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DIVERSITY PATTERNS AND HABITAT USE OF SMALL MAMMALS IN A TROPICAL MOUNTAIN AREA IN CHIAPAS, MEXICO

Thesis of PhD dissertation

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INTRODUCTION AND OBJECTIVES

Community ecology is one of the most dynamically changing fields in ecology and as such, one of the most debated, too. It is centered around two main questions: 1) what is the composition of ecological communities and 2) what are the underlying processes determining them. Investigating biodiversity has considerable impact on the advances in community ecology, as comprehensive surveys of biodiversity constantly improve species lists of an area, the datasets collected refine theories, modify patterns and provide a more solid foundation for our understanding of processes. Results of scientific research in community ecology, as well as its ever-improving theoretical background play an increasingly important role in conservation biology and practical nature conservation. One of the most influential examples is the shift from species protection strategies to the protection of habitats and landscapes, and from preservation to active restoration.

Rodents and chiropterans are the most diverse groups of mammals both in terms of species richness and variety of ecological roles. Two thirds of currently known species (a total of 5000) belong to these two groups: 2277 species of rodents and 1116 of bats. Due to their large population sizes, rodents and bats contribute a great amount to the biomass of terrestrial ecosystems. They also form a huge number of ecological niches and their foraging habits are very diverse. They include pollinators, dispersers of seeds and hyphas, insectivores, carnivores and herbivores. Predominant processes and patterns of energy and material flow in ecosystems are driven by the most numerous populations within each functional group or guild. Therefore, rodents and bats play a fundamental role in all terrestrial communities. Neotropical bats deserve special attention as their diversity in this biome is outstanding. Rodents and bats are indispensable in maintaining ecosystem dynamics and in regenerating disturbed areas. Any change in the composition or structure of their communities affects local and regional biodiversity either directly or indirectly.

Earlier research in temperate and tropical regions documented the impacts on habitat change and fragmentation on mammals in general, and highlighted differences among different species, species groups and guilds. Disappearance, fragmentation and conversion of the original forests can induce a number of changes in the structure and composition of ecological communities. Population viability in a fragmented landscape depends on several genetic, ecological, anthropogenic and stochastic factors. The three most studied factors are the ecological, morphological and behavioural characteristics of a given species, evolutionary biology and biogeography of the species and spatial attributes of the landscape.

Mexico is among the first ten countries of the planet as concerns biodiversity and the third regarding mammalian richness. Three quarters of terrestrial mammal species in Mexico are rodents and bats. Rodents belong to 8 families, 46 genera and 233 species of which a half are endemic, whereas bats are represented by 139 species in 63 genera of 9 families of which 15 species are endemic. In Chiapas, the southernmost state of Mexico, bat diversity (106 species) is much higher than rodent diversity (48 species), a phenomenon typical of the Neotropics. There are several endemic species of rodents in the area. In this thesis, I present the results of a comprehensive investigation on mammalian diversity carried out in the Lagos de Montebello National Park. The main research objective was to document and analyse mammalian diversity in the Montebello region, as well as to investigate the effects of habitat disturbance on the diversity and distribution patterns of rodents and bats.

Specific research directions were as follows:

a) Taxonomical and zoogeographical survey and assessment of mammal diversity in the area
b) Estimate the efficiency of the survey creating a model of the expected maximum number of species based on γ-diversity and sampling effort, and make suggestions on future research directions
c) Analyse and compare small mammal community composition and diversity among natural and disturbed habitat types (cloudforest, pine-oak-liquidambar forest, pine-oak forest, shade coffee, corn field, pasture).
d) Pinpoint habitat attributes important for small mammal communities and reveal species habitat preference patterns.
e) Evaluate methods applied for sampling small mammals with regards to their efficiency for different species or species groups, and make suggestions for improving methodology.
f) Select species or species groups that can serve as indicators for biodiversity monitoring protocols prescribed by managements plans of the area.
g) Make suggestions for habitat conservations priorities based on diversity indices of small mammal communities.

MATHERIALS AND METHODS

Study area

The Lagos de Montebello National Park is situated in the South Mexican State of Chiapas, next to the Guatemalan border, on the transition zone between the Lacandon rainforest and the Highlands of Chiapas (Figure 1).

