

Rodent Diversity and Land Use in Montebello, Chiapas, Mexico

Anna Horváth¹, Ignacio J. March¹ and Jan H. D. Wolf²

¹Dept. de Ordenamiento Ecológico, El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas, Mexico

²Dept. of Ecology and Terrestrial Systematics, El Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas, Mexico

Abstract

We analyzed the abundance and diversity of Heteromyid and Murid rodents in the Lagos de Montebello National Park and adjacent areas, Chiapas, Mexico. We sampled three habitat types with different degrees of disturbance: pine-oak-liquidambar forest, ecotone and crop farming lands. Habitat types were defined considering characteristics such as heterogeneity, structural complexity and arboreal cover. We obtained ancillary habitat data considered important for small mammal requirements. Data on rodent communities were obtained by capture-mark-recapture between February and October 1996. We made 410 captures in 3820 trap-nights effort. Ten species were recorded, including one endemic with restricted distribution in Chiapas. Mouse diversity in the forest was significantly higher than within the farm lands. A Kendall correlation analysis showed positive relationship between rodent community species richness and habitat heterogeneity. Diversity of rodents was associated with the habitat complexity and structural elements, and negatively correlated with farming intensity. We found a high beta diversity and low similarity of the rodent communities in the three different habitats. Community composition strongly changed from the forest through the ecotone into the farm lands, with five species gained and seven species lost. The highest species richness was found in the ecotone; however, it showed a strong dominance of a single species that can convert into a plague of crops, and relatively low abundance of the other species. The pine-oak-liquidambar forest had the highest diversity indices, sheltering a particular rodent community within the study area, it therefore probably has the most important role in the conservation of the local biodiversity.

Resumen

Se analizó la abundancia y diversidad de roedores de las familias Heteromyidae y Muridae en la región del Parque

Nacional Lagos de Montebello, en Chiapas, México. Los muestreos se llevaron a cabo en tres tipos de hábitat con diferentes grados de transformación: bosque de pino-encino-liquidambar, ecotono y cultivo. La definición de los tipos de hábitat se realizó según sus características principales en cuanto a la heterogeneidad del hábitat, complejidad estructural y cobertura arbórea. Además de estas características se tomaron otros datos del hábitat, que se consideraron importantes para los mamíferos pequeños. Los datos de las comunidades de ratones se obtuvieron a través de captura-marcaje-recaptura entre febrero y octubre de 1996, realizándose 410 capturas con un esfuerzo de 3820 noches-trampa. Se registraron diez especies, una de ellas endémica para Chiapas. Se encontró que la diversidad de ratones en el bosque es significativamente mayor que en los cultivos. Un análisis de correlación demostró asociación positiva entre la riqueza de la comunidad de ratones y la heterogeneidad del hábitat, así como entre los índices de diversidad y la complejidad y cantidad de los elementos estructurales del hábitat. Se encontró una correlación negativa entre la diversidad de ratones y la intensidad del cultivo agrícola. Se observó una alta diversidad beta de ratones y baja similitud entre las comunidades en los hábitat considerados. La composición de las comunidades cambió desde el bosque a través del ecotono hasta el cultivo. El ecotono presentó la mayor riqueza, sin embargo mostró una fuerte dominancia de solo una especie, la cual puede convertirse en plaga del cultivo, y abundancias relativamente bajas del resto. El hábitat con mayor índice de diversidad fue el bosque de pino-encino-liquidambar, que alberga una comunidad de ratones particular para el área de estudio, por lo que probablemente juega el papel más importante en la conservación de la biodiversidad local.

Keywords: Diversity, abundance, rodent community, habitat structure, land use, Lagos de Montebello National Park, Chiapas.

Received: 18 September 1998

Accepted: 20 June 2001

Correspondence: A. Horváth, El Colegio de la Frontera Sur (ECOSUR), Carretera Panamericana y Periférico Sur S/N, AP. 63, C.P. 29290, San Cristóbal de las Casas, Chiapas, Mexico. Fax: +52 967 82322; E-mail: ahorvath@scelc.ecosur.mx

Introduction

The drastic changes occurring within natural forests during recent decades have provoked three important trends: 1) towards the reduction of the surface extension of the forest; 2) towards the simplification of the forest communities in structure and composition, promoted by the selective extraction of the forest resources and subsequent reforestation with few species; 3) towards increased fragmentation, resulting in smaller and more isolated patches of native forests, original habitats being replaced by agricultural fields, pastures, industrial and urban zones (Harris, 1984). Even the protected natural areas of Mexico are not excluded from these processes, as parts of them are rapidly being integrated into the agricultural matrix. In the Lagos de Montebello National Park in the State of Chiapas, more than 1000 inhabitants were dwelling within its boundaries in 1990. It has been estimated that in the 1970s there still existed 4753 ha of forest in good condition, 71.9% of the Park's total surface of 6022 ha. Nevertheless, by 1993 the forested area has been reduced to 264 ha, or 4% of the Park's total area (March & Flamenco, 1996). The rest is covered by transformed and fragmented forests, such as agricultural lands and human settlements, which produce a heterogeneous landscape.

