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Patterns of frugivore species richness and abundance in forest islands and in agricultural habitats at Los Tuxtlas, Mexico

A. Estrada [1], R. Coates–Estrada [1], D. Meritt, Jr. [2], S. Montiel [3] & D. Curiel [1]
[1] *Estación de Biología 'Los Tuxtlas', Instituto de Biología–UNAM, Apartado Postal 176, San Andrés Tuxtla, Veracruz, Mexico;* [2] *Lincoln Park Zoological Gardens, 2200 North Cannon Drive, Chicago, Ill, USA;* [3] *Universidad Veracruzana, Cordoba, Veracruz, México*

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Abstract

Destruction and fragmentation of tropical rain forest result in a loss of species and of generating capacity of the ecosystem via animal vectors such as seed dispersal agents. To gather quantitative data regarding this ecological problem, birds and mammals were censused in 30 forest fragments, 15 agricultural islands representing five types of vegetation (coffee, cacao, citrus, pepper and mixed–crops) and in three pastures in Los Tuxtlas, southern Veracruz, Mexico. More than 6000 animals of 257 species were detected thus suggesting the existence of a rich species pool in the fragmented landscape. Frugivores accounted for 60% of species, for 72% of individuals censured and for 85% of the total animal biomass recorded. Clusters of small forest fragments (< 100 ha) were richer in species and individuals than clusters of large area (> 100 ha) forest islands. Pastures were especially poor in forest birds and mammals. While the agricultural islands studied contributed to only 1% of the total area of vegetation sampled, they contained 58% of all species detected and 34% of all individual birds and mammals censured. Recaptures indicated inter–island movements of forest birds and mammals. Forty percent of the species were detected in forest habitats only, the rest were detected in forest and in agricultural habitats. Seeds of forest interior plants dispersed by birds and bats were detected in the agricultural habitats. The value of agricultural islands as landscape features providing some degree of biotic connectivity among fragmented animal populations is discussed.

Introduction

Tropical rain forest are the most diverse and complex terrestrial ecosystems on this planet. They harbor about 50–70% of all existing species of organisms and are a source of climatic stability and of many resources used today by man, ranging from food crops to pharmaceutical products (Myers 1988). In Latin America the conversion of tropical rain forest to pastures to raise cattle has meant the destruction and fragmentation of the natural habitats of a great number of tropical vertebrates whose ecology, behavior, and sensitivity to fragmentation is poorly known. This process has also meant the severe and sometimes irreversible weakening of the regenerating and self sustaining capacity of the tropical ecosystem. Further, the disappearance of these resources represent an irreversible loss to the world community and to the countries in which they occur.

As natural habitats are destroyed by man, they become fragmented and their component populations are subdivided and reduced, with local and regional extinction of species a common result (Gilbert 1988; Karr 1982a, 1982b, 1990; Lynch & Whitcomb 1978; Lovejoy *et al.* 1984). When animals are capable of migrating between fragments the effects of small population size may be partly or greatly mitigated. The demographic and genetic contributions of immigrants can provide a buffer against extinction (Brown & Kodric–Brown 1977; Burkey 1989; Laurance 1991; Lomolino 1986). Because food and other resources of ecological specialists are often patchy in space and time these species tend to be rare and more vulnerable to habitat destruction (Diamond 1984; Hubbel & Foster 1986; Karr 1982a, b; Terborgh 1976, 1986; Wilcox 1978). Specialists can be threatened also by successional changes in fragments (Picket & Thompson 1978), by the collapse of coevolved mutualisms or food webs (Gilbert 1980) or by edge effects (Janzen 1983; Lovejoy *et al.* 1986).

Frugivores depend on a type of food that is patchy in space and time and thus display high sensitivity to fragmentation and isolation of their habitat (Laurance & Yensen 1991; Leighton & Leighton 1983; Terborgh 1986). However, in a fragmented landscape frugivore species that are good dispersers and ecological generalists may continue to survive (Gilbert 1980; Laurance 1991). Interfragment dispersal may promote survival of forest species through the genetic and demographic contribution of immigrants (Brown & Kodric–Brown 1977; Laurance 1991). Such dispersal may be a critical prerequisite as a source of seeds of rain forest trees and other plants (Hopkins & Graham 1984) with arrival of viable seeds declining sharply as distance between fragments increases. Precise evaluation of the effects of fragmentation on the regenerating capacity of tropical rain forests is difficult because the ecology of the majority of the species is poorly known and reliable data on responses of entire guilds or assemblages to habitat fragmentation are rare (e.g. Klein 1989; Lovejoy *et al.* 1986; Zimmerman & Bierregaard 1986; Willis 1974).

Tropical rain forests in Mexico today consist of a collection of fragments of various sizes and with different histories of isolation. These fragments continue to be reduced in size at a rate of 4000 ha/yr. In the region of Los Tuxtlas, in southern Veracruz tropical rain forest reaches its northernmost distribution in the American continent and is notable for its high biological diversity (Estrada *et al.* 1985). Of the original 2,500 square kilometers of tropical rain forest that once covered the region of Los Tuxtlas, only about 10% remains today in a very fragmented condition (Estrada & Coates–Estrada 1988).