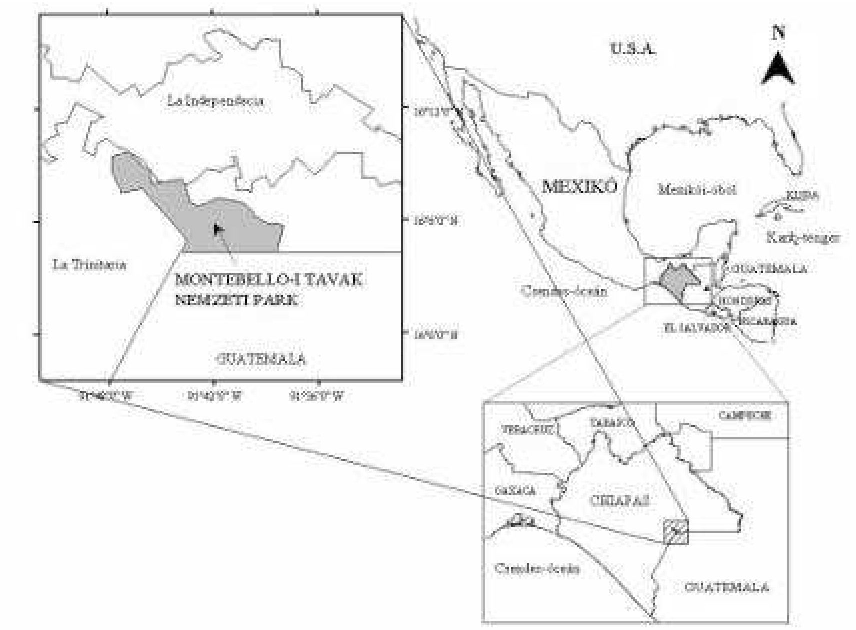

Figure 1: Localization of the Lagos de Montebello National Park in Chiapas, Mexico.

Due to its geographical and ecological situation, the Montebello region is a high diversity area with a considerable proportion of endemisms. The study area is characterized by a landscape mosaic formed by natural heterogeneity and by the particular agricultural, livestock production and urbanization processes of the region during the last few decades, which have frequently been influenced by social and political conflicts. I differentiated five major habitat types considering also the microhabitat diversity of the area: tropical mountain cloud forest, pine-oak-liquidambar forest, pine-oak forest, shade coffee plantation and open vegetation like corn fields or pasture. The habitat types were determined by vegetation structure, dominant tree species and agricultural land use forms. Data were obtained from a total of 73 sampling sites, from which I have 12 sites in cloud forest habitat type, 19 in pine-oak-liquidambar forest, 23 in pine-oak forest, 4 in shade coffee plantation and 15 in open vegetation (corn field or pasture).

Sampling mammals

I collected information on the mammalian fauna between 1996 and 2005, carrying out 6-14 days monthly field work, on 67 occasionsl. Data were obtained using three basic field methods according to the size, mobility, feeding habits, behavioral characteristics, vertical and horizontal use of space of different mammal species or species groups: 1) Direct or indirect visual observations 2) Trapping and 3) Mist netting. Captured bats were marked semi-permanently on the right forearm with ink, small rodents and marsupials were marked individually by applying a permanent marking system by ear-cutting. After marking and taking data, captured individuals were released.

Analysis of habitat data

Data on vegetation structure were obtained from three sampling sites by each habitat type (15 sites). The following habitat variables were analysed: percentage of canopy cover, canopy height, percentage of herbaceous cover, depth of leaf-litter, basal area of trees per hectare, number of tree individuals per sampling quadrate, number of arboreal species per sampling quadrate, relative quantity of epiphytes, amount of fallen logs and rockiness. Differences between habitat variables were analysed using one factor ANOVA (habitat type) and by *t*-tests between pairs of habitat types. Discriminant and Principal Component Analysis were applied in order to examine if the habitat types can be separated by the measured habitat variables.

Faunistic and biogeographic characterization of the mammal community and estimating the expected species richness

The total number of species was considered as the mammal species richness of the whole study area. Based on the complete list of the recorded species I analysed the composition of the mammal community of the Montebello area considering taxonomic, biogegraphic and conservation issues.

The Clench accumulation model was used to estimate the expected maximum number of species as a function of the sampling effort. I analysed the completeness of the mammal diversity survey as compared to the expected species number estimated by the Clench-model, taking the criteria of 90 % as reference. Results were evaluated by the total area and species number, and by species groups and by habitats as well. That contributed significantly to the comparison of mammal communities between habitat types and to the evaluation of the conservation situations of each habitat type.

Diversity and abundance by habitat types

I calculated capture rates as a percentage of captures of the total capture effort. Unit of capture effort was trap-night (that is one trap functioning for one night) and in case of bats, mist net-hour (that is, one 12 m long mist net functioning for one hour). Recapture rate means the percent of recaptures within te total captures. Species richness of each site was considered as the total number of recorded species (by capture or by observation) in a given sampling site. Sampling sites and points of observation were grouped and data were pooled by habitat types in order to obtain the species richness and abundance of each one.

Small rodent and bat community-level analysis.

