

Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico

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The rapid and extensive conversion of Neotropical rain forests to a landscape consisting of pasture lands and other agricultural habitats has meant the local disappearance, fragmentation and isolation of vertebrate populations. To avoid further losses in biodiversity in Neotropical rain forests, it is imperative to determine how the different species that constitute the different vertebrate communities have responded to the anthropogenic alterations of their natural habitats. To provide data in this direction, we sampled non flying mammals in 35 forest fragments, in six disturbed forest sites, in 12 regenerating forests, in 20 arboreal agricultural habitats (cacao, coffee, mixed, citrus and allspice), in four live fence sites and in four pasture sites at Los Tuxtlas, Veracruz, Mexico. Sampling indicated that area of forest fragments and isolating distance were important variables influencing species richness. Disturbed forest had fewer species and individuals present and supported a lower non flying mammal biomass than undisturbed and regenerating forests. Shaded plantations (cacao, coffee and mixed) were richer in species and in individuals than unshaded ones (citrus, allspice). Species richness in forests and agricultural habitats were associated to horizontal plant diversity and vertical foliage diversity. Pasture habitats were the poorest man-made habitats in non flying mammal species. Live fences supported a higher biomass and species of non flying mammals than pastures and were similar to forest and shaded man-made habitats in species assemblages.

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Introduction

The rapid and extensive conversion of Neotropical rain forests to a landscape consisting of pasture lands and other agricultural habitats has meant the local disappearance, fragmentation and isolation of vertebrate populations. To avoid further losses in mammalian biodiversity in Neotropical rain forests, it is imperative to determine which mammal species have survived the fragmentation and isolation of their tropical rain forest habitat and how they are responding to the environmental change. Reports exist only for a few localities in Central and South Amer-

ica (see Lovejoy et al. 1984, 1986) and more recently for Mexico (Estrada et al. 1993a).

Such information is fundamental to determine what remains of the original biological diversity, as represented by particular animal taxa, and to assess the adaptive responses of animals to tropical rain forest fragmentation and replacement by agricultural vegetation (Saunders et al. 1991, Terborgh 1992). These data may be useful in designing conservation scenarios for wildlife involving different sets of species under different types of land management systems. As a necessary corollary to this, we also need basic information on the little known

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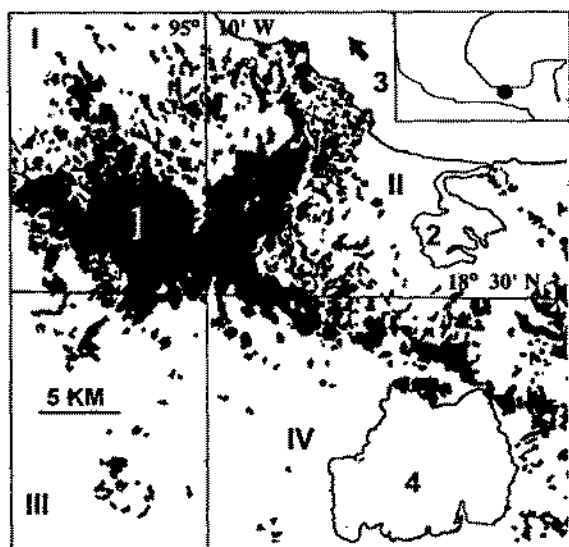


Fig. 1. Northeastern section of the region of Los Tuxtlas in southern, Veracruz, Mexico. Lowland rain forest remaining shown as dispersed fragments. The area was divided into four zones following longitude and latitude ($95^{\circ}10'W$, $18^{\circ}30'N$). Study sites (forests, agricultural habitats and live fences) located in zones II and IV. Map drawn from satellite images taken in April 1990. 1 = San Martin Volcano (1600 m), 2 = Lake Soñtecomapan, 3 = Gulf of Mexico, 4 = Lake Catemaco.

patterns of species composition and distribution for different animal communities in various localities in the neotropics.

In the region of Los Tuxtlas, in southern Veracruz, Mexico, lowland tropical rain forests reach their northernmost distribution in the American continent and are notable for their high biological diversity (Pennington and Sarukhan 1968, Estrada et al. 1985, Dirzo and Garcia 1992). However, land management practices have converted 80–90% of these forests to pastures for cattle ranching. The remaining forests in the landscape consist of collections of fragments of various sizes and with different histories of isolation scattered throughout the region (Estrada and Coates-Estrada 1988). Within this context, agricultural activities occur sporadically in time and space in a "sea" of pastureland and occupy only c. 3% of the land. These consist of cultivation of arboreal plants such as citrus *Citrus sinensis*, Rutaceae, allspice *Pimenta dioica*, Myrtaceae, and cacao *Theobroma cacao*, Sterculiaceae. Farmers cultivate coffee *Coffea arabica*, Rubiaceae as a single crop. Less common is the cultivation of plots of mixed crops that include coffee, cacao, citrus, and banana *Musa* spp., Musaceae. Rain forest trees left by farmers provide shade in the case of cacao, coffee and mixed plantations.

It is a common practice among farmers and ranchers of Los Tuxtlas as elsewhere in the lowland wet Neotropics to use live posts of *Bursera simaruba* (Burseraceae) and *Gliricidia sepium* (Leguminosae) to hold barbed wire

fences to divide the pasture land into smaller plots, to delimit the boundaries of their properties, and, in some cases, to rotate their cattle from one pasture plot to another. Because these posts grow rapidly in height and trunk width and produce moderately foliated crowns, some single rows of these live fences resemble corridors of vegetation criss-crossing the pasture lands.

This paper presents information on how the non flying members of the mammalian community are responding to (a) biogeographical aspects of forest fragmentation (e.g., size and isolating age and distance of forest patches), (b) the continued deterioration of isolated forest patches, and (c) the conversion of forest to pastures and to other agricultural habitats at Los Tuxtlas in southern Veracruz, Mexico.

To achieve this, we examined field data on relative abundance and detection rates of mammal species present in isolated rain forest fragments, in disturbed and regenerating forest habitats, in man-made vegetation islands representing five types of agricultural vegetation, in live fences and in pastures. The data presented are a complement to information published on the flying mammals of this animal community and on the frugivore guilds of the avian and mammalian communities (Estrada et al. 1993a, b).