Land in this region is used primarily for cattle ranching. The cultivation of plants such as coffee, cacao, citrus and allspice, among others, is in the form of small parcels which occur sporadically in a 'sea' of pastures and represents only 3% of the total land use. The land–use pattern allowed us to experimentally assess the effects of rain forest destruction and fragmentation on the fate of two of the most sensitive animal components of this ecosystem: birds and mammals. In addition, it enabled us to assess the value of man–made islands of vegetation to frugivorous forest birds and mammals.

The specific aims of this paper are to report data on the bird and mammal species richness detected in forest fragments occurring amidst pastures in Los Tuxtlas southern Veracruz, Mexico. Further papers will report additional and complementary data both at the community and species level.

In addition to the forest fragments studied, birds and mammals were also censured in five types of agricultural vegetation: coffee (*Coffea arabica*), cacao (*Theobroma cacao*), allspice (*Pimienta dioica*), citrus (*Citrus sinensis*) and mixed crops (coffee, cacao, citrus, banana). Shade in the case of the coffee, cacao and mixed plantations was provided by tall (> 15 m) rain forest trees left by the farmers. Since pastures are now the dominant form of vegetation in Los Tuxtlas, we also conducted faunistic surveys in these habitats to determine the presence of forest birds and mammals.

Because of the important role played by frugivores as dispersal agents in the reproductive strategy of tropical rain forest plants and in the regenerating capacity of the ecosystem, special attention was paid to the occurrence of the frugivore components of these two animal communities.

Methods

The sector in the region of Los Tuxtlas in which field work was carried out encompasses 100–800 square kilometers within which the biological field station of 'Los Tuxtlas' of UNAM is located. Original vegetation cover in this area was tropical rain forest. The altitudinal gradient ranges from sea level to 1600 m above sea level and the landscape, dominated by pastures, contains forest fragments and a few agricultural islands which were the subject of our biological surveys (Fig. 1).

We studied forest fragments differing in size and in years of isolation. Area of each fragment was measured by digitizing aerial photographs and by corroboration in the field. Time since isolation was determined using aerial photographs taken at 5–10 year intervals during the last 30 years and by field surveys. The forest fragments we studied represented different stages of regeneration and disturbance. In the case of the five agricultural habitats (coffee, cacao, allspice, citrus and mixed crop), we sampled three replicates per habitat type to control for spatial variation in animal composition and distances to forest sites, but their selection depended on their

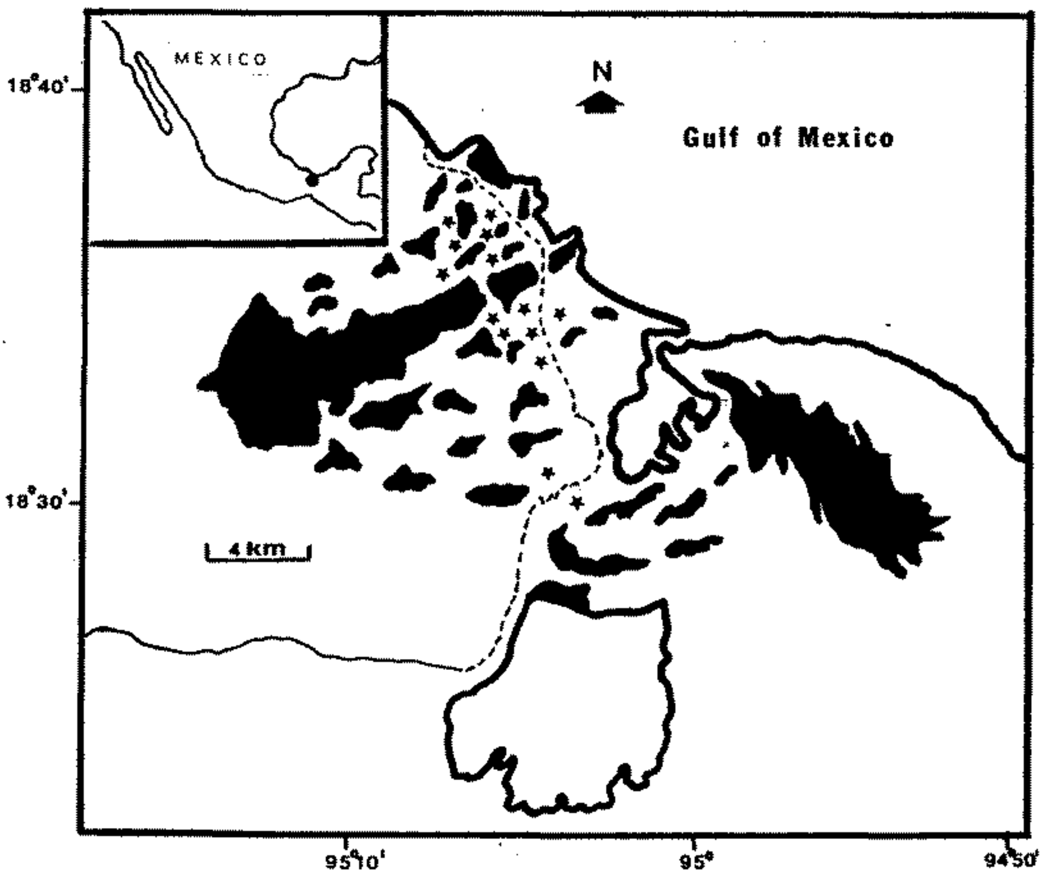

Fig. 1. Region of Los Tuxtlas in southern Veracruz, Mexico where the study was conducted. Major islands of rain forest remaining are shown in dark. Not shown are forest fragments < 100 ha in size. The approximate location of the agricultural islands studied is indicated by stars. The discontinuous line is a dirt road, Lake Catemaco is the large open area at the bottom and the paved road to Veracruz City is the continuous line bottom left.

availability because less than 3% of the land is currently used for growing these particular crops. Three areas of pasture totally devoid of the original forest vegetation were also studied; the three replicates permitted comparison with forest and agricultural islands of similar area.