For the community analysis in groups, I used relative abundance indices by standardizing the number of individuals by sampling effort unit, for each species, each habitat type and in total. The following variables were utilized in order to characterize and analyse bat and small mammal communities in each habitat type: number of species, total abundance, number and percentage of rare species, number and percentage of habitat-specific species (those that occurred in only one habitat type), relative dominance (percentage of individuals of the most abundant species) and the Shannon-diversity index. Abundance ranks were calculated as the contribution of rare species to the diversity of each habitat type. Shannon-diversity indices were compared between the five habitat types using the modified t-test by Hutcheson. Morisita-Horn similarity indexes were calculated in order to compare small rodent and bat fauna between the different habitat types.

I analysed the diversity partition of small rodent and bat communities, which are the patterns of alpha, beta and gamma diversities and the complementarity of the communities in the study area. Relations between average number of species by habitat type (α diversity) and total number of species on the whole area (γ diversity) were estimated with the Whittaker beta diversity index (β_W). Beside this landscape-level beta diversity value, I analysed in detail the species turnover through the gradient of the conservation status of the habitat types.

Habitat preferences of small mammals were examined by using a new habitat preference index, in which I weighted the relative abundance indices of species in each habitat type with the percentage of recapture of a given species in a given habitat type. This parameter expresses not only the abundance of each species, but also the permanence of individuals on the given habitat type. Ordination of habitat preference indices helped to explore if the habitat types can be separated by the occurrence of the species. Furthermore, I searched for those species or species groups that can be considered representative for some habitat types based on the level of association with a given habitat type.

Analysis of the relation between habitat factors and small mammal diversity

To explore associations between habitat and small mammal community variables I considered data only from those 15 sampling sites where vegetation structure data were also taken. Possible associations were analysed using rank correlations, and a Canonical Correspondence Analysis (CCA) helped to examine if there was any effect of habitat variables on the occurrences of small mammal species in the different habitat types.

Evaluating the conservation situation of mammal fauna

I reviewed the representation of the mammal species of Montebello region in the updated nature conservation legislation in Mexico and also in the different categories of international conservation acts (IUCN and CITES). Then I compared this with the local situation of the species in the study area. To evaluate the local conservation situation of mammals in the Montebello region I used a ranking system that took into account nine criteria grouped in three main themes: *I. Biological characteristics:* 1) Systematic status, 2) Population density, 3) Distribution, 4) Ecological specialization, 5) Habitat or vegetation type. *II. Conservation status*: 6) Presence in the Mexican or international conservation legislation. *III. Characteristics of the species in the study area*: 7) Occurrence, 8) Relative abundance, 9) Utilization by local people, hunting.

RESULTS

Habitats

Habitat variables differed significantly among the five studied habitat types (n=45, p<0.0025: Av F=11.628, L% F=118.517, Lm F=25.718, Lsz% F=17.184, Tha F=4.931). Habitat types were separated by the combined effects of the variables of the vegetation structure, as there was a significant difference between group centroids (λ=0.011, F=13.627, p<0.0001). Habitat types could be categorized into two main groups: forest habitat with arboreal structural elements and those open habitats without arboreal components. Between groups of forested habitats other differences were observed: values of basal area and canopy cover separate cloud forest from other forested habitats, while canopy height and the number of trees per sampling quadrate differentiate the pine-oak-liquidambar forets. Therefore, there is no simple distinction between forested and open habitats but more and less complex forested habitat types can be clearly differentiated. Most of the variance was explained by canopy height, canopy cover, herbaceous cover and the basal area.

Faunistic and biogeographical analysis

65 mammal species were recorded in the study area, belonging to eight orders, 19 families and 46 genera. Mammals of the Lagos de Montebello National Park - in 6022 ha surface -, represent 13.5% of all terrestrial mammal species of Mexico and almost one third ((31.4%) of the mammals known for Chiapas can be found here. Mammal fauna of the study area is characterized by neo-tropical affinity: 46 spp (72 %) belong the Neo-tropical Biome, that is, their South-Mexican distribution range is shared with South- or Central-America. A very little portion of the mammal fauna (4 spp, 6%) has a geographical distribution range shared with North-America and 13 spp (20%) have a range that is shared with both North- and South-America. Within the Neo-tropical species group - the most of the mammal fauna of Montebello -, Mesoamerican endemism is particularly important: a third part of the species (22 spp, 34%) is distributed only in the Mesoamerican Bioregion. In the Montebello region there is an endemism even more limited in range: the Chiapan Deer-mouse (*Peromyscus zarhynchus*) is known only from the state of Chiapas.