Despite this alarming fragmentation and loss of the natural ecosystems within Lagos de Montebello National Park, there exists very little information about its faunal diversity. The principal objective of this study was to identify the tendencies in diversity and composition of field mouse communities (Rodentia: Heteromyidae and Muridae) in habitats of three different grades of disturbance: 1) pine-oak-liquidambar forest; 2) ecotone and 3) agricultural areas (mainly corn fields). These habitats are the principal components of the heterogeneous landscape in the area, resulting from different land use practices.

Small mammals, in particular rodents of the Heteromyidae and Muridae families, generally play important roles in ecological processes. Beyond their considerable contribution to the ecosystem's diversity, they are potential prey for other terrestrial vertebrates, consumers of massive amounts of vegetal parts (leaves, roots, fruits, seeds), predators of insects and other invertebrates, and even small vertebrates, as well as dispersers of seeds and certain mycorrhizal fungi. Moreover, they can be vectors and reservoirs of human diseases, and use a wide range of ecological niches (August, 1983; Bergallo, 1994; Cameron & Spencer, 1981; Carey & Johnson, 1995; Corney & Baker, 1986; Janzen, 1986; López-Arevalo et al., 1993; López-Vidal & Alvarez, 1993; McClearn et al., 1994; Sánchez-Cordero, 1993; Sánchez-Cordero & Fleming, 1993). Due to their key ecological role and ease of capture and handling, these rodents are suitable for ecological studies, offering significant information about the dynamics of local biodiversity in relation to conservation levels of the different habitat types within a landscape.

Materials and methods

Study area

The Lagos de Montebello National Park is situated in the Southeast of the State of Chiapas, Mexico, close to the Guatemalan border, and within the transition zone between the region of the Central Plateau and the Lacandona Tropical Forest (Fig. 1). The average elevation of the area is 1500 m. The prevailing climate is semi-tropical, with summer rains, A(C)w''2(w), according to the Köppen classification, modified by Garcia (Cardoso, 1979). The average annual temperature is 18°C and the average annual precipitation is 1836 mm. The dominant natural vegetation types are pine forest, pine-oak-liquidambar forest, and tropical mountain rainforest (Breedlove, 1981; Carlson, 1954). The dominant woody species are: *Ardisia* sp., *Liquidambar styraciflua*, *Oreopanax xalapensis*, *O. sanderianus*, *Pinus oocarpa*, *P. montezumae*, *Quercus laurina*, *Q. polymorpha*, *Q. sapotae-folia* and *Q. peduncularis* (Carlson, 1954). The presence of over 50 lakes of different sizes is a major characteristic of the landscape. The most common land uses are the cultivation of corn, beans, tomato, coffee, and pasture for extensive cattle ranching. Utilization of the forested areas includes the extraction of firewood, wood, and other non timber-yielding products such as blackberry, mushrooms, bromeliads, orchids and pine needles.

Characterization of habitats

Ten representative sampling sites were chosen: 3 in forest (sites no. 1–3), 4 in the ecotone (sites no. 4–7) and 3 in the crop culture (sites no. 8–10) (Fig. 1, Table 1). The determination of habitat types was realized considering their principal characteristics of heterogeneity, structural complexity and canopy level cover. Several authors have utilized the terms of complexity and heterogeneity as important characteristics of

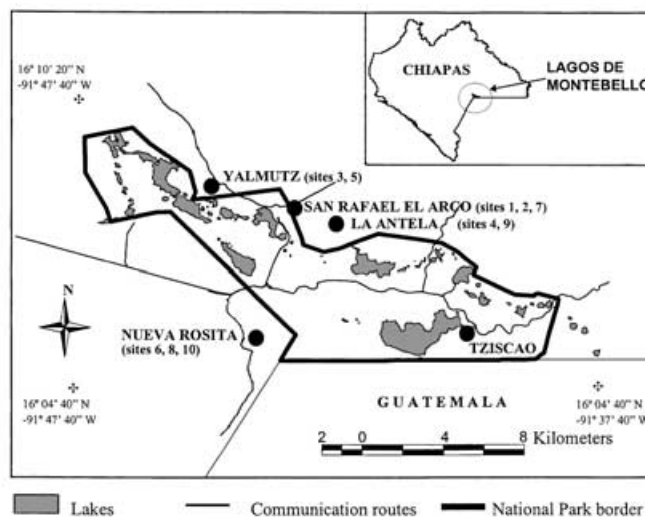


Fig. 1. Location of the Lagos de Montebello National Park in the State of Chiapas, Mexico, and of the different sampling sites.

Table 1. Habitat characteristics of the sampling sites in the Lagos de Montebello National Park, Chiapas, Mexico in 1996.