Our interest in contrasting the biological richness across sites and vegetation types led to emphasize an equal or similar sampling effort in each island of vegetation. Thus, the number of nets (day and night; N = 11 in each period), net hours per day (125), net hours per night (50), number of diurnal visual and nocturnal censuses (2 in each case) as well as number of traps (46 Sherman and 15 Tomahawk), and trap nights (1), were standardized across all sites and vegetation types. The sampling quadrat or the area where netting, trapping and visual censuses were carried out in all sites (except the very small ones (1.0 ha), was 140 m in length by 80 m in width. At all sites the sampling quadrat was located at least 30–50 m from the fragment's border(s). In the case of very small sites (1.0 ha), the sampling area was adjusted in shape to have all sampling units at least 5–10 m from any border. A standard number of replicates (N = 3) per condition (e.g. island size class, vegetation type) was used in the comparisons presented below.

Sampling of birds and mammals was carried out during two days at each site. At each fragment one transect of 11 adjacent mist nets (12 m long × 3 m high) about 140 m long bisecting the site was set up. Nets were operated to capture understory birds from 0600 to 1130–1200 for two consecutive mornings and for 2–3 beginning at dusk on two consecutive nights to capture understory bats. In another parallel transect, located about 50 m away, 46 Sherman (bait = oats and vanilla) and 15 Tomahawk traps (bait = sardines) were placed on the forest floor every 5 and 10 m, respectively, and were operated for one full night (12 h). Visual censuses of birds and mammals were conducted at six sampling points at 30 m intervals along the latter transect. For each animal detected we recorded species, sex, age, height in the vegetation, time at which it was observed, and general activity.

Nocturnal censuses were carried out using flash lights and a nightvision scope (Javelin Electronics, model 221) to minimize disturbance to detected animals. Captured animals were identified to species and marked with coloured and numbered bands. Body weight, wing and/or forearm length, incubation patch and/or reproductive condition, age, molt, and the presence or absence of ectoparasites were recorded before releasing each animal. Average body weights obtained from the literature and from our own surveys were assigned to those animal records derived from visual censuses for calculations of total and partial animal biomass.

Species were classified in one of six foraging guilds: frugivore–insectivore, granivore, insectivore, insectivore–carnivore, carnivore and nectarivore–insectivore according to their foraging preferences as reported in the literature and by direct field observations by us at Los Tuxtlas over the last 15 years. For the purposes of this paper, analysis here is restricted to the frugivore (seed dispersers) and granivore (seed predators) components of these guilds which were classified as fruit–users; for some analyses these two groups were treated separately.

At each site the vegetation was censused in six random located plots measuring 10 × 10 m and separated by at least 30 m. All trees ≥ 5.0 cm in dbh and 1.5 meters in height that occurred within the plot were counted, measured (dbh, height) and identified to species. We also measured maximum canopy height and foliage density (number of foliage interceptions along a vertical pole at each of the following height classes: 1 = 0–0.50 m; 2 = 0.50–1.0 m and 3 = 1.0–3.0 m) at four random locations within each plot.

Results

Number of organisms detected

Data for this paper came from 30 forest islands, 15 agricultural islands and three pastures. The total area of vegetation accumulated by forest fragments was 7158 ha. The 15 agricultural islands encompassed 45 ha and the three pastures totaled 100 ha. A total of 8050 net hours, 184 visual censuses, 598 hours of censusing and 2806 trap nights were completed. This resulted in the censusing of 6846 animals (65% birds and 35% mammals) of 257 species, of which 189 were birds and 68 were mammals (34 species of bats and 34 species of non flying mammals (NFM from here on). Ninety percent of the species detected occurred in forest islands, 58% occurred in agricultural habitats and 4% occurred in pastures. Sixty five percent of all individuals were censused in forest fragments, 34% were detected in the agricultural habitats and 1% in the pastures (Table 1). Total animal biomass recorded in all vegetation islands was 1.607 kg of which 84% came from forest fragments and 16% from agricultural islands.

Ten of the 189 bird species detected (*Cyanocorax morio*, *Habia fuscicauda*, *Henicorhina leucosticta*, *Amazona autumnalis*, *Phaethornis superciliosus*, *Turdus grayi*, *Dendroica magnolia*, *Wilsonia citrina*, *Hylocichla mustelina* and *Oporornis formosus*) accounted for 37% of individual records and the remaining species (95%) accounted for 63% of the bird records. The community of 34 bat species detected was strongly dominated by seven species (*Carollia brevicauda*, *Sturnira lilium*, *Pteronotus parnelli*, *Vampyrops major*, *Artibeus phaeotis*, *A. toltecus*, *A. jamaicensis*) which accounted for 79% of all bat records. The remaining 27 species (79%) accounted for 22% of the remaining records. One species, *C. brevicauda*, accounted for 24% of all bats captured. Of the 34 NFM species recorded, two marsupials (*Didelphis marsupialis* and *Philander opossum*) and a rodent (*Peromyscus mexicanus*) accounted for 46% of the individuals censused. The remaining species (91%) accounted for 54% of the NFM records.