Methods

We conducted field work in the northeastern area of the region of Los Tuxtlas ($95^{\circ}00'W$, $18^{\circ}25'N$; max. 1600 m

Table 1. Non flying mammal species and individuals censused at the habitats investigated. Numbers between parentheses are species and individual mean (\pm SD) detection rates per site in each habitat.

Habitat	Sites	Species	N	Mean \pm SD Biomass kg
Forest*	35	38 (10.8 \pm 6.8)	1518 (44.7 \pm 35.3)	3298 (89.0 \pm 215.0)
Cacao	4	16 (5.0 \pm 0.81)	144 (36.0 \pm 19.2)	277 (17.0 \pm 26.0)
Coffee	4	13 (4.5 \pm 1.2)	106 (26.5 \pm 14.4)	308 (24.0 \pm 36.0)
Mixed	4	13 (8.0 \pm 0.81)	145 (36.2 \pm 19.0)	427 (33.0 \pm 49.0)
Citrus	4	8 (2.0 \pm 0.81)	38 (9.5 \pm 4.5)	49 (6.0 \pm 5.0)
Allspice	4	7 (2.0 \pm 1.1)	42 (10.5 \pm 3.8)	59 (8.0 \pm 8.0)
Livefence	4	11 (8.0 \pm 1.8)	83 (20.2 \pm 6.8)	123 (12.0 \pm 12.0)
Pasture	4	4 (2.0 \pm 0.81)	93 (23.2 \pm 3.8)	57 (14.0 \pm 12.0)
Total	63	39	2169	

* Forest size classes: <2000 ha N = 3, <1000 ha N = 3, <800 ha N = 3, 600 ha N = 3, <400 ha N = 3, <200 ha N = 3, <100 ha N = 3, <50 ha N = 3, <20 ha N = 3, <10 ha N = 3, <5 ha N = 3, 1 ha N = 2.

a.s.l.) in southern Veracruz, Mexico (Fig. 1). Mean annual temperature is 27°C and mean annual precipitation is 4964 mm (SD + 862 N = 20 yr) with a seasonal distribution (Estrada et al. 1985). Non flying mammals were censused between 1990–1992 in 35 undisturbed forest fragments (isolated forest sites without apparent further human intervention), in six disturbed forest fragments (strong edge effect, hunting and selective removal of hardwoods, firewood and other), in six old second growths (regenerating forests 20–35 yr old) and in six young second growths (5–15 yr). In addition, non flying mammals were censused in 20 agricultural habitats, in four live fences and in four pastures.

We selected the study sites in two zones within the study area to have some control over spatial variation in distribution of the organisms under investigation (Fig. 1). Sites ranged in elevation from sea level to c. 800 m. The 35 undisturbed forest fragments studied varied in isolating distance (distance to edge of the nearest forest fragment: 0.2–8.0 km). Area of forest fragments, obtained by digitizing aerial photos and by corroboration in the field, ranged from 1 to >2000 ha (Table 1).

At each site we estimated time (years) since isolation (isolation = complete separation of forest from major forested land mass) by examining vegetation maps for the period before 1967, aerial photographs taken in 1967 and 1979, satellite images taken in 1986 and 1990 and by field surveys. Isolating age ranged from 5 to 35 yr. Six undisturbed forests fragments selected at random from our data base were compared to the six disturbed forest habitats and to the six young and six second growth habitats in species richness and composition.

We sampled non flying mammals in four replicates of each of the following arboreal and perennial agricultural habitats: cacao, coffee, mixed crops, citrus, and allspice. Tall (> 15 m) rain forest trees left by the farmers provided shade in the case of cacao, coffee, and mixed plantations. The agricultural plots ranged in size from 2–10 ha and ranged in age from 12–15 yr; all habitats were fruit productive. Straight line distance to the nearest forest fragment regardless of size ranged from 200 to 6000 m; distance to the nearest plantation ranged from 200 to 1000 m.

We also censused non flying mammals in four live fence sites c. 2 km long each located across the pasture land and in the vicinity of the forest and agricultural habitats studied; each of these sites was at least 5 km away from the others. We surveyed the non flying mammals in four areas of pasture, 25 ha each, totally devoid of the original forest vegetation and at least 5 km apart from each other, but within a 5 km radius of the forest sites we studied. In the pastures, we located the sampling area in the center of each of the 25 ha pasture plots.

We conducted visual census of non flying mammals along existing trails or along trails demarcated by us with a cotton thread. These trails were walked at a slow pace c. 2 km and both sides of trail were scanned visually. Length of census trails at each site was 400 m for forest

patches ≤ 50 ha, 600 m for patches ≤ 100 ha, 800 m for patches ≤ 200 ha, 1000 m for patches ≤ 400 ha, 1500 m for patches ≤ 800 ha, 2000 m for patches ≤ 1000 ha, 2500 m for patches ≤ 2000 ha.

Census routes were chosen to minimize trail overlap within and between days and nights and thus the probability of viewing the same individual more than once. The census trails were at least 10 m from the edge of the vegetation patch under investigation. We recorded the number of individuals of each species detected. We conducted the censuses between 0600 h and 1200 h and between 1600 h and 1800 h and between 1900 h and 2400 h. We used at night, in addition to flash lights, a night vision scope (Javelin Electronics, model 221) to minimize disturbance to detected animals in the nocturnal censuses. On most cases 2–3 people walked together with either of the two senior authors.

To sample terrestrial species with relatively small home ranges (most rodents < 200 g) and medium size species that are cryptic in their behavior and thus difficult to detect by visual means, we set up at each site 50 wire-mesh cage traps (size ranged from 48 × 17 × 17 cm to 66 × 24 × 24 cm, Tomahawk Live Trap Co.; 25 baited with sardines and 25 baited with fruits and vegetables) and 200 Sherman traps (23 × 8 × 8 cm) baited with oats, peanut butter and vanilla along 4 parallel lines; distance between lines was 20–25 m.