Bats and rodents have nearly the same species richness (25 and 22) and jointly provide the ¾ part to the total richness of mammals (47 spp, 73%). Small carnivore diversity is relatively high, I recorded 10 species belonging five families (Carnivora: Felidae, Canidae, Mustelidae, Mephitidae, Procyonidae). Marsupials (Didelphimorphia: Didelphidae) with three opossum species, shrews (Soricomorpha: Soricidae) with two species, lagomorphs (Lagomorpha: Leporidae) and armadillos (Cingulata: Dasypodidae) with another two species contribute to the total mammalian diversity. White-tailed Deer (*Odocoileus virginianus*, Artiodactyla: Cervidae) is the only big mammal species that still occurs in the study area.

Evaluating the efficiency of sampling methods applied for mammals

In total, 5472 records were obtained including both captures and observations. From these, we got data visually or by indirect methods on about 47 individuals of 18 species, from 13 families and six orders. These observations provide seemingly insignificant part of the total data obtained (0.85%); however, visual or indirect observational methods contributed significantly to the complete species list, since nearly one third of the total number of species (28%) could be recorded only by this kind of methods.

Most of the data were obtained by captures through trapping or mist-netting. Total trapping effort applied for non-flying small mammals were 33950 trap-nights with Sherman traps and 2070 trap-nights with Tomahawk traps. We captured 24 species from which 17 were small rodents (Rodentia: Cricetidae and Heteromyidae), three opossums, (Didelphimorphia: Didelphidae), three small carnivore species (Carnivora: Mephitidae and Procyonidae) and one shrew (Soricomorpha: Soricidae). Capture success obtained with Sherman traps was high (13.4%) while capture success of Tomahawk traps were a quite lower (2.3%). Total mist-netting effort applied for bat capture was 5612 netting-hours reaching 14.8% capture success. More than half (50.7%) of the total captures were recaptures; however, this very high recapture rate was given only by small rodents and opossums.

Composition and structure of small rodent assembly

1789 individuals of 17 small rodent species (Rodentia: Cricetidae and Heteromyidae) were captured during the study. Small rodent assembly of the Montebello region is still very rich as compared with Neotropical high biodiversity conditions, and is characterized by a high proportion of the strongly habitat-associated or/and rare species. The species highlighted from the conservation point of view, contribute more then one third (35.3%) of the total number of the small rodent fauna of the study area. Six rare species and six strictly habitat specialist species (those which occurred only in a single habitat type) were found. Of these, four species are both rare and habitat specialists, hence they can be considered like indicators of habitat quality: the Mexican Wood-rat (*Neotoma mexicana*), Big-eared Climbing Rat (*Ototylomys phyllotis*), the Aztec Deermouse (*Peromyscus aztecus*) and the Northern Climbing Rat (*Tylomys nudicaudus*).

The highest number of species and the Shannon diversity index were found in the cloud forest (13 spp, H'= 0.80), and proportions of rare and habitat specific species were also the highest in this habitat type. The following six small rodent species were the most abundant: Mexican Harvest Mouse (*Reithrodontomys mexicanus*), Mexican Deermouse (*Peromyscus mexicanus*), Sumichrast's Harvest Mouse (*R. sumichrasti*), Hispid Cotton Rat (*S. hispidus*), Alfaro's Rice-rat (*Oryzomys alfaroi*) and the Chiapan Deermouse (*P. zarhynchus*).

The situation of the endemic Chiapan Deermouse (*P. zarhynchus*) deserves a particular mention. Based on the total abundance index, this species is the sixth of the most abundant small rodents. However, this species is strictly associated to the structurally complex non disturbed forests, stable populations occurred only in the cloud forest (where it is the 2nd most abundant species) and in the pine-oak-liquidambar forest. In these habitat types had a very high recapture rate (80%) and a long permanence of individuals was observed (up to 3 years), these parameters being the highest among all species that occurred in the entire study area.

Highest total capture rates per habitat type were observed in the cloud forest and in the pine-oak forest (16% and 15% respectively); while in the shade coffee plantation was one order of magnitude less (<1%). Total recapture rates showed a decreasing tendency from the cloud forest toward the disturbed habitat types. In the cloud forest, the high recapture rate together with the low relative abundance suggests a longer permanence of the individuals in the small rodent community living in this habitat type. This would mean the dominance of the territorial or K-strategist species, and, on the other hand, suggests relative stability of resource availability as a result of the processes of intrespecific competition in the structurally complex habitats. The lowest recapture rate was found in the shade coffee plantation and agricultural lands (crop or pasture), but unlike the cloud forest, this low recapture rate was associated with a high relative abundance, suggesting a quick replacement of the individuals in the populations of the community. This could be explained by the dominance of r-strategist species adapted to the frequent shifts of resource availability in this kind of very disturbed and simply-structured agricultural habitats; and on the other hand, also by the occasional occurrence of individuals of those species in the adjacent forested habitats that occasionally emigrate but are unable to form stable populations for a long time in this kind of dynamical habitat with open vegetation.