Fruit–eating birds and mammals

We detected the presence of 153 fruit–eating species representing 60% of all species detected (N = 257) and for 72% of all animal records. Within this category frugivores accounted for 110 (72%) of these species and for 83% of all fruit–eating animals censused (N = 4896); granivores represented 28% of fruit–eating species and 17% of all fruit–eating animals censused (Table 2).

In forest habitats we detected 86% of fruit–eating species and 65% of fruit–eating individuals. Fruit–eating species recorded in agricultural habitats represented 62% of all fruit–eating species detected and 35% of fruit–eating individuals censused at these sites (Table 2). Fruit–eating birds and mammals accounted for 85% of the total animal biomass recorded (1.607 kg) with frugivores accounting for 71% and granivores for 14%.

Table 1. Birds and mammals detected in 30 forest islands, 15 agricultural islands representing five types of vegetation (cacao, coffee, mixed, citrus and allspice) and 3 pastures. The number of forest islands sampled per size class and the number of sites sampled per agricultural habitat as well as the number of pastures studied are shown at the bottom of the table.

Organism	Forest		Agricultural		Total		Pasture		Total	
	Spp	N	Spp	N	Spp	N	Spp	N	Spp	N
Birds	165	2806	120	1665	189	4471	8	13	189	4484
Nonflying mammals	34	630	8	56	34	686	1	16	34	702
Bats	33	1037	22	623	34	1660	0	0	34	1660
Total	232	4473	150	2344	257	6817	9	29	257	6846

Forest size classes: 1000 ha N = 2, <800 ha N = 2, <600 ha N = 2, <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 = 3.
Agricultural habitats: cacao 9 ha N = 3, coffee 9 ha N = 3, mixed 8 ha N = 3, citrus 9 ha N = 3, allspice 10 ha N = 3.
Pastures: 100 ha N = 3.

Table 2. Occurrence of fruit-eating birds and mammals in forest and in agricultural habitats.

	Forests		Agricultural		Total	
	Spp	N	Spp	N	Spp	N
Frugivores						
Birds	59	1383	55	921	72	2304
Bats	23	846	17	554	24	1400
Nonflying mammals	14	333	5	38	14	371
Subtotal	96	2562	77	1513	110	4075
Granivores						
Birds	23	314	15	197	30	511
Bats	0	0	0	0	0	0
Non flying mammals	13	292	3	18	13	310
Subtotal	36	606	18	215	43	821
Grand total	132	3186	95	1728	153	4896

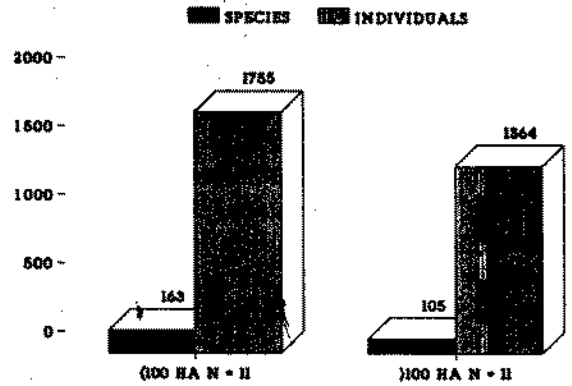

Fig. 2. Species richness and individual birds and mammals censused in forest islands < 100 ha in size and in forest islands > 100 ha in size. In this comparison, sampling effort and number of sites are equal in each condition.

Birds accounted for 67% of the species detected and for 54% of organisms censused in the fruit–eating category, mammals accounted for 33% of the species detected and for 42% of the animals censused. Bats accounted for 47% of the fruit–eating mammal species and 67% of the fruit–eating mammals censused. Birds accounted for 65% and for 70% of the frugivore and granivore species recorded and for 56% and 62% of the frugivore and granivore individuals censused. Bats were the second most numerous component among frugivores accounting for 22% of the species and for 34% of the individual records (Table 2).

Proximate effects of forest destruction and fragmentation

Replacement of forest by pasture. Our surveys in three pastures totalling an area of 100 ha resulted in no detections of forest interior birds and mammals and in the census of only nine open habitat species. These species were one rodent (*Sigmodon hispidum*) and eight bird species, four raptors (*Buteo magnirostris, Falco peregrinus, F. rufigularis, F. sparverius*), three opportunistic seed–eaters (*Dives dives, Sturnella magna, Quiscalus mexicanus*) and a specialized seed–eater (*Sporophila turqueola*). A comparison with a similar area of forest habitats (100 ha) represented by three forest islands, showed that forest habitats were significantly richer in forest interior birds and mammals and contained significantly higher numbers of frugivorous animals than pastures. Even a 1.0 ha forest patch was significantly richer in forest birds and mammals than the pasture habitat (Fig. 4).

Fragmentation of forest. A comparison among forest sites, varying in size, but with sampling effort kept constant, showed that, in general, larger forest fragments tend to have more bird and mammal species ($r = 0.857$, $P < 0.05$) and more frugivore species ($r = 0.746$, $P < 0.05$) than smaller forest fragments. However, broken down by type of organism (birds, bats, NFM), the trend held true only for NFM (number of species $r = 0.74$ $P < 0.05$; number of individuals $r = 0.763$ $P < 0.05$; $N = 11$ size classes).