We placed Sherman traps in pairs at 3 m intervals and single Tomahawk traps at 5 m intervals. Trap lines were at least 10 m from the site's borders. At the live fence sites, we formed three trap lines separated from each other by 50 m and running parallel to the barbed wire fence. We operated traps at all sites for two consecutive nights (dusk to 2300–2400 h) and for two consecutive afternoons (1600 h to dusk). We recorded the species detected, its body weight and when possible its sex and age before releasing each mammal. The number of traps was constant across all sites because we wanted to maximize the number of animals detected by this means. Preliminary probes in 10 sites with number of traps kept constant showed that our trapping success was c. 10–20%. Varying the number of traps per area of forest sites showed that in the smaller sites trapping success was nil, but that increasing the number of traps resulted in detections of animals. Detection success was found to reach an asymptote with the use of 40–50 traps.

To control for seasonal variations in the presence and activity of mammals, surveys in the man-made habitats included eight samples per habitat under investigation, two in each quarter of the year (8 × 28 = 224 samples). In forest sites, samples took place in each site in each bi-monthly period of the year (4 × 53 sites = 212 samples).

While the use of trail censuses and traps are complementary methods, they have certain biases. With the traps, we only sampled one level of the habitats studied during the day and night and species of non flying mammals may be caught unequally by traps. However, this is the only way to assess the presence of small terrestrial

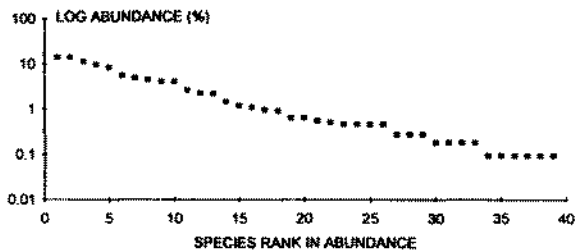


Fig. 2. Dominance diversity curve for the non flying mammal community detected. Note the asymmetry of the curve and the relatively high dominance of first five species.

and/or cryptic mammals. With trail censuses, one runs the risk of counting very mobile and active mammals more than once. Bearing these considerations in mind and our efforts to minimize these biases, the reported data may represent a biased portrait of the mammal community present in the region. Taxonomic nomenclature for mammals followed Hall (1981). We obtained measurements of body weights from our own field records and from the literature (Emmons 1990).

To census the vegetation we recorded, at each site, in six 10×10 m plots, all trees ≥ 10 cm in circumference at breast level and ≥ 1.5 m in height. We located the plots randomly within the area where we sampled the mammals; the plots were at least 30–40 m from each other. We recorded for each tree censused, the species (taxonomic nomenclature for plants follows Ibarra and Sinaca 1987), maximum height and circumference.

We measured vertical foliage density at four randomly selected spots within each of the six plots by scoring vegetation intercepts along a vertical pole at the following intervals: 0–0.5 m, 0.51–1.0 m, 1.1–2 m, 2.1–3 m, 3.1–5 m, 5.1–8 m, 8.1–10 m, 10.1–15 m, > 15 m. In this later case we expressed intercepts at each height interval as the proportion of total intercepts recorded per site/habitat. We expressed horizontal plant diversity per habitat as the mean number of tree species censused per site/habitat and vertical foliage diversity using the Shannon-Weaver information index (H') (Ludwig and Reynolds 1988).

Because mammals were censused using two different methods (traps and visual census), we compared data across vegetation types using proportions and mean detection rates of species and individuals per site in each habitat (site/habitat from here on). We used rarefaction as an alternative to species richness indices to compare species richness among habitats where sample sizes differed (James and Rathburn 1981). We used the dissimilarity index (PD) and the polar ordination procedures of Bray-Curtis (Ludwig and Reynolds 1988) to measure the degree of resemblance when comparing forests and man-made habitats in species assemblages. We used Spearman rank correlation, partial correlation analysis and "t" tests for dependent samples when comparing variables and means between groups (Ludwig and Reynolds 1988,

Fitch 1992). We present means (\pm SD) throughout the text.

We did not consider in our study the aquatic mammal *Trichechus manatus* (Trichechidae) because our surveys were mainly terrestrial (but see Coates-Estrada and Estrada 1986). Likewise, we ignored in our comparison two introduced rodents, *Mus musculus* and *Rattus rattus*, as well as the coyote, *Canis latrans*. We never encountered the introduced rodents, but they are common in human settlements. The coyote has recently expanded its range into Los Tuxtlas as a result of tropical rain forest conversion to pasturelands. We observed this mammal at the forest edges, but never in the forest interior. We refer, for the sake of economy, to non flying mammals as NFM in the rest of the paper.

Results

General aspects

In our sample of 35 undisturbed forest fragments and the agricultural habitats including pastures, we censused 2169 NFM of 39 species. Five species accounted for 66% of all records (*Didelphis marsupialis*, *Peromyscus mexicanus*, *Alouatta palliata*, *Philander opossum*, *Sciurus aureogaster*), but 87% contributed to $\leq 5\%$ of the records (Fig. 2 and Appendix 1). Sherman traps captured all murid and heteromid rodents recorded (7 species, 552 individuals) and Tomahawk traps captured only three marsupials, *D. marsupialis*, *Didelphis virginiana* and *P. opossum*. Traps recorded 84% of the individuals censused of these three species ($N = 626$).

Non flying mammal species in undisturbed forest fragments

In these habitats we censused 1518 NFM representing 38 species. Of these, species such as *P. mexicanus*, *A. palliata*, *D. marsupialis* and *P. opossum* accounted for 50% of the records. The rest of the species contributed to 1% or less of detections (Appendix 1). Because the cumulative species curve in the forest sites tended to level off after the accumulation of > 2000 ha, we feel our sample

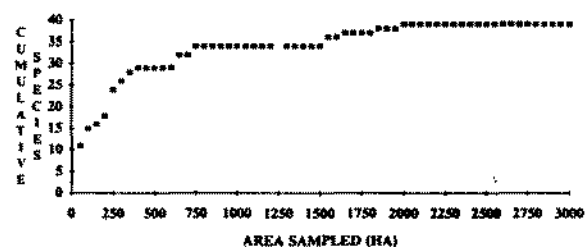


Fig. 3. Cumulative number of non flying mammal species detected and cumulative area sampled in forest fragments.

