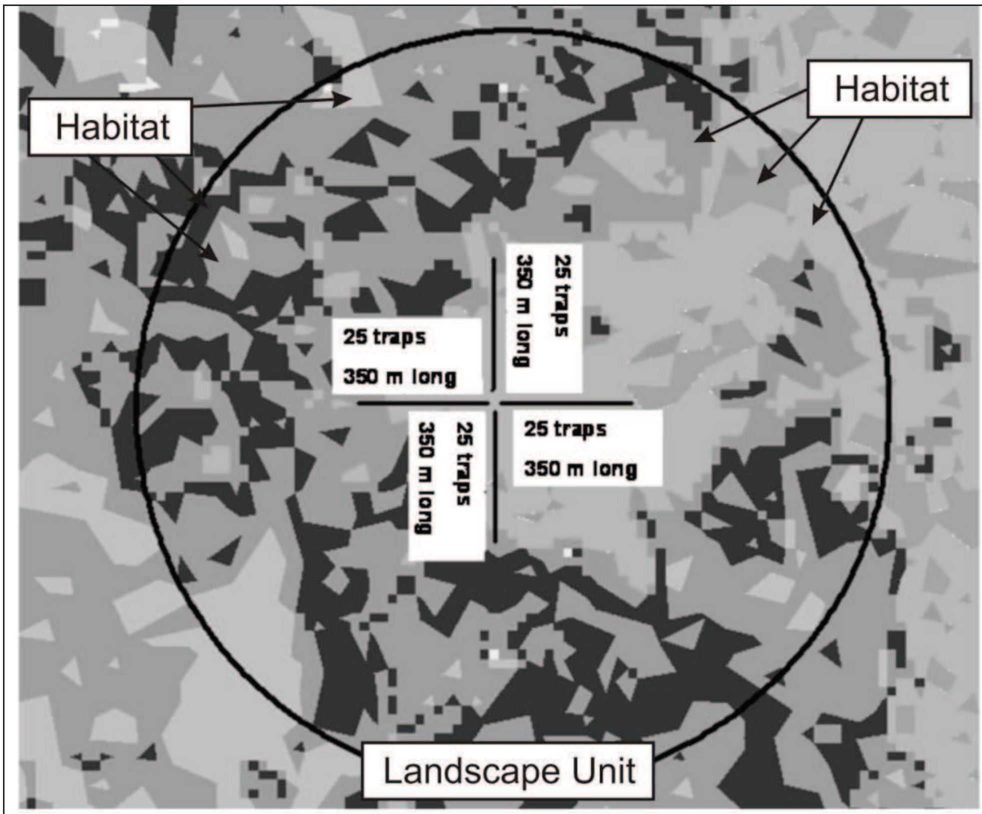

Fig 2. Sampling design and transect location in the middle of each landscape unit. 25 Sherman™ live traps were placed every 14 meters along each 350-meter-long transect resulting in 100 traps on the four transects, per landscape unit. For bats, 12-meter-long mist nets were hung in the center of each unit.

Diversity and species dissimilarity estimates

Shannon's diversity index [27-30] was chosen to calculate the diversity of rodents and bats because it takes into account rare species. Diversity was compared between pairs of units following Solow's [31] method. All calculations were performed with the program Diversity [32]. For landscape units the values of species richness and abundance per night (previously log10 transformed) were compared with a one-way analysis of variance (ANOVA) and Tukey-Kramer tests using SPSS™ 12.0 software [33]. Species dissimilarity was first calculated with the Morisita-Horn sample similarity index, using Estimates software [34] as follows:

$$C_{mh} = \frac{2\sum_{i=1}^{s}[(an_i)(bn_i)]}{(da+db)(aN)(bN)}$$

Where:
S = total number of species at both sites
aN = total number of individuals of all species collected at site A
bN = total number of individuals of all species collected at site B
an_i = number of individuals of the i^{th} species collected at site A
bn_i = number of individuals of the i^{th} species collected at site B
and, in the denominator, the two sum terms are defined as:

$$da = \frac{\sum_{i=1}^{s}(an_i)^2}{(aN)^2} \quad \text{and} \quad db = \frac{\sum_{i=1}^{s}(bn_i)^2}{(bN)^2}$$