An examination of the number of new species added when forest islands were ordered from small to large showed that an area of only about 60 ha contributed by several small forest fragments was necessary to account for 70% of the species recorded; addition of new species was very slow as additional area was added. A cluster of new species was added to the species' pool between 300–1000 ha (Fig. 3). This cluster con-

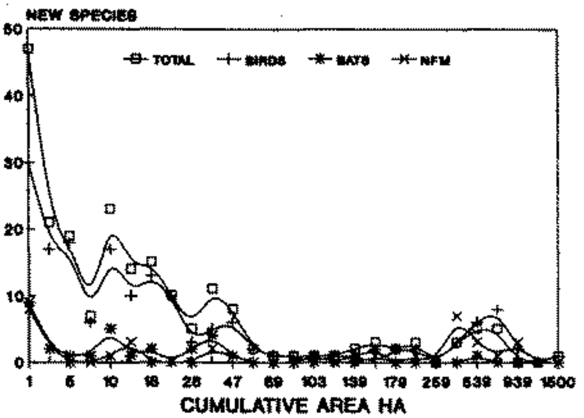

Fig. 3. Cumulative area of forest fragments and addition of new species. Note the rapid accumulation of species between 1–60 ha and the cluster of new species added with larger accumulated areas (>200 ha) of rain forest. Shown also are the patterns detected for birds, bats and nonflying mammals (NFM).

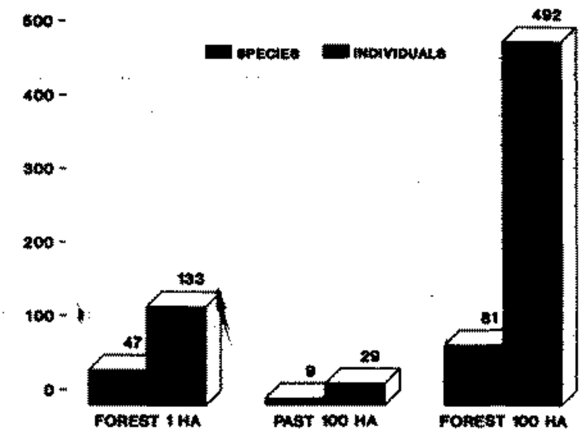

Fig. 4. Comparison of species richness (forest birds and mammals) between pastures and forest islands of equal area with sampling effort kept constant. Also shown is the species richness detected at a forest iland 1.0 ha in size. None of the species detected in pastures were forest interior birds and mammals.

sisted of frugivores such as *Ateles geoffroyi* and granivores such as *Tinamus major*, *Crax rubra* and *Penelope purpurascens*. Other species recorded in censuses at large sites were carnivores such as *Felis concolor*, *F. pardalis*, and *Spizaetus ornatus*.

An area effect was consistently found when we compared large (>100 ha; range 200–1000 ha N = 11) versus small (<100 ha; range 1–150 ha N = 11) forest islands in species richness. Small forest islands had significantly more species (small = 163; large = 105; $p<0.001$) and more individuals (small = 1755; large = 1364; $p<0.001$) than large forest islands (Fig. 2).

Forest birds and mammals in agricultural habitats

The five types of agricultural vegetation studied contained a total of 120 different species of birds and 30 different species of mammals (22 bats and 8 NFM species). Total animal biomass at these sites was 282 kg (range 28.0 kg (allspice) to 107 kg (mixed)) with frugivore biomass accounting for 73% of the total (Table 3). While agricultural sites contributed only 1% of the total area of vegetation sampled, they accounted for 58% of all species and 62% of all fruit–eating species (N = 153)

Table 3. Number of birds and mammals detected at each of the agricultural habitats studied (3 replicates per habitat).

	Birds		Bats		Nonflying animal		
					Mammals		Biomass
	N	Spp	N	Spp	N	Spp	kg
Cacao	463	75	277	15	17	7	60
Coffee	186	64	53	12	9	5	37
Mixed	330	63	89	15	25	5	107
Citrus	458	53	78	16	4	2	50
Allspice	228	39	126	14	1	1	28
Total	1665	120	623	22	56	8	282

censused. Fruit–eating species accounted for 79% (77% frugivores, 18% granivores) of all species and for 73% of all birds and mammals detected at these habitats (N = 2344).

The number of bird species detected at each type of agricultural vegetation (N = 5; 3 replicates per type) ranged from 39 (allspice) to 75 (cacao). Mammal species recorded varied from 2 (allspice) to 30 (mixed) (mean ± sd = 15.2 ± 4.0). Mean (± sd) number of bat species detected was 14.6 (± 1.7; range 12–16) and mean number of NFM species was 4.0 (± 1.1; range 1–7) (Table 3).

More bird species (63–75 spp) were detected at shaded (cacao, coffee, mixed) than at unshaded (citrus and allspice) habitats (39–53 spp). NFM species were significantly more numerous at shaded than at unshaded habitats (mean ± sd = 5.6 ± 1.1 vs 1.5 ± 0.71 spp; $P < 0.05$). In the case of bats, no difference existed in the mean (± sd) number of species detected at shaded ($\bar{X}$ = 14.0 ± 1.7) and unshaded (15.5 ± 0.71) agricultural habitats (Table 3).

