Bat- and Bird-Generated Seed Rains at Isolated Trees in Pastures in a Tropical Rainforest

JORGE GALINDO-GONZÁLEZ,*‡ SERGIO GUEVARA,* AND VINICIO J. SOSA†

*Departamento de Ecología Vegetal, Instituto de Ecología, A.C., Apartado Postal 63, 91000, Xalapa, Ver., México
†Departamento de Ecosistemas Templados, Instituto de Ecología, A.C., Apartado Postal 63, 91000, Xalapa, Ver., Mexico

Abstract: *Bats are abundant and effective seed dispersers inside the forest, but what happens when a forest is fragmented and transformed into pasture? The landscape at Los Tuxtlas, Mexico, originally rainforest, is greatly fragmented and covered with pastures. We analyzed the seed rains produced by frugivorous bats and birds under isolated trees in pastures in the fragmented landscape and the contribution of this process to vegetational recovery. We surveyed bats and obtained fecal samples under isolated trees in pastures. We also collected seed rain below the canopy of 10 isolated* Ficus *trees, separating nocturnally dispersed seeds from diurnally dispersed seeds. We caught 652 bats of 20 species; 83% of captures were frugivores. The most abundant species were* Sturnira lilium *(48%),* Artibeus jamaicensis *(18%),* Carollia perspicillata *(12%), and* Dermanura tolteca *(11%). Fecal samples contained seeds of 19 species in several families: Piperaceae (50%), Moraceae (25%), Solanaceae (12%), Cecropiaceae (10%), and others (3%).* Sturnira lilium *was the most important disperser bat in pastures. Seed rain was dominated by zoochorous species (89%). We found seed diversity between day and night seed captures to be comparable, but we found a significant interaction of disperser type (bird or bat) with season. Seven plant species accounted for 79% of the seed rain:* Piper auritum *(23%),* Ficus *(hemiepiphytic-strangler tree) spp. (17%),* Cecropia obtusifolia *(10%),* P. amalago *(10%),* Ficus *(free-standing tree) spp. (8%),* P. yzabalanum *(6%), and* Solanum rudepanum *(5%). Bats and birds are important seed dispersers in pastures because they disperse seeds of pioneer and primary species (trees, shrubs, herbs, and epiphytes), connect forest fragments, and maintain plant diversity. Consequently, they might contribute to the recovery of woody vegetation in disturbed areas in tropical humid forests.*

Dispersión de Semillas Generada por Murciélagos y Aves Bajo Arboles Aislados en Pastizales de una Selva Alta Perennifolia

Resumen: *Los murciélagos son abundantes y efectivos dispersores de semillas en la selva húmeda alta. Pero, ¿qué sucede cuando la selva es fragmentada y convertida en pastizales? El paisaje en Los Tuxtlas, México, cuya vegetación original era la de bosque lluvioso, está fuertemente fragmentado y dominado por pastizales. Analizamos la lluvia de semillas producida por murciélagos y aves frugívoras bajo árboles aislados en pastizales del paisaje fragmentado, y la contribución de este proceso a la recuperación de la vegetación. Capturamos murciélagos y obtuvimos muestras fecales bajo árboles aislados en pastizales. Colectamos la lluvia de semillas bajo 10* Ficus *aislados, separando las semillas "nocturnas" de las "diurnas." Capturamos 652 murciélagos de 20 especies, el 83% de ellos fueron frugívoros. Las especies dominantes fueron:* Sturnira lilium *(48%),* Artibeus jamaicensis *(18%),* Carollia perspicillata *(12%), y* Dermanura tolteca *(11%). Las muestras fecales contenían semillas de 19 especies de varias familias: Piperaceae (50%), Moraceae (25%), Solanacea (12%), Cecropiaceae (10%), y otras (3%).* Sturnira lilium *resultó ser el murciélago dispersor más importante del pastizal. En la lluvia de semillas el 89% de las especies fueron zoócoras. No se encontró diferencia en la diversidad de semillas depositadas en la noche o en el día; sin embargo, hubo una interacción significativa del tipo de dispersor (ave o murciélago) con la época del año. Siete especies dominaron el 79% del total de la lluvia:* Piper auritum *(23%),* Ficus *(hemiepífito-matapalo; 17%),* Cecropia obtusifolia *(10%),* P. amalago *(10%),* Ficus *(terrestre; 8%),* P. yzabalanum *(6%) y* Solanum rudepanum *(5%). Los murciélagos y las aves son impor-*