Sampling sites	Forest			Ecotone				Farm land		
	1	2	3	4	5	6	7	8	9	10
Heterogeneity	1	1	1	2	2	2	3	1	1	1
No. of vertical strata	4	4	3	3	3	3	3	1	1	1
Cover of arboreal stratum (%)	90	80	75	50	30	40	60	2	0	0
Cover of high shrub stratum (%)	70	50	0	0	0	0	0	0	0	0
Cover of low shrub stratum (%)	60	70	85	45	80	60	60	0	0	0
Cover of herbaceous stratum (%)	50	40	60	75	75	75	50	100	90	80
Soil type	2	2	3	3	4	3	2	3	3	3
Slope	1	2	1	2	0	0	1	0	1	0
Rockiness	2	2	1	2	1	0	1	0	2	0
Logs	3	2	2	3	1	1	2	0	0	0
Agricultural system	0	0	0	1	0	0	2	2	1	1
Mono/Polyculture	0	0	0	1	0	0	2	1	1	1
Farming intensity	0	0	0	2	0	3	1	1	2	3
History/Phase of succession	4	4	4	3	3	3	2	3	1	3

Heterogeneity = No. of different habitat types in a sampling site.

Soil type: 1 = sandy; 2 = muddy; 3 = clayey; 4 = flooded

Slope: 0 = low; 1 = moderate; 2 = pronounced

Rockiness: 0 = no; 1 = low; 2 = medium; 3 = high

Logs: 0 = no; 1 = some; 2 = relatively abundant; 3 = very abundant

Agricultural system: 0 = no, 1 = annual; 2 = perennial

Mono/polyculture: 0 = no agriculture, 1 = monoculture; 2 = polyculture

Farming intensity: 0 = no; 1 = extensive (manually without use of agrochemicals); 2 = semi-intensive (manually with use of agrochemicals); 3 = intensive (mechanical with use of agrochemicals)

History/phase of succession: 1 = <5 yrs; 2 = 5–10 yrs; 3 = 10–20 yrs; 4 = >20 yrs

a habitat (August, 1983; Gallina et al., 1996). Habitat complexity refers to the vertical structure of the vegetation (number of strata) while the horizontal variation of the habitat's features is expressed in the heterogeneity of the habitat patches (August, 1983). Based on these structural aspects and canopy cover, three different habitat types were defined: 1) forest habitat with three or more strata and with a canopy tree cover of more than 75%; 2) heterogeneous habitat or ecotone with no more than 3 strata and with a canopy tree cover of less than 60% (forest, or coffee culture, partly with shadow); 3) homogeneous habitat with crop culture, containing only the herbaceous stratum (Table 1). Apart from the above characteristics, some qualitative habitat data considered important to the supposed requirements of small mammal communities were also recorded (August, 1983; Carey & Johnson, 1995; Gallina et al., 1996) (Table 1).

Sampling design

Mice were sampled with Sherman live traps arranged in 7 × 7 grids with a trap-spacing of 10 m. Traps were not placed on standing trees. A total capture effort of 3820 trap-nights was applied over 9 months, from February to October of 1996. At each sampling site the same capture design and effort was applied, with 3 temporal repetitions of a 3 day

series of capture-recapture. To avoid the influence of different nearby habitat types, within the forest and the cropland the trap grid was placed as far as possible from the edge of adjacent habitats of different type. In the ecotones the quadrats were established in such a way that their central line followed either the ecotones' center or the border between the two different habitats. In the latter case, the two halves of a quadrat fell on the two neighboring habitats. Oat flakes mixed with peanut butter and vanilla essence were used as bait. The traps were checked twice a day, in the evening and early in the next morning. The first captured individuals (three at most) of each species were prepared as scientific specimens for reference and were placed in the Mammal Collection of ECOSUR (CHIS.MA.013.0497). Subsequently captured individuals were identified according to their external characteristics, permanently marked by an earmark-system, and then released at the capture site.

Data Analysis

Species abundance was estimated using the multiple recapture Jolly-Seber open-population model (Krebs, 1989; Seber, 1986). This model consists of a 'hyperpopulation' that includes all members of the population alive at present or to be born during the experiment. Abundance data are considered by sampling site, or by habitat type, not by surface unit.

We use the term habitat referring to any use of such habitat by the registered species.

Generally, heteromyid and murid rodents do not roam large distances and have restricted home ranges which do not exceed 5000 m², varying by species, sex, age or season (López-Arevalo et al., 1993; López-Vidal & Alvarez, 1993; Quintero & Sánchez-Cordero, 1989). Hence, we assume that species are associated with a particular habitat. In this study, a species was defined as characteristic for a habitat-type, when more than 75% of individuals were captured in that habitat (Fig. 3). From this criterion, species that were recorded just by one captured individual were excluded from the calculations.