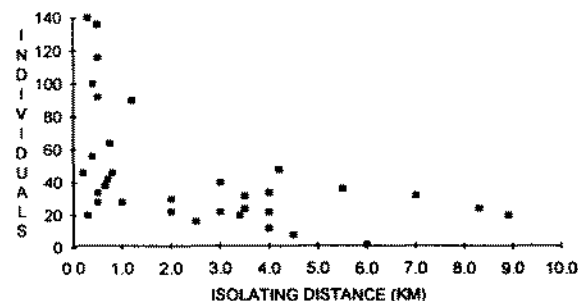
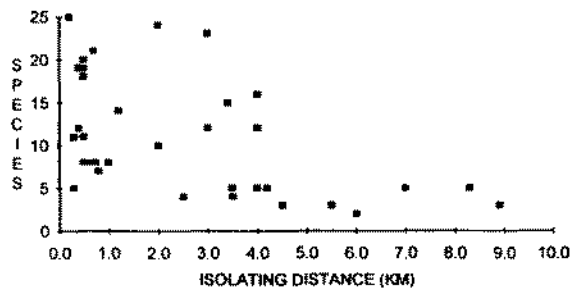


Fig. 4. Relationship between non flying mammal species richness and individuals censused and isolating distance of forest fragments.

provides a reasonably good representation of the species present in the forest remnants studied (Fig. 3). The mean number of species detected per site was 10.8 (SD \pm 6.8) and mean number of individuals censused per site was 44.7 (SD \pm 35.3) (Table 1). On average, forest sites had 25% of the species in common.

Area, age and isolating distance of undisturbed forest fragments and species richness

Species richness and area of forest fragments were related ($r_s = 0.85$, $p < 0.001$), but species richness and number of individuals censused per site were not found associated to isolating age of forest fragments ($r_s = -0.12$, $p = 0.25$; $r_s = -0.20$, $p = 0.12$). However, a significant negative relationship existed between site species richness and isolating distance of forest fragments ($r_s = -0.77$, $p < 0.02$) and between this latter variable and number of individuals censused per site ($r_s = -0.50$, $p < 0.02$) (Fig. 4).

Partial correlation analysis showed that when the influences of area and isolating distance were partialled out, species richness was best correlated with isolating distance (area partialled out $r = -0.60$, $p < 0.001$, isolating distance partialled out $r = 0.37$, $p = 0.01$). An examination of new species accumulated in our sample and cumulative area (ha), showed that c. 45% of the species were present in small forest patches ≤ 200 ha, 60% were present in fragments ≤ 250 ha, and 80% in fragments ≤ 650

Table 2. Species and individual detection rates in four types of forest habitat. Numbers between parentheses refer to number of sites sampled per habitat and distance to the edge of the nearest undisturbed forest site.

Habitat	Mean (\pm SD) number of species per site/habitat	Mean (\pm SD) number of mammals per site/habitat
Undisturbed (N = 6)	14.1 \pm 3.3	37.6 \pm 6.1
Disturbed (N = 6; 350 m \pm 10.0 m)	6.7 \pm 3.4	15.6 \pm 3.7
Old growth (N = 6; 340 m \pm 11.1 m)	5.3 \pm 1.3	14.6 \pm 2.3
Young growth (N = 6; 380 m \pm 7.3 m)	4.8 \pm 1.7	13.0 \pm 3.9

Comparison species: Uf-Df $t = 3.6$, $p = 0.01$; Uf-Yg $t = 5.4$, $p = 0.003$; Uf-Og $t = 5.3$, $p = 0.003$; Df-Yg $t = 1.2$, $p = 0.26$; Df-Og $t = 1.08$, $p = 0.32$; Yg-Og $t = 0.5$, $p = 0.58$.
Comparison individuals: Uf-Df $t = 15.7$, $p = 0.001$; Uf-Yg $t = 20.5$, $p = 0.0001$; Uf-Og $t = 17.1$, $p = 0.0001$; Df-Yg $t = 4.4$, $p = 0.007$; Df-Og $t = 1.1$, $p = 0.31$; Yg-Og $t = 1.3$, $p = 0.24$.

ha; we detected the rest of the species in forest fragments ≥ 700 ha in size (Fig. 3). In this later case were large bodied species that require large areas and found in forest habitats only such as *Tayasu tajacu*, *Ateles geoffroyi*, *Eira barbara*, *Felis concolor* and *Agouti paca* among others (Appendix 1).

Species richness in undisturbed forests, disturbed forests and in second growth habitats

We detected a significantly higher mean number of NFM species and individuals censused per site in undisturbed than in disturbed forests (Table 2). Undisturbed forests were richer in species and individuals than young and old second growth habitats. Young and old second growths did not differ in the mean number of species detected per site or in the mean number of individuals censused per site (Table 2). Data also showed that of the 30 species detected in undisturbed forests, only 14 (46%) were present in disturbed forests, 11 (36%) in old second

Table 3. Species richness in equivalent areas of pastures and forests. Shown also is the species richness detected in 100 ha of agricultural habitats, in 1 ha forest patch and in 1.5 ha of live fences.

Habitat	Number of species	Number of mammals
Pastures 100 ha (4 sites)	4	93
Forests 100 ha (4 sites)	16	175
Forest 1 ha (1 site)	8	14
Agricultural habitats 100 ha (20 sites)	17	475
Live fence (8 km, 1.5 ha) 4 sites	10	81

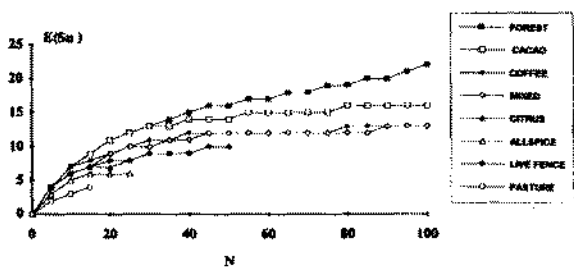


Fig. 5. Rarefaction curves for all habitats examined. $E(S_n)$ is the expected number of species in a random sample of size n where S is the sum of the probabilities that each species will be included in the sample. Comparisons can be made of the expected number of species at different sample sizes.

growths and eight (26%) in young second growth habitats.