Then we subtracted from unity, the proportion of shared species between two landscape units being compared (C_{mh}) in the form:

$$ST = 1 - C_{mh}$$

Where:
ST = species dissimilarity between the two landscape units compared
C_{hm} = Morisita-Horn similarity index

Habitat heterogeneity, conserved areas, and those disturbed by human activity (%) were correlated with Pearson's coefficient using SPSS™ 12.0 software. Also, we calculated the difference between the degree of human disturbance (proportion of pastures, towns and cropland) and the percentage of each of the different habitats (habitat heterogeneity) in each landscape unit.

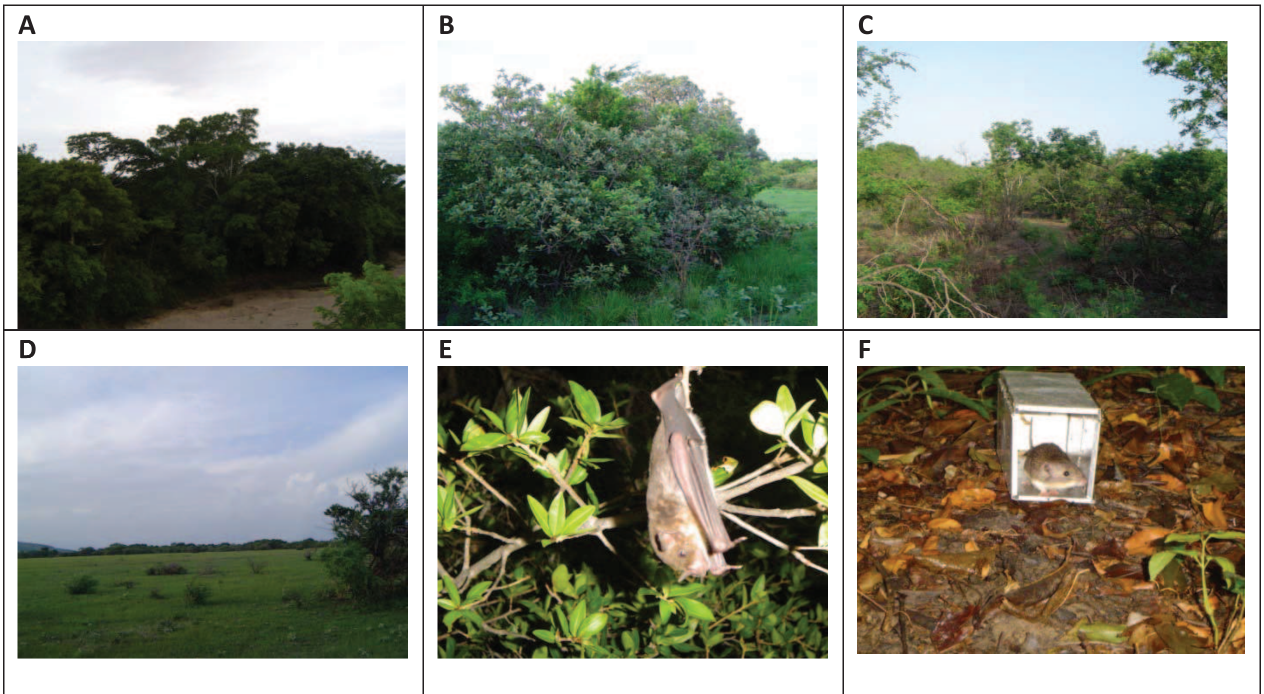

Fig. 3. (A) Riparian vegetation; (B) Nanche grove; (C) Thorny heat; (D) Pastures; (E) Bat: *Phyllostomus discolor*; (F) Rodent: *Liomys pictus.* Photos by F. Barragán.