Habitat preference of small rodents

11 species occurred in two or more habitat types. Of these, only four species occurred in all the five habitat types: Mexican Deermouse (*Peromyscus mexicanus*), Mexican Harvest Mouse (*Reithrodontomys mexicanus*), Sumichrast's Harvest Mouse (*R. sumichrasti*) and the Hispid Cotton Rat (*Sigmodon hispidus*). However, ordination of habitat preference indices provided an interesting result indicating that three of these four species showed a marked preference for a given habitat type. Based on the habitat preferences of the small rodent species, habitat types would be well separated, indices of habitat preference were not arranged randomly but the occurrence of the species depended on the given habitat type (χ^2 = 1437.41, p = 0.0001, d.f. = 64).

Comparing small rodent assemblies among habitat types

No differences were found among diversity indices of small rodents among habitat types, only a marginally significant difference was observed between the cloud forest and the pine-oak forest (t = 2.148, d.f. = 10, p = 0.057, n = 13). Interestingly, it concerns the two most species-rich communities. This points out that more important differences among small rodent communities in the studied habitat types are not in the value of the H' diversity index itself that includes both the number of species and their abundance proportions, but in the species composing the communities. The most similar small rodent communities were found in the cloud forest and pine-oak-liquidambar forest. However, the value of this highest similarity index was only 69 %, that is, composition of small rodent communities in these two habitat types, which showed to have most similar vegetation structures and locate spatially nearest, are dissimilar from each one at least by 30%. These two habitat types form a group concerning species composition, but even together they do not share more then 50% of the species of small rodent communities of the other three habitat types. The remarkable differences in the community composition have two main origins: differences in relative abundance proportions and the presence of habitat specific species.

Diversity partition of small rodent communities

Species richness per habitat types (α diversity) ranged from 7 to 13, average number of species was α_{av}= 9.4. It is low in relation to the total number of small rodent species in the whole study area (γ = 17), which clearly pointed out a high level of complementarity through a high species turnover between the habitat types. Landscape level beta diversity was also very high, β_W = 0.55, meaning that in each habitat type only occurs over a half of the total species richness (γ diversity) of the Montebello region. From the biological conservation point of view this means that the disappearance or strong alteration of any present habitat type would lead to the loss of at least a half of the total small rodent fauna in the study area, hence small rodent communities in the different habitat types do not overlap but considerably complement each other. Among natural forested habitat types, complementarity (species turnover beta diversity) indices between pine-oak forest and pine-oak-liquidambar forest as well as between pine-oak forest and cloud forest were found the highest.

Composition and structure of bat assemblies

A total of 828 individuals of 25 bat species (Chiroptera) were captured during the study. More then a half of the bat fauna of the area (13 spp) are considered rare. Despite the high proportion of rare species, relatively few habitat specific species were observed occurring in only one habitat type (12%). Three such species were found: one nectarfeeding (Commissaris's Long-tongued Bat *Glossophaga commissarisi*) and two forest-interior feeding insectivorous bats (Ghost-faced Bat *Mormoops megalophylla*, Elegant Myotis *Myotis elegans*).

The number of bat species, like rodents', was highest in the cloud forest (17), however this habitat type showed only the third higher diversity index and the fourth total relative abundance. Pine oak liquidambar forest had the highest diversity index value (H'= 0.91) where the lowest number of species was observed (14), which is due to the lower relative dominance, that is, the evenness of the relative abundances of the species in this community. Number of species per habitat type almost does not vary; there is a difference of only three species between the richest cloud forest and the pine-oak-liquidambar forest where the fewest species was recorded. No significant differences were found between the diversity indices in neither of the habitat types. Considering the total abundance data, the following six phyllostomid bat species are the more frequent in the Montebello area: *Sturnira ludovici*, *Desmodus rotundus*, *S. lilium*, *Anoura geoffroyi*, *Artibeus intermedius* and *A. jamaicensis*.

Interestingly, the highest total abundance was recorded in the habitat type with open vegetation (corn field/pasture land). Furthermore, in this habitat type the absence of any dominant species and relatively high species richness (16) were observed. On the contrary, in both original natural forested habitat types (cloud forest and pine-oak-liquidambar forest), the lowest abundance was observed and in the cloud forest and the shade coffee plantation dominance indices were found to be the highest, where the dominant species (*S. ludovici*) occupied almost a half of the total abundance of these two communities (47.2% and 41.3% respectively). However, we can assume that most of the species captured in the cornfield or pasture would not feed in this habitat type (i.e. fruit-eating bats), thus probably the open habitat type serve like transit routes for several bat species between roosting sites and feeding areas. There is no doubt that in the open habitat more bat species live than in the cloud forest, but we were able to capture more bats that trespassed open habitat.