‡*email galindoj@ecologia.edu.mx*
Paper submitted September 24, 1998; revised manuscript accepted May 31, 2000.

tantes dispersores en pastizales ya que dispersan semillas de especies pioneras y primarias (árboles, arbustos, hierbas y epífitas); conectan remanentes de selva y mantienen la diversidad vegetal. Consecuentemente pueden promover la recuperación de la vegetación leñosa en áreas perturbadas de regiones tropicales húmedas.

Introduction

Habitat fragmentation is a widespread phenomenon in both tropical and temperate regions. It affects ecological characteristics such as species richness and relative abundance and may result in the extinction of species (Turner 1996; Whitmore 1997). Understanding the effects of fragmentation on ecological processes is a major challenge for ecologists and conservation biologists (Forman & Godron 1986; Crome 1997; Laurance & Bierregaard 1997; Guevara et al. 1998). In tropical regions, the rapid conversion of rainforest into grazing pastures and croplands, is one of the most important practices that transforms continuous forest into a fragmented landscape. Such converted forest regions are typically a vegetational mosaic of cattle pastures and agricultural fields surrounding forest remnants. This is the situation in Los Tuxtlas, Veracruz, Mexico, where the remaining forest cover is <20% of the original (Dirzo & García 1992).

Abandoned pastures make up a large portion of the fragmented Neotropical landscape; there is little information on forest recovery in these areas (Brown & Lugo 1990; Aide & Cavelier 1994; Guevara et al. 1998). Regeneration of tropical rainforest in abandoned pastures depends on, among other factors, the distance of the pastures from seed sources and the mechanisms of seed dispersal.

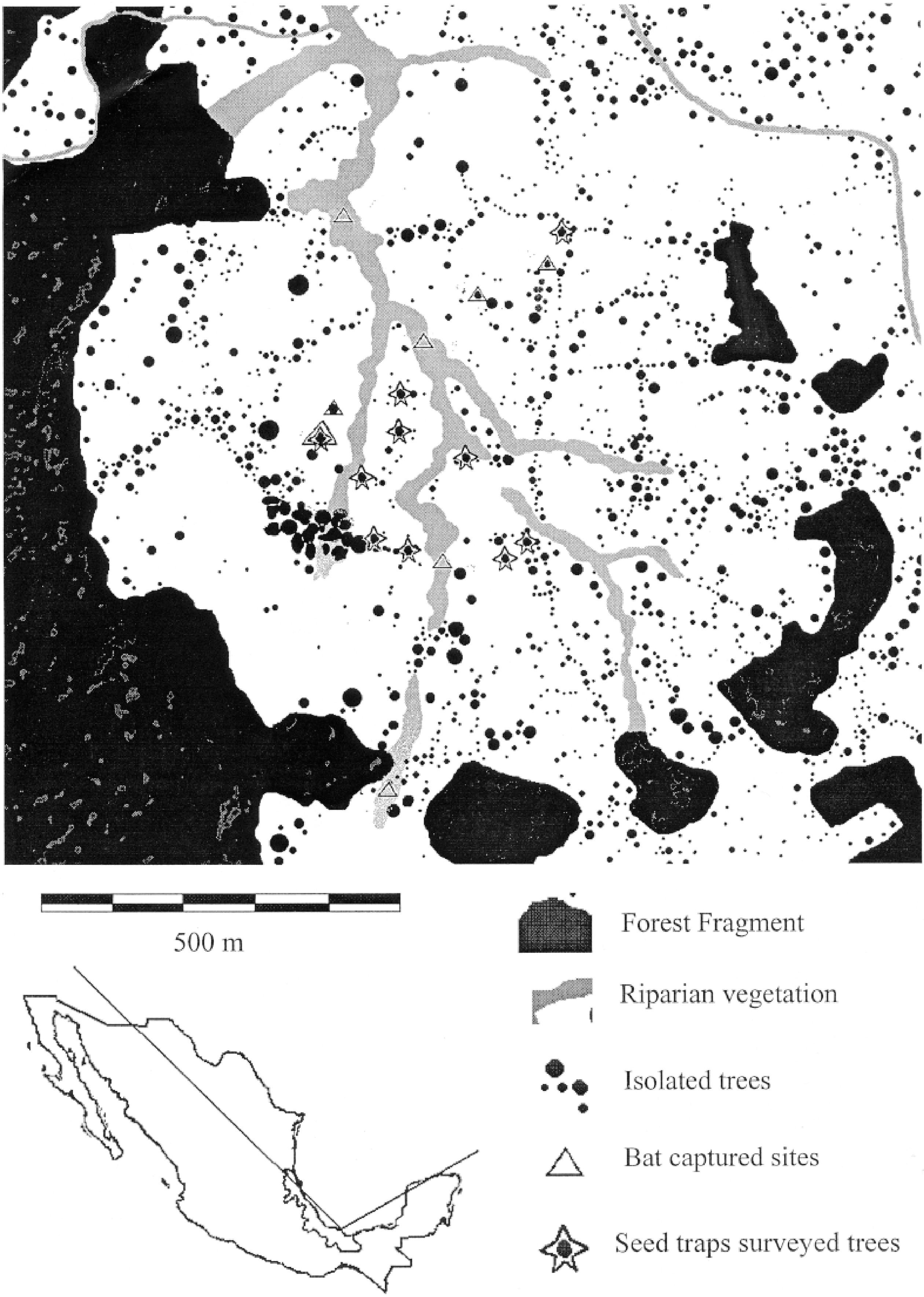
In Neotropical rainforests, more than 80% of tree and shrub species depend on frugivorous vertebrates for seed dispersal (Howe & Smallwood 1982). Frugivorous bats and birds are ideal vectors for long-distance seed dispersal, but little is known about their ability to disperse seeds where the landscape has been transformed into pastures. Aide and Cavelier (1994) found a strong decrease in seed-rain and seed-bank densities with distance from the forest edge toward pastures. We are aware of only three papers analyzing both bats and birds as agents of seed dispersal in tropical forests (Thomas et al. 1988; Gorchov et al. 1995; Medellín & Gaona 1999); in general, birds have been better studied as seed dispersers (Stiles 1980; van Dorp 1985; Murray 1988; Robinson & Handel 1993; da Silva et al. 1996) than bats (Fleming & Heithaus 1981; Fleming & Williams 1990).