Three parameters were used for the characterization of rodent communities: the richness (total number of species present), the total abundance of individuals, and the Shannon-Wiener diversity index (H') (Magurran, 1988; Pielou, 1975). The 10-base logarithm was used for the calculation of indices. To improve the statistics at the H' diversity-index estimation for each habitat type, jack-knifing was applied (Magurran, 1988). Diversity indices of habitat types were compared with paired t tests (Sokal & Rohlf, 1981; Zar, 1996).

We used the similarity index of Morisita to determine the similarity level (Wolda, 1981) and indices of beta diversity of Whitaker (β_w) and of Wilson and Shmida (β_T) to quantify the composition change of the species between habitat types (Magurran, 1988). The index β_w was used to indicate the relationship between the average number of species at the different habitats and the total richness of the area, while the index β_T was considered as the measure of the species turnover among the different habitats (Magurran, 1988; Schluter & Ricklefs, 1993).

The relationship between properties of the rodent community and environmental variables was evaluated in the non-parametric correlation analysis of Kendall Tau (Sokal & Rohlf, 1981).

Results

Species richness

We recorded 10 rodent species, 1 heteromyid and 9 murids (Table 3). Two of these species are new records for the Montebello region (*Oligoryzomys fulvescens* and *Peromyscus mexicanus*).

Capture success and temporality

Capture success was high (10.7%) with 410 captures, including 115 recaptures. Highest capture and recapture rates were registered in the forest and during the rainy season (August, September, October), however, in the forest habitat during the whole study and independently of the season, the number of the captures remained high and stable (Table 2). The most often recaptured species was *P. zarhynchus*.

Table 2. Number of mice captured per habitat and season in the Lagos de Montebello National Park, Chiapas, Mexico, in 1996.

	Forest	Ecotone	Farm land	Total
Feb–Apr	57	61	18	136
May–Jul	58	35	15	108
Aug–Oct	60	68	38	166
Total	175	164	71	410

Diversity and composition of the communities

The ecotone was the richest habitat type harboring 9 of the 10 recorded species. Nevertheless, it also showed the greatest dissimilarity in abundance of the species (Table 3, Fig. 2). Three species, *O. fulvescens*, *O. couesi* and *P. zarhynchus*, were only registered once, while *R. mexicanus* alone accounted for 68% of the total abundance. Hence the ecotone had a lower diversity index than the forest, where fewer species were found, but numbers of individuals were more evenly distributed between species (Fig. 2). The lowest total abundance and diversity indices were obtained in the croplands (Table 3). In contrast, the highest diversity index and the most balanced composition of rodent communities were found in the forest (Fig. 2). The forest had a significantly higher diversity of mice than both the crop land ($t = 2.493$, $0.025 < p < 0.05$) and the ecotone ($t = 2.138$, $0.025 < p < 0.05$).

Characteristic species

In the forest, 2 of the 5 species present were identified as characteristic, *H. desmarestianus* and *P. zarhynchus*, whereas *P. mexicanus* and *R. mexicanus* are characteristic for the ecotone. The latter is the only species recorded in all habitat-types and occurred in the highest total abundance. In the cropland zones, only *S. hispidus* is characteristic (Fig. 3). *O. fulvescens* and *O. couesi* were not taken into account for the calculation.

Beta diversity and similarity

The high degree of association between habitat and heteromyid and murid rodents is also reflected in high beta diversities, either expressed as the average number of species per sampling site with respect to the total richness of area ($\beta_w = 0.76$), or as the species turnover among habitat types (Table 4). From the cropland, through the ecotone to the forest, 7 species were gained and 5 were lost. Among the mouse communities, little similarity and a high level of species turnover were observed in the three habitat types. The highest similarity was found between forest and ecotone (44%), while similarities between ecotone and cropland and between forest and cropland were low, 16% and 2.8% respectively.

Table 3. Abundance of the recorded species and diversity indexes in the different habitat types in the Lagos de Montebello National Park, Chiapas, Mexico, in 1996.

Species	Abundance (Estimated number of individuals)			Total	F (%)	R.A.I.
	Forest	Ecotone	Farm land			
<i>Heteromys desmarestianus</i>	8	—	—	8	10	0.21
<i>Oligoryzomys fulvescens</i>	—	1	—	1	10	0.03
<i>Oryzomys alfaroi</i>	37.4	14	—	51.4	60	1.34
<i>Oryzomys couesi</i>	—	1	—	1	10	0.03
<i>Peromyscus levipes</i>	15	6	—	21	20	0.55
<i>Peromyscus mexicanus</i>	—	15	—	15	20	0.40
<i>Peromyscus zarhynchus</i>	31.66	1	—	32.66	30	0.85
<i>Reithrodontomys mexicanus</i>	21	122	3	146	90	3.82
<i>Reithrodontomys sumichrasti</i>	—	10	21	31	60	0.81
<i>Sigmodon hispidus</i>	—	7	32.5	39.5	40	1.03
Richness	5	9	3	10		
Total abundance	113	177	57	347		
H' (<i>Jack-knife</i>)	0.746	0.569	0.459			
	(s.e. = 0.098)	(s.e. = 0.149)	(s.e. = 0.060)			
1/D (<i>Jack-knife</i>)	4.639	2.048	2.759			
	(s.e. = 1.174)	(s.e. = 0.767)	(s.e. = 0.346)			

F = Frequency of the occurrence of each species (Number of sites of occurrence / Total number of sites × 100).