Habitat preference of bats

It was not possible identify any habitat preference pattern for bat species, habitat types were not separated by ordination of the relative abundance indexes. The results of the permutation test of the correspondence analysis showed that rows (species) and columns (habitat types) were independent from each other, that is, habitat type did not have any influence on the species occurrence (χ^2 = 31.784, p = 0.996, d.f. = 56).

Comparing bat assemblies among habitat types

The most important difference among the bat communities in the five studied habitat types were found concerning species composition. Morisita-Horn similarity indices calculated for pairs of habitat types showed two groups similar only in 50%. This division clearly differentiates the original natural forests of the Montebello region (cloud forest and pine-oak-liquidambar forest) from the altered or disturbed habitat types as result of the human activities in the area.

Diversity partition of bat communities

Species number by habitat types (α diversity) ranged from 14 to 17. The average number of species α_{av} = 15.6 is low in relation to the total species number of the whole area (γ diversity = 25). According to this, a high beta diversity was observed, β_W = 0.63, that is, each habitat type contained a little more then a half (60%) of the whole landscape-level diversity (γ) in the Montebello region. These results, as in the case of rodents, suggest a high degree of complementarity (species turnover) among the studied habitat types. This means that bat communities in the different habitat types share only a small proportion of the species and in fact complement each other in more than 40%. Pine-oak-liquidambar forest showed the highest species turnover index in relation to the other habitat types.

Effects of habitat variables on small mammal diversity

Species number and proportion of rare species in small rodent communities showed a positive relationship with some habitat variables, suggesting that more complex vegetation structure and higher floristic diversity could support higher small rodent diversity. Furthermore, proportion of habitat specific species was related to abiotic structural elements like rockiness and amount of fallen logs. Habitat-associated small rodent species recorded in the study area are characterized by some specific shelter and nesting requirements. *N. mexicana* and *T. nudicaudus* often refuge and nest in caves and rocky cavities, while *P. zarhynchus* nests in underground hollows between kickstand grassroots of the older trees that form more frequently in rocky grounds. In the open habitat type the proportion of the very common species abruptly increases in the total abundance of the community.

Fewer correlations were found in case of bats probably because of their habitat use properties due to their mobility by flying. This suggests the need for analysis on the species composition level rather than searching for assumed relations between bat community parameters and variables of vegetation structure. Despite some correlations encountered between small mammal community parameters and habitat variables, only between Shannon diversity index of small rodent communities (H') and the height of canopy level was found acceptable linear regression (R= 0.5817, R^2 = 0.3384; $F_{1,13}$ = 6.6497, p = 0.0229, s.e. = 5.2926). Multivariate data exploration (CCA) gave high correlations between the species and the habitat variables axes, in case of both bats and rodents, indicating habitat variables' influence on species composition. Bat species were arranged in a clear gradient-pattern among both axes, which is defined by habitat factors representing vegetation cover (canopy cover, herbaceous cover, leaf litter depth) and by floristic diversity. Number of tree individuals and canopy height draw the species' points around the second axis showing the influence of the habitat structure on the arrangement of the species. The largest group of bat species was arranged near the arrow representing tree species richness. Small rodents formed two groups: species that prefer open habitat types can be found along the arrow of herbaceous cover, and species that prefer forested habitat types are found near the arrows represented by the canopy cover. Species coordinate scores did not spread more along the first axis, that is, there is no more differentiation among forested habitat types in accordance with the changing values of habitat variables. However, another gradient can be observed along the second axis in species occurring in forested habitat types only: the extreme coordinates belong to a cloud forest associated species (*Otoylomys phyllotis*), and two pine-oak forest associated species (*Neotoma mexicana*, *Peromyscus aztecus*).

Assessing the completeness of faunistic inventory of mammals

We can expect the presence of 76 mammal species as maximum in the study area, the number of recorded species reaches 85% of this estimate. To record the 11 more species predicted by the accumulation model we should duplicate at least the applied total sampling effort. The completeness criteria of 90% would be reached by recording 68 species; three more than were recorded during the study. Species not recorded but probably present in the study area are some rare small carnivores like *Eira barbara* and other species or groups that are difficult to observe or capture with the applied sampling methods such as shrews (Soricidae), underground-living pocket gophers (Geomyidae), and high-flying insectivorous bats (Molossidae, Natalidae). The species list of small rodents is near complete, from the 18 estimated by the model, 17 were recorded surpassing the 90% criterion.

Evaluating conservation values and priorities of habitat types

The accumulation curves confirm the importance of the two forested habitat types (cloud forest and pine-oak-liquidambar) in preserving biodiversity in the Montebello region. Not only species richness is highest in these two habitats (45 and 37 species, respectively), but complementarity is remarkably high and habitat specific species are also very characteristic, placing these habitats high on the priority list of conservation. The slope and direction of the accumulation curve shows that the proportion of rare species that have already been observed is higher, and there are potentially more present that could be recorded by higher effort sampling. The model points out the importance of forested and other habitat types partially wooded. Thus, even in a strongly disturbed and structurally and floristically simplified shade coffee plantation, the estimated number of species is almost as high as in forested habitats.