Based on the analysis of bat foraging behavior and feeding habits and on seed-rain studies in pastures, Galindo-González (1998) concluded that frugivorous bats are important in the regeneration of tropical rainforest in abandoned Mexican pastures. Another study demonstrated that bats are present at grazing pastures and use habitats such as isolated trees and riparian corridors in pastures (J.G.-G & V.J.S, unpublished data). By monitoring seed rain under isolated trees in tropical pastures, Guevara and Laborde (1993) found that birds or bats dispersed more than 80% of the seeds. Even though numerous studies have examined the importance of bats as seed dispersers in tropical regions (review by Galindo-González 1998), information on their impact on forest restoration in pastures is lacking. Many researchers have investigated the feeding behavior of bats and the plant species they consume (van der Pijl 1957; Janzen et al. 1976; Janzen 1978; Fleming & Heithaus 1981; Fleming 1988; Thomas et al. 1988), but almost nothing is known about the fate of seeds they process outside the forest.

After cattle were excluded, rainforest plants grew quickly under isolated canopy trees in pastures in the Los Tuxtlas region (Guevara et al. 1992, 1998). Isolated trees in pastures function as seed-concentration sites, where seeds are deposited mainly by birds and bats (Guevara et al. 1986) and create "nuclei of regeneration" (Yarranton & Morrison 1974; McDonnell & Stiles 1983; Guevara et al. 1986, 1992; McClanahan & Wolfe 1987; Belsky et al. 1989; McClanahan 1993; Nepstad et al. 1996). Frugivorous birds are important for seed dispersal under isolated trees in pastures (Guevara & Laborde 1993), but the difference between the plant species dispersed by birds and those dispersed by bats and the different roles they play in seed dispersal and vegetation recovery are not clear. Fig trees present tow dispersal syndromes, those with green syconia are supposedly bat dispersed and those with small, red syconia are bird dispersed.