The majority of the species missing from the disturbed forests and second growth habitats were arboreal mammals such as *A. palliata*, *A. geoffroyi*, *T. mexicana*, and *C. mexicanus*, carnivores such as *F. pardalis*, *F. weidii*, and *F. concolor* and other large mammals such as *M. americana* and *T. tajacu* among others (Appendix 2). The total NFM biomass detected at disturbed forests was only c. 50% of the NFM biomass detected in undisturbed forest habitats, confirming the loss of medium and large size mammals. Regenerating forests accumulated <15% of the biomass present in undisturbed forests suggesting the colonization of these forests by small size species (Appendix 2).

Non flying mammal species richness in pastures

Our surveys in four pasture sites totalling 100 ha resulted in the census of 93 NFM of only four species. One species (*Sigmodon hispidus*) accounted for 69% of the records. The other species were *D. marsupialis*, *D. virginiana* and *P. opossum* (Appendix 1). Mean detection rates of NFM species in pastures were among the lowest ($\bar{X} = 2.0 \pm 0.8$ species per site; Table 1).

Non flying mammals in agricultural habitats

We censused at these habitats 649 NFM of 17 species. Five species numerically dominated (≥ 30 individuals each) the sample accounting for 60% of the records. Among such species were habitat generalists such as *D. marsupialis*, *P. opossum* and *Orthogeomys hispidus*, and forest dwellers such as *Alouatta palliata* and *Sciurus aureogaster* (Appendix). Mean number of NFM species detected per site/habitat ranged from 8.0 (mixed) to 3.5 (cacao) and the mean number of individuals censused per site/habitat ranged from 9.5 (citrus) to 36.2 (mixed)

(Table 1). These habitats had, on average, 59% of the species in common (Appendix 1).

Shaded man-made habitats (cacao, coffee and mixed plantations) accumulated 17 species of NFM. Unshaded habitats (citrus and allspice) accumulated only eight species. These two habitats only had seven species in common. Arboreal mammals such as *A. palliata*, *B. sumichrasti* and *P. flavus* were a predominant component among the NFM detected in shaded habitats (Appendix 1). We found significant differences between shaded and unshaded habitats in mean number of species detected per site/habitat (shaded $\bar{X} = 5.8$ range 3–9, unshaded $\bar{X} = 3.6$ range 3–4; $t = 2.34$, $p = 0.05$) and in the mean number of individuals censused per site/habitat (shaded $\bar{X} = 19.7$ range 2–72, unshaded $\bar{X} = 4.0$ range 3–19; $t = 4.1$, $p = 0.001$).

Mixed plantations differed from the other shaded habitats (cacao and coffee) in the mean (\pm SD) number of species detected per site (mixed $\bar{X} = 8.0 \pm 0.82$ vs cacao $\bar{X} = 5.0 \pm 0.82$; $t = 3.6$, $p = 0.03$; mixed vs coffee $\bar{X} = 4.5 \pm 1.2$; $t = 4.04$; $p = 0.02$), but did not differ in the mean number of individuals detected per site (mixed $\bar{X} = 36.2 \pm 19.2$ vs cacao $\bar{X} = 36.0 \pm 19.2$; $t = 0.02$, $p = 0.98$; mixed vs coffee $\bar{X} = 26.5 \pm 14.4$; $t = 0.69$, $p = 0.53$) (Appendix 1).

Non flying mammals in live fences

We censused 83 NFM of 11 species in these habitats. Species detected at these habitats represented 53% of the species detected at the man-made habitats only, excluding pastures. Mean number of species detected per site was 8.0 (range 6–10) and mean number of individuals censused per site was 20.2 (range 14–28) (Table 1, Appendix 1). Species such as *S. aureogaster*, *D. marsupialis*, *P. mexicanus*, *P. opossum*, *D. virginiana* and *C. mexicanus* accounted for 85% of the records in these habitats (Appendix 1).

Vegetation types used by non flying mammal species

We recorded 49% of the species in our sample in both forests and in non forest habitats and 51% in forest habitats only (Appendix 1). Only three species (*D. marsupialis*, *P. opossum* and *D. virginiana*) were present in both forest habitats and in the seven man-made vegetation habitats studied, 14% were present in 6–7 man-made habitats in addition to the forests and 30% were present in forests and in 2–5 agricultural habitats (Appendix 1).

We found no correlation between the number of vegetation types in which a species occurred and the species' mean body mass ($r_s = -0.19$, $p = 0.11$), but an association existed between the number of habitats in which a species was present at and the rank order of individuals censused per species ($r_s = 0.83$, $p < 0.01$). This later variable was

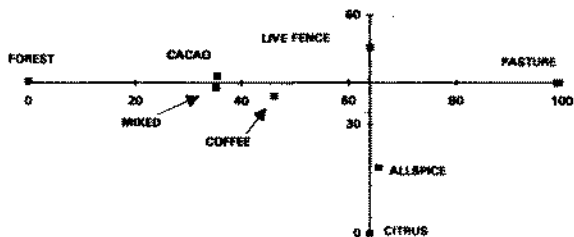


Fig. 6. Polar ordination of PD index for the habitats studied. Note the similarity to forest habitats in species assemblages of shaded man-made habitats (cacao, coffee, mixed) and live fences and the dissimilarity of pastures and unshaded man-made habitats.

negatively correlated with the species mean body mass ($r_s = -0.33$, $p = 0.02$), but partial correlation analysis showed that when the influence of body mass and abundance rank were partialled out, only the latter variable was significantly correlated with the number of vegetation types in which species were present ($r_{xy} = 0.66$, $p = 0.001$).

Undisturbed forests and agricultural habitats

Rarefaction curves showed that pastures were the poorest habitat in species. This analysis also showed that the most diverse habitats were the forests followed by cacao, coffee and mixed plantations and the live fences. Of all the arboreal agricultural habitats examined, citrus and allspice were the least diverse (Fig. 5). Polar ordination showed that the mixed, cacao and coffee plantations and live fences were the habitats most similar to forest fragments in species assemblages. The least similar were citrus and allspice. Pastures were the most dissimilar with respect to the other habitats studied (Fig. 6).