R.A.I. = Relative abundance index of each species (Total number of individuals / total capture effort × 100).

H' = Shannon-Wiener diversity index.

1/D = Inverse Simpson dominance index.

s.e. = Standard error of the estimated diversity indexes by *Jack-knifing*.

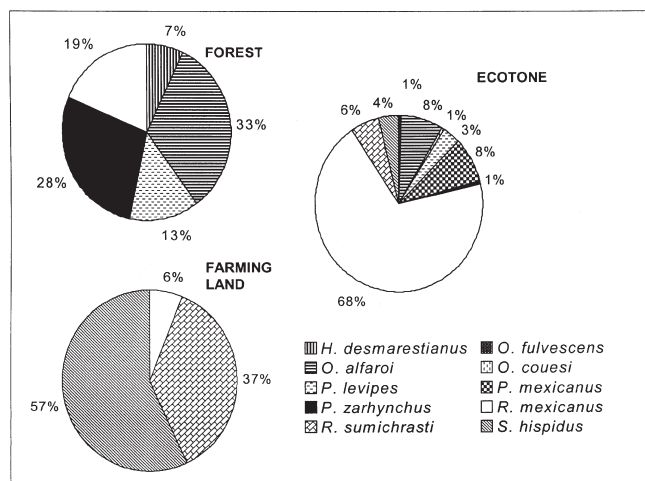


Fig. 2. Mouse community composition in the three habitat types at the Lagos de Montebello National Park, Chiapas, Mexico.

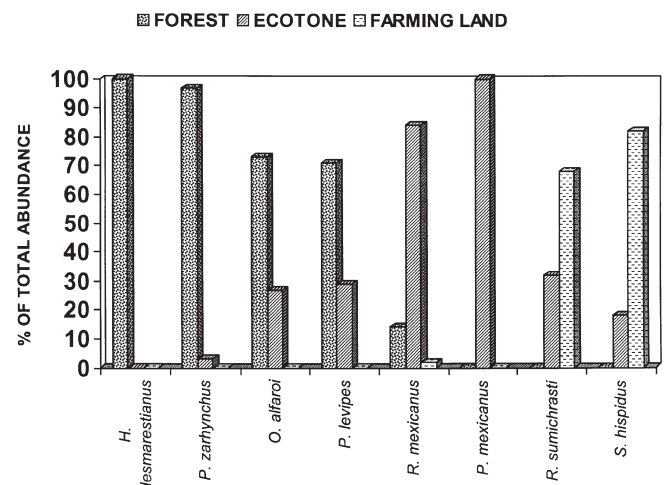


Fig. 3. Distribution of the abundance of mouse species by habitat types (*O. fulvescens* and *O. couesi* are not considered) in the Lagos de Montebello National Park, Chiapas, Mexico, in 1996.

Characteristics of habitat and diversity of mice

The diversity of the rodent communities, expressed as species richness, is positively correlated with the heterogeneity of the habitat ($\tau = 0.527$; $p = 0.0339$). There are also positive correlations between the diversity expressed as Shannon-Wiener's index and the complexity ($\tau = 0.597$; $p =$

0.0163), the coverage of the arboreal stratum ($\tau = 0.629$; $p = 0.0113$), the rockiness ($\tau = 0.493$; $p = 0.0472$) and the quantity of logs ($\tau = 0.662$; $p = 0.0077$). A negative correlation was found between the diversity expressed as Shannon-Wiener's index and the intensity of the agricultural activity ($\tau = 0.547$; $p = 0.0278$).

Table 4. Beta diversity indices of Wilson and Shmida between the habitat types in the Lagos de Montebello National Park, Chiapas, Mexico in 1996.

	Forest	Ecotone
Ecotone	0.43	—
Farm land	1.06	0.5

Discussion

It has been suggested that a high level of complexity and heterogeneity in a habitat promotes high species diversity by providing a great quantity of potential ecological niches distributed both vertically and horizontally (August, 1983; Bridgewater, 1988; Carey & Johnson, 1995; Gallina et al., 1996; Noss, 1983). The results of the present study agree with the above hypothesis, reporting a higher diversity of mice in the forest, which is the most complex of the three habitats studied. In the forest, the elevated number of vertical stratification of the vegetation coincides with the highest categories of arboreal cover, the quantity of fallen trunks and rockiness. These characteristics provide a series of resources for mice such as shelter, places for nests and food and presumably are the determining factors for the high diversity of the small mammals, above all mice.