Results

Landscape units

Landscape unit 4 had the highest number of habitats (10), the most representative being pasture, which occupied 53% of the total unit area. In contrast, landscape unit 1 had only five habitat types, and the most representative among them was the nanche (*Byrsonima crassifolia*) grove, known locally as *nanchal,* which occupied 33% (Table 1; Figure 3). The sum of the proportions of disturbed habitats indicated that unit 3 had the highest proportion of human disturbance (62%), while unit 1 had the lowest proportion of human disturbance at 26% (Table 1).

MAMMAL DIVERSITY, LANDSCAPE HETEROGENEITY AND HUMAN DISTURBANCE

1,133 individuals of 26 bat and 13 rodent species were caught. The rodent species richness reported here represents 23.2% (13 of 56 species) of all the species reported for the state of Oaxaca, while bat species richness represents 31.7% (26 of 82 species) of the state's bat richness [35]. *Liomys pictus* (spiny pocket mouse) was the most abundant species and represented 65% of all the rodents collected, followed by *Baiomys musculus* (14.1%) and *Oligoryzomys fulvescens* (12.3%). For bats, *Artibeus lituratus* and *A. jamaicensis* were the most abundant species and represented 26.6% and 15.2% of all the bats collected, respectively, followed by *Uroderma bilobatum*, *A. intermedius*, *Choeroniscus godmani* and *Phyllostomus discolor* (Appendix 1).

Landscape unit 2 had the highest rodent species richness (11 species) and abundance (137 individuals), with *L. pictus* (52 individuals) the most abundant species. In landscape unit 3, the highest number of bat species (16) and individuals (313) was recorded, and the most abundant species were *A. lituratus* (56) and *Choeroniscus godmani* (51; Appendix 1). Mean rodent abundance was significantly different among landscape units (ANOVA test $F_{3,28}$ = 3.81; P = 0.03), particularly between units 1 and 2 (Tukey-Kramer test). There were no statistical differences in bat mean abundance among landscape units (P < 0.05).

Table 1. Habitat types and proportion of each habitat occupied in each landscape unit. Numbers in italics show the habitat with the highest percent occupancy in each unit.

Habitat	Unit 1		Unit 2		Unit 3		Unit 4	
	Hectares	%	Hectares	%	Hectares	%	Hectares	%
Thorny heath	117.34	9	0	0	32.39	3	50.89	4
Water	0	0	11.72	1	0	0	258.22	21
Nanche grove	*412.06*	*33*	10.08	1	0	0	59.32	5
Pastures*	319.25	26	105.45	8	*449.5*	*36*	*656.89*	*53*
Grassland with bushes	0	0	15.45	1	160.34	13	14.01	1
Towns*	0	0	21.13	2	11.43	1	12.15	1
Riparian vegetation	62.05	5	186.4	15	104.83	8	62.16	5
Mature secondary vegetation	339.56	27	277.99	22	169.39	14	45.81	4
Croplands*	0	0	*431.54*	*35*	306.54	25	0	0
Bare Sand	0	0	0	0	0	0	48.49	4
Forest	0	0	0	0	0	0	42.34	3
Unknown	0	0	190.51	16	15.85	1	0	0
Human disturbance		26		45		62		54

* Proportion of each habitat occupied in each landscape unit was added to estimate the degree of human disturbance in each landscape unit.

There were differences among landscape units in mean rodent richness (ANOVA test $F_{3,28}$ = 18.08; P < 0.0001); and a Tukey-Kramer test indicated that unit 2 was significantly different from units 1, 3 and 4. Differences between landscape units in mean bat richness were also statistically significant (ANOVA test $F_{3,28}$ = 5.22; P = 0.009), and unit 4 had lower species richness than unit 3 accordingly to a Tukey-Kramer test.