An examination of the vegetation data showed that horizontal diversity of the vegetation (mean number of tree species detected per site/habitat (MTSSH)) and foliage vertical diversity (FH') were related ($r_s = 0.97$, $p = 0.001$). Forests and shaded crops were the most complex habitats. Partial correlation analysis showed that when the influence of MTSSH and FH' were partialled out, the mean number of NFM species detected per site in each habitat and the mean number of individuals NFM per site in each habitat were associated only to the horizontal diversity of the vegetation (MNSSH $r = 0.66$, $p = 0.03$; MNMSH $r = 0.68$, $p = 0.03$).

Non flying mammal biomass

We found a negative association between total NFM biomass detected per site and area of forest fragments ($r_s = -0.43$, $p = 0.005$). Forest habitats had the highest mean biomass detected per site among the habitats investigated (forest = 89 kg; man-made habitats = 6–33 kg (Table 1)). Partial correlation analysis showed that mean biomass

per site in each habitat was best correlated with MNTSSH (FH' $r = 0.65$, $p = 0.04$; MNTSSH $r = 0.88$, $p = 0.003$). The mixed, cacao and coffee plantations contributed to 78% of the total biomass recorded at the man made habitats; live fence habitats accounted for 10% and the citrus and allspice plantations and pastures accounted for 13% (Table 1). Shaded man-made habitats (cacao, coffee, mixed) had a higher mean biomass per site than unshaded habitats (citrus, allspice and pastures) (shaded $\bar{X} = 24.6 \pm 9.1$, unshaded $\bar{X} = 9.3 \pm 4.1$; $t = 6.5$, $p = 0.02$).

Discussion

Our study showed that a rich pool of forest NFM species still exists in the fragmented landscape of Los Tuxtlas (c. 70% of the species historically reported; Coates-Estrada and Estrada 1986). The majority of the species, however, were present in very low numbers and their representatives exist in isolated forest fragments scattered in the landscape. In spite of our intensive and extensive surveys we did not detect 11 NFM species expected to appear in the forest fragments studied. These were small mammals such as *Cryptotis mexicana* and *C. parva* (Soricidae), *Liomys pictus* (Heteromyidae), *Oryzomys fulvescens*, *Nyctomys sumichrasti*, and *Reithrodontomys fulvescens* (Muridae). Some of these species are arboreal, very cryptic and nocturnal, features that would make them difficult to detect. It is possible that they were present in some of the forest habitats we studied.

Other larger species are known to be locally extinct in many parts of the region. In this case we have *Cyclopes didactylus* (Mirmecophagidae), *Felis onca* (Felidae), *Tapirus bairdii* (Tapiridae), *Tayassu pecari* (Tayassuidae) and *Odocoileus virginianus* (Cervidae). While small (< 200 ha) forest fragments studied harbored many mammal species, c. 45% of the species detected were present only in large tracts (≥ 400 ha) of rain forest vegetation. In this later case we detected large species such as *Felis concolor*, *F. pardalis*, *M. americana*, *Ateles geoffroyi* and medium size carnivores such as *Eira barbara* and *F. yagouaroundi*. The disappearance of some of these carnivores from the remaining forests, may have important consequences in the overall structure and dynamics of the mammalian community and the ecosystem (Terborgh 1992).

In our study, disturbed forest sites were significantly poorer in species and NFM biomass than undisturbed sites, probably the result of continued human activity, mainly hunting and removal of hardwoods and firewood. In contrast to disturbed forest sites, regenerating forests contained significant numbers of mammals, with older regenerating forests supporting more NFM species and biomass.

Proximity of regenerating forests to undisturbed forest fragments, the complexity of the vegetation along vertical and horizontal dimensions as well as the presence of

many fruiting tree species (e.g. *Cecropia obtusifolia*, *Ficus* spp., *Bursera simaruba*, *Spondias mombin*, *Stemmadenia donnell-smithii*) coupled with the presence of a diverse fauna of insects and small vertebrates (birds, flying mammals, small reptiles and amphibians) at these habitats (Estrada et al. 1993a, b, Estrada and Coates-Estrada pers. obs.) means the existence of protective cover, potential resting and nesting sites and food resources for NFM visiting and establishing residency in these sites. The potential connection provided by live fences could enhance colonization of these habitats by NFM.

The almost total absence of forest NFM in pastures suggests that these are unsuitable habitats for them. Even species such as *D. marsupialis*, *D. virginiana* and *P. opossum* that numerically dominated the total sample and were present in all habitats studied had higher detection rates in the forest and in the arboreal man-made habitats than in pastures. Lack of food resources, the extreme climatic conditions of pastures and the greater exposure to predators in these habitats would make them inappropriate for continued mammal habitation. We observed raptors such as *Buteo magnirostris*, *Falco sparverius*, *F. peregrinus* and *Herpethotheres cachinnans* and dogs chasing and preying on small NFM at the edge of forest fragments suggesting that predation may be greater at the edge of the forest patches.

Shaded agricultural habitats supported not only more species and individuals than unshaded habitats, but also contained a higher biomass of NFM represented by large arboreal mammals such as *A. palliata* and *P. flavus*, absent in the unshaded habitats. The presence at these habitats of tall rain forest trees of plant families such as Moraceae (*Ficus* spp., *Poulsenia armata*, *Brosimum alicastrum*), Fabaceae (*Pterocarpus rorhii*, *Lonchocarpus guatemalensis*), Sapotaceae (*Manilkara zapota*, *Pouteria campechiana*), Anacardiaceae (*Spondias radlkoferi*), Lauraceae (*Nectandra ambigens*, *Ocotea* spp.), Annonaceae (*Rollinia jimenezii*) among others permits the existence of a contiguous canopy cover for these mobile NFM. Some of these tree species are also an important source of leaves and of fruit for the monkeys and other fruit-eating mammals (Estrada 1984, Estrada and Coates-Estrada 1986).

Our data showed that isolating distance was a variable, that in conjunction with loss of area of natural habitat, influenced species richness and presence of NFM at the forest fragments studied. While there is potential danger of predation and higher time and energy expenditure due to exposure and the distances covered, NFM species capable of reaching forest and man-made habitats outside of the patch in which they reside may encounter a greater variety of habitats in which to find resources and meet survival requirements.