We addressed the following questions: (1) Do frugivorous bats use pasturelands while transporting seeds across the landscape? (2) Which plant species are dispersed by bats to isolated trees in pastures and which

Figure 1. Study area at the northeastern portion of the Sierra de Los Tuxtlas, Veracruz, Mexico (lat 18° 36′ N, long 95° 05′ W), 2.7 km north-northeast of the Estación de Biología Tropical Los Tuxtlas, Universidad Nacional Autónoma de México. Monitored sites, forest fragments, riparian vegetation, and isolated trees are shown.


500 m
Forest Fragment
Riparian vegetation
Isolated trees
Bat captured sites
Seed traps surveyed trees

are dispersed by birds? (3) Do frugivorous bats contribute to the seed supply in abandoned pastures as birds do and thus similarly facilitate recovery of the tropical rainforest? (4) Do frugivorous bats and birds disperse seeds under isolated fig trees in pastures according to dispersal syndromes?

Methods

Study Area

Our study was carried out in pastures in the Los Tuxtlas region, Veracruz, Mexico (lat 18°34′–18°39′N, long 95°02′–95°07′W; elevation 200 m above sea level; Fig. 1), where lowland tropical rainforest with canopy trees up to 30–35 m in height was the original vegetation. The plant community structure in the original forest was dominated by the palms *Astrocaryum mexicanum* and *Chamaedorea* spp. in the understory, *Pseudolmedia oxyphyllaria* (Moraceae) in the middle stratum, and *Nectandra ambigens* (Lauraceae), *Ficus yoponensis*, *F. tecolutensis* (Moraceae), and *Ceiba pentandra* (Bombacaceae) in the canopy (Bongers et al. 1988; Ibarra-Manríquez et al. 1997).

The current landscape of the study site is a mosaic of pastures and isolated trees, agricultural fields, forest remnants, riparian corridors, and "live fences" (small trees used as poles for barbed-wire fences that cross pastures) (Fig. 1). Sampled isolated trees were more than 50 m away from any live fence or riparian vegetation and between 280 and 381 m from the nearest forest fragment. Excluding grasses, the plant community is dominated by pioneer species from the Piperaceae, Solanaceae, and Melastomataceae families and by fruit trees with fruits attractive to frugivores in Moraceae (*Brosimum, Poullsenia, Ficus*), Lauraceae (*Nectandra*), and Cecropiaceae families. The study area was transformed into grazing pasture 30 years ago, cows graze year-round, and fire is not used as a land-management tool. Annual rainfall is approximately 4725 mm, with a relatively dry period between March and May (111.7 ± 11.7 mm/month) and a rainy period between June and February (486 ± 87.0 mm/month). Mean annual temperature is 27° C (Guevara et al. 1992).

Bat Captures

We used mist nets to capture frugivorous bats from October 1995 to September 1996. Two mist nets (each 12 × 2.5 m) were set up in an L shape at ground level under the canopy of each of four isolated trees in each pasture. One 6 × 2.5 m net was placed across streams at four riparian sites (Fig. 1). We captured bats once per month close to the new moon. Average sampling effort was 3.33 ± 0.19 nights/month (mean ± SE) during 4.2 ± 0.05 hours/site/night (mean ± SE). Sampling effort was standardized, with net hours as the unit of effort (one 12-m-long mist net set for 1 hour equals 12 net hours). Total sampling effort was 235 hours, with 1112 m of net over 40 sampling nights.

We used a field guide to identify captured bats (Medellín et al. 1997) and individually labeled each with a four-color coded plastic necklace (Dennison Secur-A-Tie). Sex, reproductive condition, time, and site of capture were recorded.

Seed Collection

Seeds were collected from bat feces or removed from seed traps. Under each mist net we placed a plastic sheet (12 × 1.2 m) in which to collect feces defecated while the bats were entangled in the net. Seeds were separated from the fecal material and placed in small cellophane bags. All captured bats were kept in separate canvas bags for 30 minutes before being released because the average time of food transit in frugivorous bats is 15–30 minutes (Fleming 1988); then the bags were searched for seeds. We dried all seeds and identified them to species level in the laboratory using a reference collection.