In terms of habitat heterogeneity, landscape unit 2 had the highest value (H' = 1.787) and unit 1 had the lowest (H' = 1.439). The highest values of Shannon's index were obtained in unit 2 for rodents (H'=1.485), and in unit 3 for bats (H'=2.23; Table 2). Shannon's indices were compared among landscape units following Solow's [31] method. Unit 1 differed from units 2 and 3, unit 2 differed from unit 3, and unit 3 differed from unit 4 for both rodents and bats. Unit 2 also differed from unit 4 only in rodents (Table 2).

Table 2. Shannon's index and comparisons of diversity values for habitat types (heterogeneity), rodents and bats in each landscape unit on the Isthmus of Tehuantepec, Oaxaca. Same letters indicate that there are no statistically significant differences (P>0.001).

Sample	Habitats	Rodents	Bats
Unit 1	1.439	0.2712 *a*	2.003 *a*
Unit 2	1.787	1.485 *b*	1.628 *b*
Unit 3	1.654	0.982 *c*	2.227 *c*
Unit 4	1.543	0.4208 *a*	1.783 *ab*

Pearson's correlation coefficient revealed a strong positive relationship between habitat heterogeneity and rodent diversity (r = 0.94) (Table 3; Figure 4). There were no significant correlations between habitat heterogeneity and bat abundance and diversity; nor were there any between human disturbance and diversity and abundance of bats and rodents.

Table 3. Pearson's correlation coefficient between species diversity and abundance with habitat heterogeneity and areas disturbed by humans (%). * = P < 0.05, d.f. = 3.

	Habitat heterogeneity	Human disturbance area (%)
Bat diversity	-0.025	0.224
Bat abundance	0.128	0.282
Rodent diversity	0.939*	0.295
Rodent abundance	0.731	0.322

Species dissimilarity

Species dissimilarity between pairs of units was closer to 50%, with the exception of units 1 and 4, for which rodent species dissimilarity was 33.3% indicating that these units share most of the rodent species collected (Figure 5). Species dissimilarity for bats was between 39% and 62%. However, units 2 and 3 had lower values (33.3%; Figure 6).

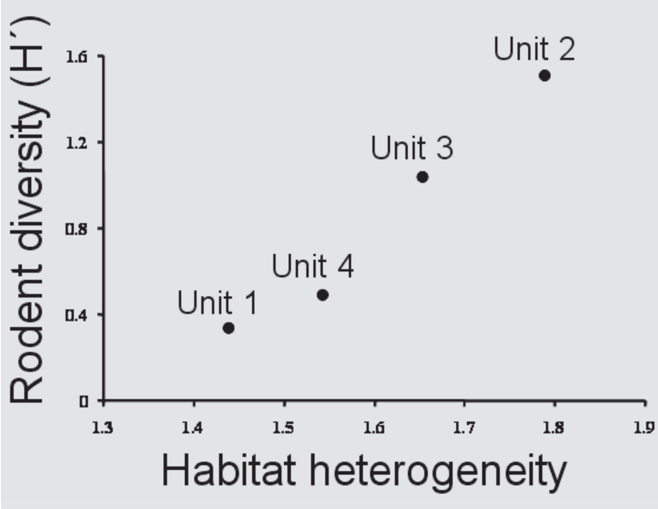

Fig. 4. Comparison of rodent diversity (H') and habitat heterogeneity. Each dot represents a landscape unit on the Isthmus of Tehuantepec, Oaxaca, Mexico.