Evaluating conservation situation of the mammal species

14 mammal species, 21.5% of the entire mammal fauna, are represented in Mexican (NOM-059-ECOL-2001) or international conservation categories (IUCN, CITES). From these, six species are enlisted in more than one conservation act: the Chiapas Deermouse (*Peromyscus zarhynchus*), Mexican Hairy Dwarf Porcupine (*Coendou mexicanus*), Jaguarundi (*Herpailurus yagouaroundi*) Margay (*Leopardus wiedii*), Cacomistle (*Bassariscus sumichrasti*) and the Kinkajou (*Potos flavus*). At least in one of these conservation acts four bat species are also included: the carnivore Woolly False Vampire Bat (*Chrotopterus auritus*), Hairy-legged Vampire Bat (*Diphylla ecaudata*), Velvety Fruit-eating Bat (*Echisthenes hartii*) and the Mexican Free-tailed Bat (*Tadarida brasilinesis*). From rodents, the Hispid Pocket Gopher (*Orthogeomys hispidus)* and Lowland Paca (*Cuniculus paca*) appear in some of the conservation lists.

Almost a half of the 25 species suggested for conservation priority (12 spp) in the Montebello region are not included in either of the official national and international conservation acts. Of these, six are small rodent species (3. *Tylomys nudicaudus*, 5. *Ototylomys phyllotis*, 14. *Nyctomys sumichrasti*, 17. *Neotoma mexicana*, 18. *Peromyscus aztecus*, 25. *Heteromys desmarestianus*), five are bats (19. *Centurio senex*, 20. *Glossophaga commissarisi*, 21. *Myotis elegans*, 22. *Micronycteris microtis*, 23. *Hylonycteris underwoodi*) and one is a shrew (*Cryptotis goldmani*).

CONCLUSIONS AND SUGGESTIONS

During nine years of fieldwork, 65 mammal species were registered in the Montebello region that belong to 46 genera of 19 families of 8 orders. The region can be typefied as having a Neotropical affinity with a high tendency of Mesoamerican endemism, including one species endemic to the state of Chiapas, the Chiapan Deermouse (*Peromyscus zarhynhcus*).
Most mammals in the region are small mammals. Rodents are characterized by a high diversity, whereas bat communities are at an intermediate level.

Althought the sampling was almost complete with regards to mammals, with serious further efforts and a wider range of field methods the species list can potentially be added to, especially as concerns bats. There is a chance of recording a small number of microcarnivores, shrews and pocket gophers that have not been recorded before. The list of rodent species is assumed to be complete, even though the presence of one additional species cannot be ruled out.

Lansdscape-scale distribution patterns of rodents and bats were quite different in several ways. A large proportion of rodent species only occur within one habitat type and most of those that occur over a range of habitats would still show explicit habitat preference. In bats, there was no clear preference for any habitat type. At the same time, relative frequency of bats was affected by structural characteristics of habitats describing vertical complexity and available food sources.

Both bats and rodents were found in the highest diversity in the two natural forest types, cloud forest and pine-oak-liquidambar forest. Therefore, protection of remaining stands, as well as restoration of this habitat type should be prioritized in management plans of the national park. The importance of cloud forest must be stressed from other aspects, too, of which the five most important ones are:

1) Cloud forests are extremely rich in mammal species (45 species, as opposed to other habitat types in this study: pine-oak-liquidambar– 37 species, pine-oak – 35 species, shade coffee / corn field / pasture – 25 species each).
2) According to the model estimating the number of species, this is the habitat, where although yet undetected, scarce species can potentially be registered.
3) This habitat harboured the highest number of habitat specialists and rare species.
4) This habitat is the one which overlaps the least with the disturbed habitat types.
5) Due to current land use tendencies, this habitat type is the most threatened not only in the Montebello region, but in its entire distribution range.

Complementarity among small mammal faunas of different habitat types within the study area is quite high, while faunistic similarity is low, therefore it can be concluded that the Montebello region has a high beta diversity. From the nature conservation point of view, this means that apart from protecting areas currently in good condition (i.e. the original forested habitats) the protection of moderately modified agricultural areas are very important for biodiversity. For this reason, it is necessary to include landscape structural arguments in the management plan of the national park and its buffer zone. The presence of open habitats can be advantageous for bat species as well as for some species of micro- and mesocarnivores. Those species that not only utilize but explicitly need a certain level of mosaicity of habitats are the larger sized species and game still persisting in the area, such as the Lowland Paca, White-tailed Deer, Nine-banded

Armadillo, Raccoon, Virginia Opossum, Eastern Cottontail. In case a management plan strongly grounded in scientific research is enforced as well as local regulations on hunting, these species can present the local population with a considerable economic potential.