We observed troops of *A. palliata* visiting cacao, coffee and mixed plantations by moving through the trees of narrow strips of forest vegetation along streams and rivers. In some instances, the troops shared their presence

with other troops at these plantations. We witnessed individuals of *G. vitatta* moving on the ground through the pasture into agricultural habitats such as the cacao plantations and from here to nearby forest patches. We made similar observations on *S. aureogaster*, *P. lotor*, *N. narica*, *B. sumichrasti*, *P. flavus*, *D. marsupialis*, *D. virginiana* and *P. opossum*. Since the farmers planted the trees after clearing the forest in the case of the citrus and allspice plantations, we can assume that all the NFM detected in these habitats probably originated from nearby forest fragments or from the pasture habitat (e.g. *S. hispidus*).

The conservation value for mammals of arboreal agricultural islands as stepping stones and as temporary refuge habitats could be enhanced by the presence of live fences. In our study 27% of the species detected in the total sample and 53% of those detected in the man-made habitats were present at the live fence sites studied. The hundreds or thousands of linear meters of vegetation in the form of live fences across the landscape are available to mammals inhabiting the many forest fragments in the region. Some live fences end at the edge of forest patches or interconnect with the forest vegetation remaining along streams and rivers, probably enhancing biotic connectivity in the area. For example, our records for forest mammals such as *P. mexicanus*, *B. sumichrasti*, *P. flavus* and *C. mexicanus* are from those live fence sites that ended at the edge of a forest patch.

The live fence trees (e.g. *Bursera simaruba*) also produce edible fruit, adding to the opportunities available to NFM in a landscape where the forest is now a limited resource. In those live fences where the vegetation has been allowed to regenerate under the trees, the presence of high concentrations of plant species of the genera *Piper* (Piperaceae) *Solanum* (Solanaceae), *Cecropia*, *Siparuna* (Mominaceae), *Eugenia* (Myrtaceae), *Psycotria* (Rubiaceae) and occasional strangler figs (*Ficus* spp.) suggests the occurrence of abundant food supplies (large numbers of fruits produced per plant and year long availability). These habitats may provide temporary sustenance not only for fruit-eating NFM, but also for those that consume insects and small vertebrates but complement their diet with important amounts of fruit. Allowing the vegetation to grow under the posts and preserving old live fences may be a favorable strategy to increase the number of NFM species and individuals visiting these sites.

Our data indicated that NFM were present in habitats other than forest patches, but the use of all the habitats examined seemingly applies to only three species (*D. marsupialis*, *D. virginiana* and *P. opossum*), the rest are less resilient. This is consistent with the generalist habitat and feeding preferences of these mammals (Coates-Estrada and Estrada 1986, Julien-Leferriere and Atramentowicz 1990, Emmons 1990). These species are also characterized by having high reproductive rates, high fecundity and rapid population turnover (Atramentowicz 1986). At the other extreme were 20 species (e.g. *Da-*

syprocta mexicana, *Tamandua mexicana*, *Felis weidii*) that occurred in forest habitats only and that have low reproductive rates, low fecundity and a slow population turnover (Robinson and Redford 1986, Eisenberg 1989).

Thus, species with higher tolerance to habitat fragmentation and isolation will be those with larger intrinsic population densities, requiring small home ranges, with generalized habitat requirements and with the ability to move between forest fragments. It is not surprising then that most of the species with high numerical representation in our censuses (e.g. *D. marsupialis*) were those species that either have small home ranges, are very mobile, and that seem to have generalized feeding habits. It is important to note here that the mammals present in unshaded man-made habitats were those with very generalized habitat and feeding requirements (Appendix 1, Coates-Estrada and Estrada 1986). Forest interior mammals with more specialized habits such as *P. mexicanus*, *H. desmarestianus*, *B. sumichrasti* and *S. deppei* (Emmons 1990) were present only in the shaded habitats. Likewise, the exploitation of persistent resources in time and space (e.g. leaves, Estrada 1984) has allowed small troops of *A. palliata* to continue surviving in isolated forest fragments.

Hence, at Los Tuxtlas, we have a small number of NFM species that seem to be able to occupy a variety of man-made habitats. However, the proximity of these sites to forest fragments and whether they are shaded with rain forest trees or not seems to influence the richness and composition of the NFM fauna existing in these habitats. For some of these species a variegated model rather than a fragmentation model of land management may be more adequate as a conservation approach at the landscape level (McIntyre and Barrett 1992). At the other extreme are about half of the species detected in our censuses. These display intolerance and exist in a truly fragmented landscape. For these, the conservation of the remaining large tracts of forest is fundamental to ensure their continued existence.

In regions such as Los Tuxtlas where only c. 300 km² remain of the original 2500 km² of tropical rain forest vegetation and where these remnants occur in the form of isolated forest fragments (Estrada 1992), a landscape arrangement in which agricultural parcels occupy some of the pasture separating archipelagos of forest fragments, including forests in process of regeneration, may reduce isolating distances facilitating the flow of animals through space. Such management of the land may preserve selected species of forest mammals and may have several important added benefits including retention of soil and of soil fertility and preservation of water resources (Gleissman et al. 1981).

The predominance of *D. marsupialis*, *D. virginiana* and *P. opossum* in our surveys suggests that unless we act promptly with alternative scenarios of land management to stop rain forest destruction and to mitigate the effects of habitat destruction, fragmentation and continued isolation on the remaining NFM species, these three species

will probably be the only components of the NFM community in the landscape of Los Tuxtlas. These three species are hardly representatives of the once rich and diverse non flying mammal fauna of the northernmost representation of the Amazon rain forest in the American continent.

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Appendix 1. Non flying mammal species and individuals censused in forest and man-made habitats.