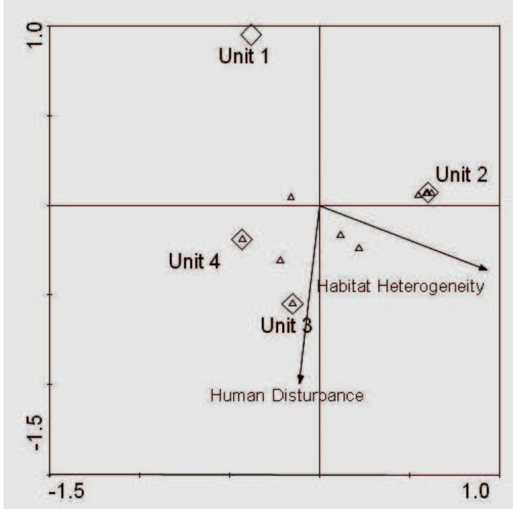

Fig. 5. Canonical correspondence analysis for rodents, relating species dissimilarity to differences in human disturbance and habitat heterogeneity in the four landscape units. Eigenvalue=0.350; F-ratio=2.288; P-value=0.0460. ◊=Landscape unit; Δ=Species.

Eight rodent species were not shared between landscape units (61.5%), but the other five species were shared (38.5%). At the landscape level, unit 2 had the highest number of exclusive species (*N*=6), and unit 1 had no unique species. Unit 2 shared most of its species with units 3 and 4 (four species in each). For bats, 12 species were not shared among units (46.2%), and 14 species were shared (53.8%). Units 2 and 3 shared the highest number of species (*N* =9), and units 2 and 4 shared only four species (Appendix 1).

The differences between the degree of human disturbance and the habitat heterogeneity occupied in each landscape unit showed that the greatest difference in human disturbance was 36% between units 1 and 3, and the lowest difference in disturbance human was 8% between units 3 and 4. The highest difference in the value of habitat heterogeneity was 0.348 between units 1 and 2, and the lowest difference was 0.104 between units 1 and 4 (Figure 5 and 6).

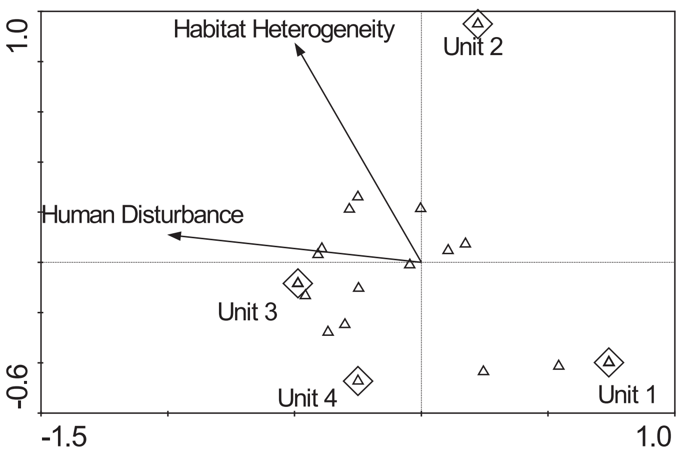

Fig. 6. Canonical correspondence analysis for bats, relating species dissimilarity to differences in human disturbance and habitat heterogeneity in the four landscape units. Eigenvalue=0.260; F-ratio=1.209; P-value=0.0460. ◊=Landscape Unit; Δ=Species.

Discussion

Mammal diversity

The differences in the pattern of species richness and abundance of rodents and bats in the fragmented landscape were quite evident. We recorded high rodent richness (13 species) compared to previous studies. For example, near the Isthmus of Tehuantepec, Horvath [36] found 10 species in the Chiapas Highlands, southwestern Mexico, while Vázquez [37] reported seven species in Manantlan, Jalisco, western Mexico. In both studies, *Reithrodontomys* was the most abundant genus. In our study area, the most abundant rodent was the spiny pocket mouse, *L. pictus* (*N*=248), a granivorous species with a wide distribution and high abundance in both disturbed and undisturbed areas in Mexico. The presence of this species in all landscape units may be explained by the availability of refuges because it inhabits either thorny scrub or deciduous forest where conditions are suitable for it to dig burrows [38]. *Liomys pictus* is favored by the semiarid conditions present over most of the landscape, and by the presence of thorny scrub [31]. The high richness of rodent species in unit 2 was likely a result of the presence of two semi-permanent sources of fresh water (these only dry up partially in the last month of the dry season). Their presence favors: 1) the presence of patches of gallery vegetation that connect with fragments of mature secondary vegetation creating a good refuge and source of food for arboreal rodents such as *N. sumichrasti* and *C. mexicanus* and also for *R. fulvescens* which is semi-arboreal; and 2) the presence of crops (sorghum and corn) that attract species such as *R. sumichrasti* and *O. rostratus,* which use this resource to survive.