For 4 months (May–June, early wet season; August–September, wet season; November–December 1996, late wet season; and March–April 1997, dry season), 100 circular seed traps (50 cm in diameter) of Tergal (French polyester fabric) were left under the canopy of 10 isolated fig trees chosen randomly from within pastures (five *Ficus yoponensis* and five *F. colubrinae*). Ten traps were placed randomly under each selected tree, covering 1.96 m^2 of ground under the tree canopy. Each trap had two separate bags (day-night traps), one for diurnal and other for nocturnal seed rain. Diurnal traps were open during daylight hours, and nocturnal traps were open at night. Seeds were collected from bags once a month. We did not observe ants or rodents removing seeds from traps. We sampled 19.63 m^2 for 120 days and nights. Because we did not see any other frugivores feeding on isolated trees (except for ficus seeds of the same species as the sampled tree), we assumed that birds dispersed the seeds found in diurnal bags and that bats dispersed the seeds in nocturnal bags. No bat day roosts were found under these trees. Seeds from traps were dried, counted, and identified to species.

Isolated trees in pastures constitute the minimum remnant of the original tropical rainforest canopy (Guevara et al. 1998). Seed traps were located under the canopy of *Ficus* trees because they were the most common isolated trees in the study pastures (Guevara et al. 1992) with fruits attractive to frugivores. There are 13 *Ficus* species in the study area, but only two subgenera could be identified on the basis of their seeds: *Urostigma*, the "hemiepiphytic-strangler" tree, and *Pharmacosycea*, the "free-standing tree." Subgenera of *Ficus* were counted as two morphospecies. Fig species in Los Tuxtlas have one of two dispersal syndromes: syconia of *F. yoponensis* (*Pharmacosycea*, bat syndrome) are large (2.1 cm diameter, SE ± 0.13, $n = 20$), yellow-green when ripe, and aromatic, whereas those of *F. colubrinae* (*Urostigma*, bird syndrome) are small (0.5 cm, SE ± 0.03, $n = 20$) and dark red when ripe. Seeds found in traps belonging to the same subgenus as the sampled fig tree were not counted, so *Ficus* seeds may be underestimated.

To determine the viability of seeds that have passed through the digestive tract of bats, we randomly took 50 seeds from each of the five most abundant species (*Piper auritum*, *Ficus* [*Urostigma*] spp., *F.* [*Pharmacosycea*] spp., *Cecropia obtusifolia,* and *Solanum rudepanum*) collected in bat feces. We placed the seeds on filter paper in five petri dishes (10 seeds in each). Dishes were incubated for 2 months in a germination chamber that was illuminated 12 hours per day. Temperatures were maintained at 30° C during the day and 25° C during the night. Distilled water was added to petri dishes every 2–3 days to maintain humidity.

Data Analysis

To evaluate the importance of each frugivorous bat species as a seed-dispersal agent in pastures, we calculated a disperser importance index (DII) based on the relative abundance of captured bat species (*B*) and the percentage of fecal samples with seeds obtained from each bat species (*S*). Samples with at least one seed were counted as one event, samples with two seed species were counted as two, and so on. The DII = $(S^*B)/1000$; the index ranged from 0 to 10. Zero represents no seeds found in feces (a rare species that disperses few seeds will rank near zero), and 10 represents a unique bat species that disperses all seeds (100% relative abundance).

Species diversity for seeds dispersed by bats and birds (day-night traps) was calculated with the Shannon diversity index (*H*). We compared differences in H' between diurnal and nocturnal seed rain using a *t* test for diversity indices (Zar 1996). We used the Morisita-Horn index (C_{mH}) to compare the similarity of plant species dispersed in diurnal and nocturnal seed rain ($C_{mH} = 1.0$ means complete similarity; Magurran 1988).

The effect of disperser (bird vs. bat), dispersal syndrome (ornithocore vs. chiropterocore), and season (dry, early wet, wet, and late wet) on overall seed rain was tested by repeated-measures analysis of variance (von Ende 1993). Each tree was considered the subject because data from the 10 traps under an individual tree were combined to avoid pseudoreplication (a disperser is likely to change perches within a tree and thus contribute seeds to more than one seed trap during a single visit). Also, variation in seed catching among traps is high because of their small size. Therefore, each treatment combination was replicated five times and measured in four seasons, for a total of 79 df. All factors except subject (tree) were assumed to be fixed. Therefore, interactions involving subjects were used as error components, and no tests of their effects were carried out. Seed-rain abundance data were normalized by square-root transformation. Bonferroni pairwise comparisons of means were conducted when an effect was significant. Finally, we used the normal approximation to the binomial test to determine differences in the proportions of deposited seeds (null hypothesis, $p = 0.5$) between day and night for each of the dispersed plant species (Zar 1996).