Comparison between agricultural and forest islands in frugivore species richness

A comparison of agricultural islands and forest islands of similar total area (35 vs 36 ha) and equal sampling effort (10 sites in each case; 2 replicates per type of agricultural vegetation type), showed that forest and agricultural islands contained similar numbers of fruit–eating species (85 vs 95) and frugivore species (77 vs 77), but significantly more granivore species (8 vs 18, $P < 0.05$) were present in the man–made habitats. Frugivore biomass accounted for 80-88% of the total biomass accounted for at the 10 sites in each case, but forest sites had a significantly higher frugivore biomass than the man–made islands (Fig. 5).

Fruit-eating North American American migrant (NAM) birds

NAM birds accounted for 24% of all bird species (N = 4471) in both forest and agricultural islands. Seven NAM bird species (*Dendroica magnolia*, *Wilsonia citrina*, *W. pusilla*, *Hylocichla mustelina*, *Vireo griseus*, *Setophaga ruticilla*, and *Oporornis formosus*) were among the top 20 ranking species in the total sample of birds censused at all sites. No difference in number of NAM fruit–eating bird species was evident between agricultural and forest sites of equal area and sampling effort but significantly more NAM birds were censused at the agricultural habitats than at the forest sites $P < 0.001$; Fig. 6).

Number of vegetation types occupied by species

The distribution of species censused was not homogeneous across six of the vegetation types studied (tropical rain forest, cacao, coffee, mixed, citrus and pepper). Only 8% of the 257 species occurred in all six types of vegetation and 42% of all species occurred in forest islands only. Only 9% of the species occurred in agricultural habitats, and 41% of the species occurred in 2–5 types

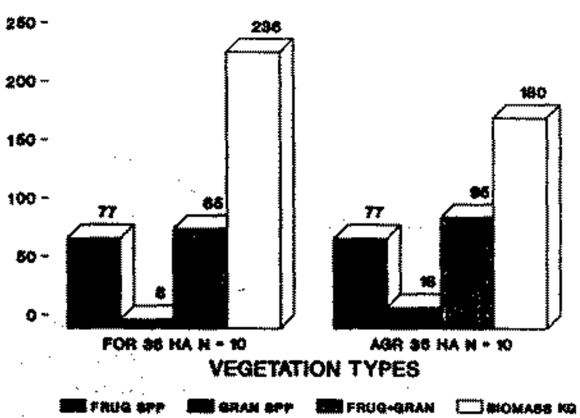

Fig. 5. Comparison of frugivore species richness and frugivore biomass in forest islands and in agricultural islands, of equal accumulated area and equal sampling effort.

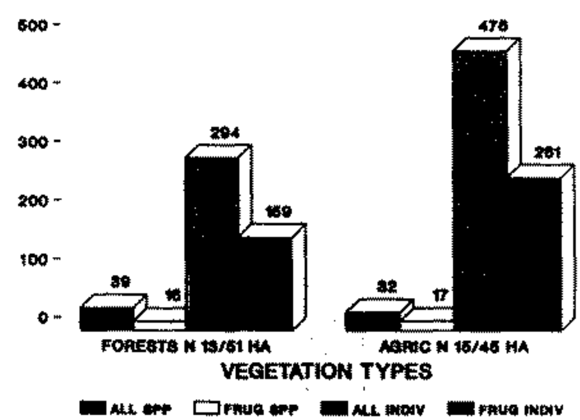

Fig. 6. Comparison of forest and agricultural habitats of similar accumulated area (sampling effort kept constant) in number of North American migrant birds censused. Also shown are the number of fruit–eating species and individuals in this subcommunity.

of vegetation which included forest and agricultural habitats (Fig. 7).

A similar proportion of bat (35%) and bird (37%) species were detected only in forest habitats, but 76% of the NFM species were detected only in this habitat. Forty seven percent of bird species were detected in agricultural habitats only and only 7% occurred in the six vegetation types studied. In the case of bats, 21% of the species were present in all six habitats, and 42% occurred in 2–5 types encompassing both forest and agricultural habitats (Fig. 7). One bat species (*Vampyrum spectrum*) was captured only in an agricultural habitat (mixed plantation). Non flying mammals showed, as indicated above, a much more restricted occurrence in the vegetation types. None of them occurred in more than four vegetation types, 24% were detected in 2–4 habitats and only one species (*Galictis vittata*; Mustelidae) was detected in one of the cacao plantations (Fig. 7).

The number of vegetation types in which a species occurred was not correlated with its mean body weight (rs birds = −0.07, rs bats = 0.04, rs NFM = −0.01, ns). The rank order of individuals censused per species was strongly correlated with the number of vegetation types used (rs birds = 0.78 $P<0.05$, rs bats = 0.92 $P<0.05$, rs NFM = 0.79 $P<0.05$).

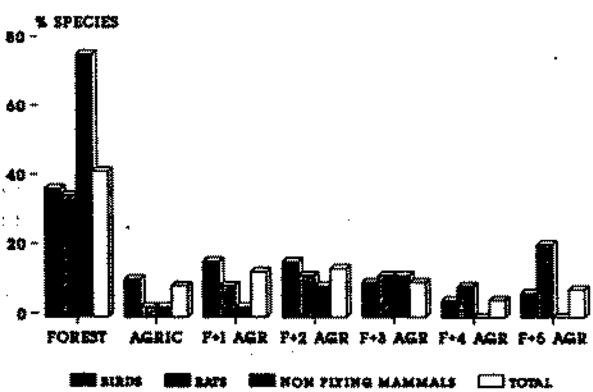

Fig. 7. Proportion of bird and mammal species detected in forest habitats only, in agricultural habitats only and in forest and agricultural habitats. F + 1 Agr indicates species occurring in forest and in one agricultural habitat. Rest of codes follow the same explanation.