The most abundant bat species in our study site was the frugivorous bat *A. lituratus*, which was found during both the wet and dry seasons. This bat also was the most abundant species in most of the landscape units (*N*=198), with the exception of unit 4 (*N*=14). In units 3 and 4, one of the most abundant species was the insectivorous/frugivorous bat *Phyllostomus discolor*. The abundance of *P. discolor* can be attributed to the availability of food resources, since this species mainly feeds on insects, an apparently abundant resource (mainly in unit 4), possibly owing to the presence of a body of water that favors some groups of insects. The habitat characteristics of the other units could be attractive to other types of species, such as *A. lituratus* which eats mostly fruit such as mango (*Mangifera indica*), the jobo or hogplum (*Spondias* spp.), fig (*Ficus* sp), the Maya nut tree or ramón (*Brosimum alicastrum*) and banana (*Musa paradisiaca*) [38]. This species has a Neotropical distribution, occupies the tropical lowlands in Mexico, and is common in the study area. *Vampyressa thyone* is a unique species captured in this study during the dry season. This frugivorous bat has been associated with wet habitats over brooks in gallery vegetation [39], but had not been reported in previous studies conducted on the Isthmus of Tehuantepec, Oaxaca [35].

Several authors have proposed that species richness increases with increasing food diversity [23, 40-43] and habitat diversity [23, 44]. In our study area, species richness is probably related to the diversity of both food resources and habitat types. Landscape unit 2 with its eight different habitat types provided evidence of this, as it had the highest values of Shannon's index for rodents, and the highest rodent species richness (*N*=11), including arboreal species (*Nyctomys sumichrasti* and *Coendou mexicanus*). Similarly, in unit 3 we recorded seven different habitats, the highest values of Shannon's index for bats, and we observed more bat species (*N*=16), including rare (*Carollia perspicillata*, *Glossophaga morenoi*) and insectivorous species (*Myotis nigricans*).

Landscape heterogeneity and human disturbance

We expected a positive correlation between habitat heterogeneity levels and mammal diversity, i.e., that mammal diversity would be higher in more heterogeneous landscape units. Our results only support this hypothesis for rodent diversity. In this study, unit 2 had a high number (11) and diversity (1.48) of rodent species. These results suggest that, in terms of richness and abundance, rodents respond favorably to more heterogeneous habitats, and bats respond favorably to habitats with moderate levels of heterogeneity.

However, we found that the richness and abundance of rodent and bat species was similar between landscape units with similar levels of human disturbance. Units 1 and 4 were the most similar in human disturbance (0.104) and bat diversity values. In contrast, differences in the diversity of rodents and bat species were found between units 1 and 2, and these had the highest difference in the degree of human disturbance (0.348), but had a similar number of bat species (11 species in unit 2, 10 species in unit 4). Thus, the presence of some bat species in each unit was unique: unit 2 had seven exclusive species, and unit 4 had six species not found in unit 2.

We also expected that rodent and bat species diversity would be lower in the landscape units with greater levels of human disturbance; however, our results do not support this hypothesis, because no correlation was found for either bats or rodents. In unit 3, we found six fewer rodent species than in unit 2, and over 89% of the individuals belonged to one species, *L. pictus*, which is associated with disturbed habitats. It is necessary to obtain more data from areas with different disturbance levels.

In summary, bat and rodent species respond differently to landscape heterogeneity. We found that rodent diversity was related to the level of landscape heterogeneity, but different levels of human disturbance to the landscape did not affect rodent or bat diversity. However, the distribution of habitats on the landscape, the presence of plant corridors and the differing displacement capacity of the animals allowed for the presence of generalist and specialist species in most landscapes units, and resulted in similar abundances among units and the presence of rare species.