The study area is part of a heterogeneous and fragmented landscape, including several habitats of very different characteristics. Each of the three habitat types has a different rodent community as evidenced by the low level or absence of similarity and by the high values of beta diversity (Table 4). Important ecological features that influence the dispersion and composition of animal communities in an agricultural landscape are the diversity of the habitat, the presence of borders or ecotones, as well as the fragmentation and dynamics of the habitat (Harris & Woolard, 1990). A high exposure to abrupt environmental changes in extensive areas of monoculture or a lack of vertical strata can work as barriers for the dispersion of certain species and thus lead to reduced diversity. For small mammals, especially mice, the extension of habitat patches seems to be very important because even relatively small patches with unfavorable habitat (cropland, little vertical complexity, lack of coverage) may exert a barrier effect (Andrén, 1994; Mills, 1995). The agricultural landscape is the most dynamic habitat, due to the short cycles of the cultivated plants and associated human activities. Therefore, crop fields cannot maintain species that have special requirements or a low tolerance to habitat transformation and only those species that are less sensitive to a rapidly changing environment are able to survive there. These generalist species acquire a competitive advantage in the occupation of the ecological niches and may often become dominant in the agricultural habitat (Harris & Woolard, 1990). This was also shown by the present study,

demonstrating *S. hispidus* as the dominant cropland habitat species. This rodent is a well-known crop plague, from the southern USA to Venezuela (Cameron & Spencer, 1981). It is adapted to disturbed habitats, by tolerating a simplified habitat structure like herbaceous cover and pastures, for shelter and food (Cameron & Spencer, 1981). Due to its high reproductive rate resulting from short gestation, numerous litter and very quick development (Cameron & Spencer, 1981) populations of *S. hispidus* are apparently able to recover quickly from the hazards caused by the abrupt deterioration of the habitat and high predation pressure. In the cropland, the captures increased considerably after August, the beginning of the rainy season, when the accelerated growth of corn and weeds provided cover and food (Table 2). Other species, like *H. desmarestianus* and *P. zarhynchus*, are less generalist and associated to a higher grade of complexity because they require structural elements for shelter and nests or burrows. Moreover, their nutrition is strongly linked to the resources of the forests (Coates-Estrada & Estrada, 1986; Horváth & Navarrete-Gutiérrez, 1997; Martínez-Gallardo & Sánchez-Cordero, 1993; Sánchez-Cordero & Fleming, 1993).

The three cropland species (*R. mexicanus*, *R. sumichrasti* and *S. hispidus*) were also captured in the ecotone. This suggests that the ecotone could serve as temporary retreat for the species of mice that can become a plague in certain periods of the agricultural cycle (Mellink, 1991; Mellink, 1995). It is also important to emphasize that the other species of the ecotone were never found in the cropland zones. This may result from biological peculiarities in these species, which appear to tolerate a minor structural complexity and take advantage of the other resources provided by the ecotone, but perhaps lack the necessary strategies to avoid increased depredation in the edge and simplified habitats such as cropland (Bolger et al., 1997; Rosenberg et al., 1997). In consequence, having reached a certain level of reduction in the structural elements and coverage, the habitat is no longer adequate for them, not even for foraging excursions.

The ecotones, as heterogeneous environments, generally provide certain habitat characteristics, such as a great variety of microhabitats and food resources, factors that can increase the richness of species (Pickett, 1994). They can also constitute corridors or transition areas. Nevertheless, the relatively large border area of ecotones also has some negative effects, such as abrupt fluctuations in the microclimate and the higher exposure to predators (Andrén & Angelstam, 1988; Bierregaard et al., 1992; Murcia, 1995; Pickett, 1994; Saunders et al., 1991). This might explain the absence or the low abundance of some forest species. The mouse communities of the different habitat types among a gradient of the level of disturbance in the area of Lagos de Montebello National Park also suggest a similar tendency. Our results show that species richness (number of species that can potentially be present) seems to increase within the ecotones. Nevertheless, it is important to take into account the quantitative composi-

tion of these rodent communities with a single species (*R. mexicanus*) clearly dominating while individuals of another species occur in ecotone habitat were captured rarely. Thus the high species richness of the ecotones simply may be due to mice passing through the ecotone at the moment of the capture but do not reflect permanent residents.

The occurrence of the endemic species *P. zarhynchus*, in the ecotone is considered to be accidental, as their populations were only stable in the forest. Thus, in spite of presenting a high richness, the ecotone does not seem to maintain a high biological diversity over a long period of time. For the conservation of the endemic and rare species it is, therefore, of lesser importance than the forest.