Recaptures from other sites

We recorded 61 recaptures of animals banded at other vegetation islands. Of these, 44 were recaptures of birds and 17 of bats. Distances from the original banding site ranged from 0.5 to 2.0 km in the case of birds, and from 0.5 to 8.0 km in the case of bats. Such recaptures provide tangible evidence for the inter–island movement of forest interior birds with strong frugivorous habits such as *Pipra mentalis*, *Icterus virens*, *Turdus gravi*, *Momotus momota* and of forest interior bats such as *Carollia brevicauda*, *Artibeus jamaicensis*, *A. phaeotis*, *Vampyrops major*, *Glossophaga soricina*, *Vampyrops helleri*, *Sturnira lilium* and *Choeroniscus godmani*, among others. In fifteen cases, birds (N = 6) and bats (N = 9) which were originally banded at forest sites were recaptured at agricultural sites.

Discussion

Although much further analysis of our data is called for, especially with respect to the relative influence of time since isolation and of isolation distance on species richness and their interaction with area effects, some general and preliminary conclusions are possible. It is obvious that at Los Tuxtlas man's management of the tropical land is having a very important impact on the survival of forest interior birds and mammals.

Our study showed that (a) disappearance of the forest totally eliminates the forest's faunistic components and that pastures, the now dominant form of vegetation, are unsuitable habitats for forest interior birds and bats, (b) a great number of species still occur in the forest fragments surveyed, but the majority of the species detected occurred in very low numbers, (c) the component most affected by forest fragmentation in the animal communities was the non flying mammals, and (d) the agricultural habitats studied were intensively used by forest birds and mammals.

The surveys also showed that fruit–eating birds and mammals constitute an important component of the animals still existing in the area. The different types of agricultural habitats merit further investigation in terms of the opportunities they may offer to forest birds and mammals. For example, shaded habitats (mixed plantation, cacao and coffee) were significantly richer in species of birds and mammals than unshaded habitats (citrus and allspice). This may possibly be a result of the greater vertical and horizontal structural complexity of the vegetation. Arboreal mammals such as *Alouatta palliata*, *Bassariscus sumichrasti*, and *Potos flavus* which require tall and structurally complex vegetation were only detected in shaded agricultural habitats.

Our study also showed that birds and flying mammals moved between forest patches and between forests and agricultural islands in the landscape at Los Tuxtlas, but this seemingly applies only to 60% of all species detected. The remaining species are less resilient. Bird species such as *Amazona autumnalis*, *Amazilia candida*, *Dendroica magnolia*, *Melanerpes aurifrons*, *Mniotilla varia*, *Tityra semifasciata*, and *Ramphastos sulfuratus* among others and bat species such as *C. brevicauda*, *A. phaeotis*, *A. jamaicensis*, *S. lilium* and *V. major* were among the very few species present in forest and in the five agricultural habitats studied. Bird species such as *Cotinga amabilis*, *Ciccaba virgata*, *Amblycercus holoseri*, *Catharus minimus* and *Onychorhynchus mexicanus*, and bat species such as *Centurio senex*, *Diclidurus virgo*, and *Macrotus waterhousi* among others were never seen and/or captured outside the forest.

While disappearance of the forest totally eliminates the forest's faunistic components, a species' capacity to use the resulting environmental matrix may have important consequences for their persistence in time and space. The ability of a species to disperse over the matrix from areas of native vegetation may depend on physical and biotic factors such as the distance at which other opportunities are located, the ability to move such distances and the availability of nutrients and the existence of competitive interactions (Saunders *et al.* 1991). The persistence of species in the matrix has been suggested to depend on enough suitable habitat to maintain sufficient numbers to avoid extinction (Soule 1987; Ewens *et al.* 1987; Neward 1991; Blake 1991). Our study showed that a species' ability to use new opportunities offered by the matrix may allow such persistence to occur.

Our study showed that about 60% of all species detected were making use of the man–made islands which were located at distances from a few hundred to several thousand meters from forest fragments. Such islands of man–made vegetation provide these species with stop–over points when moving from forest fragment to forest fragment, with energy resources which animals were observed to harvest, and with shelter from variations in climatic conditions and from predators existing in open areas. Such benefits may have the net result of reducing time and energy expenditure and exposure in addition to providing some degree of connectivity among the species' fragmented populations.

Removal of the native vegetation and the isolation of remnants, which become the only area of suitable habitat remaining for biota displaced by clearing, may lead to concentration of mobile elements of the biota in the remnants (Lovejoy *et al.* 1986). This crowding effect may be rapid and result in saturation of the remnant by some species. Crowding can alter intra and interspecific interactions, and competition and predation can increase resulting in changes in fecundity and the potential collapse of the population (Karr 1990). Resource availability may also be affected by overexploitation (Walker 1981). As a result of their value as stepping stones to birds and mammals, agricultural islands of the sort reported here may ease some of the above pressures. Species which use them, as well as some of those remaining in the forest remnants, may be buffered from the more drastic short and medium term effects of forest fragmentation and isolation.