Species dissimilarity

Species dissimilarity patterns were different for bats and rodents under distinct landscape conditions. Rodents had unequal values of species diversity across units (*i.e.*, 11 species in unit 2, in contrast with 2 species in unit 1) resulting in high species dissimilarity on this landscape of the Isthmus of Tehuantepec. Meanwhile, species diversity values for bats were more similar among units (species dissimilarity was around 3 to 6 species in all units), which means that bat species use all landscapes and not only a specific site.

Horváth [36] reported 76% replacement for rodent species in the Chiapas Highlands. Rodent species dissimilarity in our study area was 47.4%. In this study a high dissimilarity was expected because of the limited mobility and small home ranges of rodents. However, it is possible that differences in temperature and in the number and quality of habitats among landscape units were related to the high numbers of exclusive species associated with specific sites. For example, unit 2 had six exclusive species, one of them the rare *Coendou mexicanus,* which is under special protection in the current Official Mexican Regulation 2001 of the Ministry of the Environment and Natural Resources [45]. The differences between Horváth's [36] results and those of this study could be due to differences in the landscape matrices. In the Chiapas Highlands, the landscape matrix is mainly composed of pine-oak forest and it is more homogeneous, while that of the Isthmus of Tehuantepec is composed of natural pastures and is more heterogeneous.

Moreno & Halffter [10] found replacement values for bat species of 32% to 42% in Veracruz, Mexico; Sanchez-Cordero [46] found replacement values for rodents and bat species of 50% to 70% in Sierra Mazateca and Sierra Mixteca, Oaxaca, and Sosa-Escalante [47] found replacement values of around 40% for bats in the northwest of the Yucatan Peninsula. Bat replacement in this study was 36%, which coincides with analyses of replacement in bats in different habitats [10, 48]. Some authors have suggested that replacement values in fragmented landscapes should be higher (above 50%) in habitats with highly contrasting conditions that promote species dissimilarity [48], because the habitats are quite different.

Although landscape units 2 and 3 are separated by nearly 8.5 km, bat species dissimilarity was high (33%). This is probably due to the presence of a river (accompanied by gallery vegetation) that crosses the landscape and joins both units. This gallery vegetation favors the movement of bats between habitat types, functioning as a biological corridor that provides food, shelter, perching sites and other resources. On the other side, in units 2 and 4, also separated by 8 km, bat species replacement was higher (62%), perhaps owing to the lack of forest cover that could facilitate bat flight between the two units.

Our hypothesis predicted that species composition would be expected to be more similar between landscape units with similar degrees of disturbance; however, this was not found for either group of mammals. Units 3 and 4 were most similar in human disturbance (with a difference of 8%), but species dissimilarity was higher in these units than it was in the units with greater differences in human disturbance levels.

In conclusion, rodent species dissimilarity among different habitats in the landscape was generally high on the Isthmus of Tehuantepec. Therefore, species were not widely distributed throughout the landscape. In contrast, the degree of dissimilarity in bat species among different habitats in the landscape was generally low. This means, that bat species were widely distributed across the landscape, likely because of their high vagility and the spatial structure of the landscape (for example; gallery vegetation corridors).

Implications for conservation

The results of this study suggest that the presence of fragments of different habitats are important to different populations of rodents and bats, and even though different anthropogenic activities are under way, these do not have a direct effect on the diversity of these mammals. Conservation strategies should attempt to protect corridors of arboreal vegetation because, even though there are many vegetation fragments, these animals do benefit from the connectivity provided by these corridors. This is particularly true for the bats that had high beta diversity and are found dispersed across the entire Isthmus of Tehuantepec landscape. Therefore, the presence of trees and shrubs beside bodies of water favor such threatened species as the bats *Leptonycteris curasoae, Enchisthenes hartii*, and *Myotis nigricans* [45]. Species endemic to Mexico such as *Rhogeessa parvula* and threatened rodents such as *Coendou mexicanus* also benefit from this landscape configuration because the habitats provide refuge and food. It is necessary to continue monitoring these small mammal species in the region of the Isthmus of Tehuantepec to further our knowledge of local diversity in modified landscapes (with differing degrees of disturbance), and to test the hypothesis that mammal richness is related to food availability and habitat heterogeneity.