The high species richness and balanced abundances suggest that the forest is also the most stable habitat in terms of the diverse requirements of the mice such as food, shelter, diversity of microhabitat and nest sites. Thus, the forest is of primary importance for the conservation of the local diversity because it is sheltering a distinct and unique community which includes, besides a species with a locally restricted distribution in the forest habitat (*H. desmarestianus*) a small rodent (*P. zarhynchus*) endemic to Chiapas and perhaps also present in Guatemala (Horváth & Navarrete, 1997). Certainly, the only option for maintaining the whole faunal biodiversity for which this mice community stands only as one example is the conservation of the pine-oak-liquidambar forests in a good state, independently of the role of habitat interspersation.

For a better understanding of the processes influencing changes in diversity and local distribution of the species and their population dynamics, ecological studies focussing on the analyses of habitat quality, availability of resources and feeding habits, and long-term monitoring and determination of habitat-use by radiotelemetry are necessary.

Acknowledgements

This study was supported by ECOSUR and by Idea Wild. Wally Van Sickle III facilitated the field equipment. The field-work would not have been possible without the altruistic assistance of Rafael Martínez Castellanos and Roberto Castellanos Castellanos. Dario Navarrete Gutiérrez and José A. Santos helped in the taxonomic identification of some rodent species. Eduardo Naranjo and Eric Mellink reviewed and gave constructive comments on the manuscript. Judit Dorogi and Charlie Keck reviewed the English text. Finally we thank Anne Zillikens and an anonymous reviewer for the comments and suggestions on the manuscript.

References

- Andrén H (1994): Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355–366.
- Andrén H, Angelstam P (1988): Elevated predation rates as an edge effect in habitat islands: Experimental evidence. *Ecology* 69: 544–547.
- August P (1983): The role of habitat complexity and heterogeneity in structuring tropical mammal communities. *Ecology* 64: 1495–1507.
- Bergallo HD (1994): Ecology of a small mammal community in an Atlantic forest area in southeastern Brazil. *Stud Neotrop Fauna & Environm* 29: 197–217.
- Bierregaard Jr. RO, Lovejoy TE, Kapos V, dos Santos AA, Hutchings RW (1992): The biological dynamics of tropical rainforest fragments. *BioScience* 42: 859–866.
- Bolger DT, Alberts AC, Sauvajot RM, Potenza P, McCalvin C, Tran D, Mazzoni S, Soulé ME (1997): Response of rodents to habitat fragmentation in coastal southern California. *Ecological Applications* 7: 552–563.
- Breedlove DE (1981): *Introduction to the Flora of Chiapas*, Department of Botany California Academy of Sciences, San Francisco, California, USA. p. 35.
- Bridgewater PB (1988): Biodiversity and landscape. In: Firman J, ed., *Landscapes of the southern hemisphere*. Earth-Science Reviews Vol. 25. pp. 485–491.
- Cameron GN, Spencer SR (1981): *Sigmodon hispidus*. *Mammalian Species* 158: 1–9.
- Cardoso MD (1979): *El clima de Chiapas y Tabasco*. Instituto de Geografía, Universidad Nacional Autónoma de México, México, D.F. p. 99.
- Carey AB, Johnson ML (1995): Small mammals in managed, naturally young, and old-growth forests. *Ecological Applications* 5: 336–352.
- Carlson MC (1954): Floral elements of the pine-oak-liquidambar forest of Montebello, Chiapas, México. *Bulletin of the Torrey Botanical Club* 81: 387–399.
- Cervantes FA, Castro-Campillo A, Ramírez-Pulido J (1994): Mamíferos terrestres nativos de México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología*. 65: 177–190.
- Coates-Estrada R, Estrada A (1986): *Manual de identificación de campo de los mamíferos de la Estación de Biología 'Los Tuxtlas'*. Universidad Nacional Autónoma de México, México, D.F. p. 151.
- Corney JE, Baker RJ (1986): *Neotoma mexicana*. *Mammalian Species* 262: 1–7.
- Gallina S, Mandujano S, González-Romero A (1996): Conservation of mammalian biodiversity in coffee plantations of central Veracruz, México. *Agroforestry Systems* 33: 13–27.
- Harris LD (1984): *The fragmented forest. Island biogeography theory and the preservation of biotic diversity*. The University of Chicago Press, Chicago and London. p. 211.
- Harris S, Woolard T (1990): The dispersal of mammals in agricultural habitats in Britain. In: Bunce RGH, Howard DC, eds., *Species dispersal in agricultural habitats*. Institute of Terrestrial Ecology, Belhaven Press, London, New York, pp. 159–168.
- Horváth A, Navarrete-Gutiérrez DA (1997): Ampliación del área de distribución de *Peromyscus zarhynchus* Merriam,