Large forest remnants usually contain greater habitat diversity than smaller ones, but a collection of smaller forest patches may, however, contain a greater array of habitats than a single large one, simply because a single large reserve will not contain all of the habitats likely to occur in an area (Sanders *et al.* 1991). Al Los Tuxtlas, collections of small forest fragments may provide those bird and mammal species capable of reaching them with a greater variety of habitats in which to find resources and meet survival requirements. Such diversity of opportunities will increase significantly if a species can also make use of the man–made islands of vegetation. Agricultural islands are habitats that were never present before the destruction and fragmentation of the forest. The majority of animals detected there are not, as is the case in some of the forest fragments studied, part of populations that were fragmented and isolated. These animals come from nearby forest islands to specifically make use of such new opportunities. What is salient about this scenario is that (a) 40% of the species detected apparently cannot take advantage of such opportunities by being restricted to the forest habitat and thus may be in serious danger of extinction and (b) 60% of the species detected were also censused in the man–made habitats. Of these, about 93% were forest interior species.

In Los Tuxtlas, species that have very low population numbers, limited mobility and specialized habits are at risk of extinction because they cannot take advantage of the opportunities present outside of the forest habitats they occupy. In this position are the majority of the forest's non flying mammals, species that occurred in forest sites only and species with large area requirements. Some species with these characteristics such as *Eira barbara*, *Tamandua mexicana*, *Felis onca*, *Diclidurus virgo* and fruit–eaters such as *Ateles geoffrovi*, *Dasyprocta mexicana*, *Agouti paca* and *Crax rubra* among others have become extinct in several localities in Los Tuxtlas. To preserve these species, large areas of continuous rain forest are needed (Newmark 1991).

The fact that many species of birds and mammals disperse to and obtain resources at other forest fragments and at the man–made islands of vegetation means that the rate of seed rain may be relatively high in the landscape matrix which could mean the retention, via animal vectors, of some degree of genetic connectivity in plant populations. Many bats and birds captured in agricultural habitats regurgitated, defecated or were carrying seeds of forest canopy trees and plants such as *Nectandra ambigens* (Lauraceae), *Brosimum alicastrum*, *Pseudolemdia oxyphyllaria*, *Poulsenia armata* (Moraceae), *Turpinia occidentalis* (Staphylaceae), *Quararibea funebris* (Bombacaceae), *Allophylus campostachys* (Sapindaceae), *Dendropanax arboreus* (Araliaceae), and *Trichilia martiana* (Meliaceae) as well as seeds of pioneer species such as *Spondias mombin* (Anacardiaceae), *Ficus* sp. and *Cecropia obtusifolia* (Moraceae), and *Piper* sp. (Piperaceae).

Our study of seed rain in agricultural islands has shown the presence, not only of pioneer species such as *C. obtusifolia* and *Piper* sp., but also of forest species such as *N. ambigens*, *Cordia stellifera*, *Guarea grandifola*, *Sapindus saponaria* and *Cynometra retusa* among others, under the plants of allspice, cacao, citrus and coffee (AE, unpublished data). It is not uncommon to observe seedlings of many of these species in untended agricultural plots. The shade of domestic plants provides suitable conditions of humidity and light not present in pastures for seed germination and establishment. Although humans remove these seedlings as part of a regular program of crop–care, they nevertheless constitute a collection of genes removed from forest fragments by animals dispersing to other vegetation islands in the matrix. Such collections could be harvested and planted elsewhere or could be left alone to act as foci of forest regeneration if the crop–raising programs are abandoned. The conservation of collections of forest fragments not far from one another and the use of agricultural islands as stepping stones for forest animals carrying seeds and as centers of seed deposition may be a potentially effective strategy to promote forest regeneration.

Tropical rain forest destruction and reduction of area of native habitat available to birds and mammals leads in time to total extinction and to an irreversible weakening of the regenerating capacity of the ecosystem via the disappearance of animals acting as seed dispersal vectors. However, our discovery of the value of agricultural islands to birds and mammals in the remaining forest fragments suggests that these man–made islands compensate partly for the fragmentation and isolation of the forest. This may permit, if suitable breeding habitats are preserved as well, the persistence in time and space of many frugivore species and seed dispersal agents, especially those capable of taking advantage of the opportunities represented by agricultural habitats. The net impact of such a role is a potential reversal of species' extinction trends resulting from loss of area and habitat isolation.

Agricultural islands apparently allow enhanced biotic movement, provide extra foraging areas of vegetation among other benefits to forest birds and mammals. As a result of the inter–island movement (forest island–forest and forest island–agricultural island–forest island) of seed dispersal agents, agricultural islands may serve as units of connectivity among fragmented animal and plant populations. Further investigations are needed to determine the roles different agricultural habitats may play in conjunction with forest remnants in sustaining animal populations and species. Turning more pasture area into agricultural parcels of the sort studied by us rather than turning more forest into pasture may result in (1) the persistence in time and space of forest birds and mammals, (2) the retention of some degree of regenerating capacity of the ecosystem, and (3) direct economic benefits to human populations.

Conclusions

1) At Los Tuxtlas, loss of area of native habitat leads to the extinction of some forest birds and mammals.
2) The forest islands we studied contained rich assemblages of forest birds and mammals including many species of frugivores.
3) Clusters of small forest islands had greater numbers of species and more individuals than clusters of larger forest islands.
4) A significant number of species (40%) were restricted to forest habitat, but 60% were present in other types of vegetation in addition to the forest habitat.
5) Man–made islands of vegetation are temporary habitats for many forest interior birds and mammals and many provide a degree of biotic connectivity among isolated forest islands.

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