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Appendix 1. Number of individuals of bat and rodent species recorded in each landscape unit on the Isthmus of Tehuantepec, Oaxaca, Mexico. Species classification follows Ramirez-Pulido *et al.* (2005).

	Unit 1	Unit 2	Unit 3	Unit 4
Order Chiroptera				
Family Emballonuroidae				
Saccopteryx bilineata (Temmnick, 1838)	0	1	0	0
Family Mormoopidae				
Pteronotus davyi Gray, 1838	1	0	0	1
Family Phyllostomidae				
Micronycteris microtis Miller, 1898	14	0	0	0
Glyphonycteris sylvestris Thomas, 1896	0	2	5	0
Phyllostomus discolor Wagner, 1843	6	0	41	26
Glossophaga soricina (Pallas, 1766)	0	0	7	1
Glossophaga morenoi Martínez y Villa, 1938	0	0	1	0
Leptonycteris curasoae Miller, 1900	7	0	0	0
Choeroniscus godmani (Thomas, 1903)	10	5	51	9
Carollia perspicillata (Linnaeus, 1758)	0	0	1	0
Carollia subrufa (Hanh, 1905)	0	1	0	0
Sturnira lilium (É. Geoffroy St. Hilaire, 1810)	0	4	26	0
Sturnira ludovici Anthony, 1924	0	0	11	0
Uroderma bilobatum Peters, 1866	19	34	45	0
Vampyressa thyone Thomas, 1909	5	0	0	0
Enchisthenes hartii (Thomas, 1892)	1	0	0	0
Artibeus intermedius J. A. Allen, 1897	15	16	29	16
Artibeus jamaicensis Leach, 1821	32	32	28	21
Artibeus lituratus (Olfers, 1818)	71	57	56	14
Centurio senex Gray, 1842	8	0	0	2
Family Molossidae				
Molossus molossus (Pallas, 1766)	0	1	2	0
Family Vespertilionidae				
Rhogeessa parvula H.Allen, 1866	0	0	0	2
Lasiurus intermedius H. Allen, 1862	0	1	8	0
Myotis fortidens Miller y G. M. Allen, 1928	2	0	0	0
Myotis keaysi J. A. Allen, 1914	0	0	1	1
Myotis nigricans (Schinz, 1821)	0	0	1	0
TOTAL	191	154	313	93
Order Rodentia				
Family Sciuridae				
Sciurus aureogaster F. Cuvier, 1829	0	2	0	0
Family Muridae				
Baiomys musculus (Merriam, 1892)	4	22	25	3
Nyctomys sumichrasti (de Saussure, 1860)	0	1	0	0
Reithrodontomys mexicanus (de Saussure, 1860)	0	1	4	5
Reithrodontomys fulvescens J. A. Allen, 1894	0	1	0	0

*Reithrodontomys sumichrasti (*de Saussure, 1861)	0	0	3	0
Oryzomys couesi (Alston, 1877)	0	11	0	0
Oryzomys rostratus Merriam, 1901	0	1	0	0
Oligoryzomys fulvescens (de Saussure, 1860)	0	44	0	2
Sigmodon hispidus Say y Ord, 1825	0	1	1	0
Rattus rattus Linnaeus, 1758	0	0	0	1
Family Geomyidae				
Liomys pictus (Thomas, 1893)	53	52	42	101
Family Erenthizontidea				
Coendou mexicanus (Kerr, 1792)	0	1	0	0
TOTAL	57	137	75	113