The following mammal species should be the highest priority for nature conservation: *Leopardus wiedii, Herpailurus yagouaroundi, Tylomys nudicaudus, Orthogeomys hispidus, Ototylomys phyllotis, Potos flavus, Coendou mexicanus, Peromyscus zarhynchus, Sciurus deppei, Chrotopterus auritus, Nasua narica, Diphylla ecaudata, Cuniculus paca, Nyctomys sumichrasti, Bassariscus sumichrasti.*

As for biodiversity monitoring, small rodents and phyllostomid bats are the most useful indicators of habitat quality. Apart from their indicator roles, these groups can yield a loot of information with relatively little effort, and standard methodology for sampling them is readily available. These attributes are of high importance in planning monitoring. Additionally, a presence-absence survey of small carnivores, the paca and the white-tailed deer should be carried out at regular intervals.

NOVEL RESULTS

1. The present thesis summarizes the results of the first such surveys in the area of the Lagos de Montebello National Park. During a comprehensive and detailed investigation, 65 mammal species were recorded in the area. Of these, preliminary results on 52 species were already published earlier, and this thesis contains information on 13 further species occurences.

2. Small mammal diversity was analysed on both habitat and landscape level, and it can be concluded that cloud forests and pine-oak-liquidambar forests are the most diverse of all habitat types. Complementarity among small mammal faunas of different habitat types within the study area is quite high, while faunistic similarity is low, therefore it can be concluded that the Montebello Lakes region has a high beta diversity. From the nature conservation point of view, this means that apart from protecting areas currently in good condition (i.e. the original forested habitats) the protection of moderately modified agricultural areas are very important for local and regional biodiversity.

3. Habitat preference of small mammals within the Montebello region was assessed, which is an outstanding result not only on a regional or state-level, but in the whole of Mexico. Most small rodent species showed strong associations with the habitat types and six habitat specialist species were found. Of the five habitat types studied, three had their characteristic small rodent fauna types, which were the following:
cloud forests - *Heteromys desmarestianus*, *Ototylomys phyllotis*, *Peromyscus zarhynchus*, *Reithrodontomys mexicanus*, *Tylomys nudicaudu*s, pine-oak forests: *Neotoma mexicana*, *Peromyscus aztecus*, *P. levipes*, *P. mexicanus* and open habitats: *Sigmodon hispidus*, *Baiomys musculus*, *Reithrodontomys fulvescens*, *R. sumichrasti*.

4. Small rodents and phyllostomid bats were selected as potential indicator groups of habitat quality. These taxa can form the basis of future monitoring programs not only within the study area, but in other protected areas throughout the state of Chiapas.

5. By applying a species accumulation model, it could be concluded that the expected maximum number of mammal species in the area is 76, of which 85% are currently present, that is, there is a possibility of recording 11 more species in future.

6. I have pointed out nature conservation priorities within the national park and its buffer zone, that can facilitate the improvement of conservation management plans. A modified version of the practical ranking system used to assess local and regional conservation values within the Montebello region can be easily applied in other geographical areas and other taxa as well. According to the ranking system, the following 15 species should be given the highest priority in conservation: *Leopardus wiedii, Herpailurus yagouaroundi, Tylomys nudicaudus, Orthogeomys hispidus, Ototylomys phyllotis, Potos flavus, Coendou mexicanus, Peromyscus zarhynchus, Sciurus deppei, Chrotopterus auritus, Nasua narica, Diphylla ecaudata, Cuniculus paca, Nyctomys sumichrasti, Bassariscus sumichrasti*. I have also emphasized the importance of harmonizing habitat protection and species protection measures.

7. I have worked out a habitat preference index easliy applicable to small rodents that can be captured by traps. This can provide a useful tool in community ecology projects where a large number of species and habitats are targeted over a diverse area. In

general, it is very hard to find a robust estimation method to assess population sizes that can accommodate all species and habitats in question, even if sampling methodology is standardized. This novel habitat preference index allows for the involvement of all species within a small rodent community and includes the two most important factors determinig habitat preference: relative abundance of species per habitat type and individual permanence in the given habitat type.

8. I have worked out a marking method for small mammals and marsupials, based on protocols used in domestic animals. By using both ears, a total of 399 individuals can be uniquely marked. Even though the method is a lot less invasive than phalanx chipping, it is equally well recognizable. Another advantage to this method, as compared to ear tags of tattoes is that it is quick, easily applicable and very cost effective as it does not require specific equipment.

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