Results

A total of 652 bats of 20 species were collected under isolated trees and in riparian vegetation in pastures. Frugivorous bats represented 83.1% of total captures (542 individuals) and represented 14 species from the family Phyllostomidae (Table 1). Among the frugivores, four species accounted for 87.5% of the captures: *Sturnira lilium* (48.5%), *Artibeus jamaicensis* (18.3%), *Carollia perspicillata* (12.0%), and *Dermanura tolteca* (10.7%).

In total, we processed 256 fecal samples with seeds obtained from captured bats. Samples contained seeds from at least 19 plant species in six families. Piperaceae were represented by eight species (49.8% of the occurrence, presence-absence); Moraceae by two subgenera of *Ficus* (25%); Solanaceae by six species (11.9%); Cecropiaceae by one species (10.4%); Melastomataceae by one species (2.4%);

Table 1. Frugivorous bat species recorded in pastures at Los Tuxtlas, Veracruz, Mexico, over 1 year.

Species[a]	n	*Relative abundance (%)*	*Fecal samples with seeds*
Phyllostomidae			
Phyllostominae			
Phyllostomus discolor	1	0.18	1
Glossophaginae			
Glossophaga soricina[b]	10	1.85	4
Choeroniscus godmani[b]	1	0.18	—
Carolliinae			
Carollia brevicauda	1	0.18	—
Carollia perspicillata	65	11.99	39
Stenodermatinae			
Sturnira lilium	263	48.52	175
Uroderma bilobatum	14	2.58	3
Platyrrhinus helleri	1	0.18	—
Vampyrodes caraccioli	20	3.69	2
Chiroderma villosum	5	0.92	1
Artibeus jamaicensis	99	18.26	18
Artibeus lituratus	2	0.37	—
Dermanura tolteca	58	10.70	13
Dermanura phaeotis	2	0.37	—
Total	542	100.00	256

[a] *Nomenclature according to Ramírez-Pulido et al. (1996).*
[b] *Nectar-frugivorous species.*

Table 2. Frequency with which seeds of plant species of different successional category and life form were present in bat feces in pastures at Los Tuxtlas, Veracruz, Mexico, from October 1995 to September 1996.*

Species	*Fecal samples with seeds*	*Successional category*	*Life form*
Piperaceae	163		
Peperomia spp.	5	late	epiphyte
Piper auritum	75	early	tree/shrub
P. amalago	33	early/late	tree
P. yzabalanum	19	early	shrub
P. hispidum	11	early	tree/shrub
P. aequale	6	early/late	shrub
P. sanctum	3	early/late	tree
Unknown spp. 1	11		
Moraceae	81		
Ficus (Urostigma)	54	late	tree
F. (Pharmacosycea)	27	late	tree
Solanaceae	39		
Solanum rudepanum	15	early	shrub
S. diphylum	11	early	small shrub
Juanulloa mexicana	6	late	epiphyte
Physalis spp.	5	early	shrub
Lycanthes heteroclita	1	early	vine
Unknown spp. 2	1		
Cecropiaceae	34		
Cecropia obtusifolia	34	early	tree
Melastomataceae	8		
Conostegia xalapensis	8	early	shrub
Unknown	1		
Unknown spp. 3	1		
Total	326		

**The number of fecal samples was* n = *256. Some fecal samples had more than one species, accounting for a total of 326 positive results. Successional categories and life form follows Guevara et al. 1997.*

and one unknown family by one species (0.3%; Tables 2 & 3). Bats dispersed between 4 and 13 different species per month. More than 22% of each fecal sample contained seeds of at least two different plant species, and some had five, for a total of 326 seed samples. Seven species accounted for 78.8% of the seeds found in fecal samples: *Piper auritum* (23%), *Ficus* (*Urostigma*) spp. (16.6%), *Cecropia obtusifolia* (10.4%), *Piper amalago* (10.1%), *Ficus* (*Pharmacosycea*) spp. (8.3%), *Piper yzabalanum* (5.8%), and *Solanum rudepanum* (4.6%).