- 1898 (Rodentia: Muridae). *Revista Mexicana de Mastozoología* 2: 122–125.
- Janzen DH (1986): Mice, big mammals, and seeds: It matters who defecates what where. In: Estrada A, Fleming TH, eds., *Frugivores and seed dispersal*. Dr. W. Junk publishers, Dordrecht, pp. 251–271.
- Krebs CJ (1989): *Ecological methodology*. Harper and Row Publishers, New York, 654 pp.
- López-Arevalo H, Montenegro-Díaz O, Cadena A (1993): Ecología de pequeños mamíferos de la Reserva Biológica Carpanta, en la Cordillera Oriental colombiana. *Stud. Neotrop. Fauna & Environm.* 28: 193–210.
- López-Vidal JC, Álvarez T (1993): Biología de la Rata Montera, *Neotoma mexicana*, en La Michilia, Durango, México. In: Medellín RA, Ceballos G, eds., *Avances en el Estudio de los Mamíferos de México*. Publicaciones Especiales Vol. 1. Asociación Mexicana de Mastozoología, A.C., México D.F. pp. 185–195.
- Magurran AE (1988): *Ecological diversity and its measurement*. Princeton University Press, Princeton, New Jersey. p. 79.
- March IJ, Flamenco A (1996): *Evaluación rápida de la deforestación en las áreas naturales protegidas de Chiapas (1970–1993)*. El Colegio de la Frontera Sur, The Nature Conservancy, U.S.AID, San Cristóbal de las Casas, Chiapas, México, 123 pp.
- Martínez-Gallardo R, Sánchez-Cordero V (1993): Dietary value of fruits and seeds to Spiny Pocket Mice, *Heteromys desmarestianus* (Heteromyidae). *J Mammal* 74: 436–442.
- McClern D, Kohler J, McGowan KJ, Cedeño E, Carbone LG, Miller D (1994): Arboreal and terrestrial mammal trapping on Gigante Peninsula, Barro Colorado Nature Monument, Panama. *Biotropica* 26: 208–213.
- Mellink E (1991): Rodent communities associated with three traditional agroecosystems in the San Luis Potosí Plateau, Mexico. *Agriculture, Ecosystems and Environment* 33: 363–375.
- Mellink E (1995): Uso del hábitat, dinámica poblacional y estacionalidad reproductiva de roedores en el Altiplano Potosino, México. *Revista Mexicana de Mastozoología* 1: 1–8.
- Mills LS (1995): Edge effects and isolation: Red-backed voles on forest remnants. *Conservation Biology* 9: 395–403.
- Murcia C (1995): Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10: 58–62.
- Noss RF (1983): A regional landscape approach to maintain diversity. *BioScience* 33: 700–706.
- Pielou EC (1975): *Ecological diversity*. John Wiley and Sons, New York, USA, p. 165.
- Pickett STA (1994): Mosaics and patch dynamics. In: Meffe GK, Carroll CR, eds., *Principles of conservation biology*. Sinauer Associates, Inc. Sunderland, Massachusetts, USA, pp. 242–258.
- Quintero G, Sánchez-Cordero V (1989): Estudio del área de actividad de *Heteromys desmarestianus* (Rodentia: Heteromyidae) en una selva alta perennifolia. *Anales del Instituto de Biología. Universidad Nacional Autónoma de México, Serie Zoológica* 60(2): 223–240.
- Rosenberg DK, Noon BR, Meslow EC (1997): Biological corridors: Form, function and efficacy. *BioScience* 47: 677–687.
- Sánchez-Cordero V (1993): Estudio poblacional de la rata espinosa *Heteromys desmarestianus* en la selva húmeda en Veracruz, México. In: Medellín RA, Ceballos G, eds., *Avances en el estudio de los mamíferos de México*. Publicaciones especiales, Vol.1, Asociación Mexicana de Mastozoología A.C., México D.F., pp. 301–316.
- Sánchez-Cordero V, Fleming TH (1993): Ecology of tropical Heteromyids. In: Genoways HH, Brown JH, eds., *Biology of the Heteromyidae*. Special Publications No. 10. The American Society of Mammalogists, pp. 596–617.
- Saunders DA, Hobbs RJ, Margules CR (1991): Biological consequences of ecosystem fragmentation: A review. *Conservation Biology* 5: 18–32.
- Schluter D, Ricklefs RE (1993): Species diversity. An introduction to the problem. In: Ricklefs RE, Schluter D, eds., *Species diversity in ecological communities. Historical and geographical perspectives*. The University of Chicago Press, Chicago, USA, pp. 1–10.
- Seber GAF (1986): A review of estimating animal abundance. *Biometrics* 42: 267–292.
- Sokal RR, Rohlf FJ (1981): *Biometry. The principles and practice of statistics in biological research*. Second edition. W.H. Freeman and Company, New York, USA. p. 859.
- Wilson DE, Reeder DM, eds., (1993): *Mammal Species of the World. A taxonomic and geographic reference*. Smithsonian Institution, Washington, USA. p. 1206.
- Wolda H (1981): Similarity indexes, sample size and diversity. *Oecologia* 50: 296–302.
- Zar JH (1996): *Biostatistical Analysis*. Third Edition. Prentice-Hall, Inc. New Jersey, USA, p. 121.