Species	Forest	Cacao	Coffee	Mixed	Citrus	All-spice	Live fence	Pasture	Total	Average mass g
MARSUPIAWA										
Didelphidae										
<i>Marmosa mexicana</i> (Mexican mouse opossum)	6								6	95
<i>Didelphis virginiana</i> (Virginia opossum)	70	4	12	8	2	1	9	3	109	3750
<i>Didelphis marsupialis</i> (common opossum)	183	8	16	48	6	13	15	16	305	2000
<i>Philander opossum</i> (common gray four-eyed opossum)	154	12	5	4	8	9	10	10	212	320
<i>Caluromys derbianus</i> (Central American woolly opossum)	10								10	400
PRIMATES										
Cebidae										
<i>Alouata palliata</i> (mantled howler monkey)	183	16	20	25					244	6750
<i>Ateles geoffroyii</i> (Central American spider monkey)	10								10	6000
EDENTATA										
Myrmecophagidae										
<i>Tamandua mexicana</i> (northern tamandua)	2								2	5000
Dasypodidae										
<i>Dasypus novemcinctus</i> (nine-banded long-nosed armadillo)	20	7	5	9	3	2	3	49	5000	
Leporidae										
<i>Sylvilagus floridanus</i> (cotton-tailed rabbit)							2	2		
<i>Sylvilagus brasiliensis</i> (Brazilian rabbit)	4							4		
RODENTIA										
Sciuridae										
<i>Sciurus aureogaster</i> (red-bellied squirrel)	116	16	10	8	8	18	184	450		
<i>Sciurus deppei</i> (Deppe's squirrel)	98			2				100	213	
Geomysidae										
<i>Orthogeomys hispidus</i> (pocket gopher)	16	10	14	7	5	5			57	
Heteromyidae										
<i>Heteromys desmarestianus</i> (spiny pocket mice)	108	12						120	73	
Muridae										
<i>Oryzomys palustris</i> (rice rats)	26							26	65	
<i>Oryzomys alfaroi</i> (rice rats)	10							10	63	
<i>Tylomys nudicaudus</i> (naked-tailed climbing rats)	4							4	215	
<i>Peromyscus leucopus</i> (white-footed deer mouse)	2							2	18	
<i>Peromyscus mexicanus</i> (Mexican deer mouse)	262	16	5	8			11	302	50	
<i>Sigmodon hispidus</i> (cotton rat)	20				4			64	88	159
Erethizontidae										
<i>Coendou mexicanus</i> (Mexican hairy porcupine)	8						6		14	3500

cont.

Appendix 1 (cont.)

Species	Forest	Cacao	Coffee	Mixed	Citrus	All-spice	Live fence	Pasture	Total	Average mass g
Dasyproctidae										
<i>Dasyprocta mexicana</i> (Mexican black agouti)	14							14	3500	
<i>Agouti paca</i> (paca)	6							6	7000	
CARNIVORA										
Procyonidae										
<i>Bassariscus sumichrasti</i> (cacomistle)	60	12	6	8			3		89	1000
<i>Procyon lotor</i> (northern raccoon)	10	2	3	6					21	5000
<i>Nasua narica</i> (white-nosed coati)	24	5	3						32	4000
<i>Potos flavus</i> (kinkajou)	24	7	6	9			2		48	3500
Mustelidae										
<i>Mustela frenata</i> (long-tailed weasel)	8	12					4		24	350
<i>Eira barbara</i> (tayra)	4								4	3750
<i>Galictis vittata</i> (grison)	8	3							11	3000
<i>Conepatus semistriatus</i> (striped hog-nosed skunk)	8	2	1	3	2	4			20	2500
<i>Lutra longicaudis</i> (southern river otter)	4								4	4500
Felidae										
<i>Felis concolor</i> (puma)	2								2	35000
<i>Felis wiedii</i> (margay)	2								2	4000
<i>Felis yagouaroundi</i> (jaguarundi)	10								10	5000
<i>Felis pardalis</i> (ocelot)	4								4	7000
ARTIODACTYLA										
Tayassuidae										
<i>Tayassu tajacu</i> (collared peccary)	12								12	2200
Cervidae										
<i>Mazama americana</i> (red brocket deer)	6								6	15000
Subtotal	1518	144	106	145	38	42	83	93	2169	
%	108	10	8	10	3	3	6	7		
No. of species	38	16	13	13	8	7	11	4	39	
%	97	41	33	33	21	18	28	10		

Appendix 2. Non flying mammal species and individuals detected in disturbed and undisturbed forest habitats and in regenerating forests (6 sites per habitat).

Species	Undisturbed forest	Disturbed forest	Old growth	Young growth
<i>Peromyscus mexicanus</i>	44	29	27	20
<i>Didelphis marsupialis</i>	30	17	16	17
<i>Philander opossum</i>	33	18	10	11
<i>Sciurus aureogaster</i>	8	6	15	10
<i>Alouatta palliata</i>	26	4		
<i>Didelphis virginiana</i>	12	8	6	3
<i>Heteromys desmarestianus</i>	18	2	5	4
<i>Bassariscus sumichrasti</i>	12	1	1	1
<i>Sciurus deppei</i>	12	1		
<i>Oryzomys palustris</i>		1	1	10
<i>Sigmodon hispidus</i>	4	1	4	1
<i>Ateles geoffroyi</i>	5			
<i>Potos flavus</i>	1	1	1	
<i>Oryzomys alfaroi</i>	2	1		
<i>Marmosa mexicana</i>	3			
<i>Silvilagus brailliensis</i>	1	1	1	
<i>Conepatus semistriatus</i>	1		1	
<i>Caluromys derbianus</i>	1	1		
<i>Silvilagus floridanius</i>				2
<i>Dasypus novemcinctus</i>	1			
<i>Nasua narica</i>		1		
<i>Procyon lotor</i>	1			
<i>Coendou mexicanus</i>	1			
<i>Dasyprocta mexicana</i>	1			
<i>Tayassu tajacu</i>	1			
<i>Felis yagouaroundi</i>	1			
<i>Mazama americana</i>	1			
<i>Agouti paca</i>	1			
<i>Tylomys nudicaudus</i>		1		
<i>Felis pardalis</i>	1			
<i>Tamandua mexicana</i>	1			
<i>Peromyscus leucopus</i>	1			
<i>Felis wiedii</i>	1			
<i>Felis concolor</i>	1			
Total individuals	226	94	88	79
Total species	30	17	12	10
Total biomass kg	388	203	56	40
Mean (\pm SD) biomass \times site kg	73.6 \pm 45.4	23.8 \pm 14.9	9.5 \pm 3.5	6.8 \pm 4.7