The importance of each bat species as seed-dispersal agents in pastures is represented by the DII. (Table 3). *Sturnira lilium* was the most important disperser at pastures in Los Tuxtlas, with a DII of 3.4. This bat was the most abundant (48.5% of bat captures) and dispersed most of the seeds registered in fecal samples (69.4%).

A total of 4145 seeds was collected in seed traps from at least 68 species of plants in 23 families. The majority of species (34) identified from seed rain (88.7%; 3678 seeds) were zoochorous. Traps received an average of 1.56 seeds/m^2/24 hours. Seeds of 32 morphospecies (11.3%; 467 seeds) could not be identified. The most abundant species were *Cecropia obtusifolia*, *Conostegia xalapensis*, *Ficus* (*Urostigma*) spp., *Piper auritum*, *Solanum diphyllum*, *Cordia spinescens*, and *F.* (*Pharmacosycea*) spp., which accounted for 85.2% of zoochorous seed rain. During the day 1979 zoochorous seeds were collected, whereas 1699 seeds were collected during the night (Table 4).

In spite of the fact that the seeds of some species were almost exclusively encountered either during the day or at night, no differences were found in diversity indices (Shannon H') between the overall seed rain of day and night (t test for diversity indices, $t = 1.52$; df $= 3580$; $p > 0.05$). Seed rain between day and night was 73% similar (pairwise comparisons of species similarity $C_{mH} = 0.730$). Nevertheless, the binomial test revealed that the proportions of seeds recovered in day versus night differed from the hypothetically expected 1:1 for the 13 most frequently encountered species (Table 5).

There was neither effect of syndrome nor type of disperser in the overall number of seeds collected under isolated fig trees. Season had an effect on seed rain, but only marginally. Only the interaction of season with type of disperser was significant (analysis of variance; Table 6). The number of seeds recovered under fig tree spe-

Table 3. Plant families dispersed by bats in pastures at Los Tuxtlas, Veracruz, Mexico, showing percent abundance of seeds in bat fecal samples (n = 256).

	Bat species[a]					
Plant families	St. l.	Ca. p.	Ar. j.	De. t.	*O. spp.*	*Total*
Piperaceae	33.6	8.3	4.6	1.8	1.5	49.8
Moraceae	16.5	4.3	0.3	2.4	1.5	25.1
Solanaceae	9.2	1.8	0.3	0.3	0.3	11.9
Cecropiaceae	8.0	1.2	0.9	0.3	0.0	10.4
Melastomataceae	2.1	0.3	0.0	0.0	0.0	2.4
Unidentified	0.0	0.0	0.0	0.0	0.3	0.3
Total (%)	69.4	15.9	6.1	4.9	3.7	100.0
Bat abundance (%)	48.5	12.0	18.3	10.7	10.5	100.0
DII[b] (0–10)	3.37	0.19	0.11	0.05	0.04	

[a]St. l., Sturnira lilium; Ca. p., Carollia perspicillata; Ar. j., Artibeus jamaicensis; De. t., Dermanura tolteca; *O. spp., other species.*
[b]*Disperser importance index of frugivorous bat species.*

Table 4. Identified zoochorous seeds (dispersed by frugivorous birds and bats) found at seed traps (day-night) placed under isolated fig trees at Los Tuxtlas, Veracruz, Mexico, between May 1996 and April 1997.*

Family and plant species	*Day seeds*	*Night seeds*	*Successional category*	*Life form*
Actinidaceae				
Saurauia yasicae	11	36	late	tree
Annonaceae				
Cymbopetalum baillonii	9	2	late	tree
Araceae				
Anthurium scandens	1	0	late	epiphyte herb
Monstera acuminata	1	1	late	epiphyte herb
Araliaceae				
Dendropanax arboreus	11	10	late	tree
Oreopanax obtusifolius	44	17	late	epiphyte tree
Boraginaceae				
Cordia spinescens	94	6	ruderal	herb
Bromeliaceae				
Aechmea bracteata	13	12	late	epiphyte
Burseraceae				
Bursera simaruba	11	2	pioneer	tree
Cactaceae				
Rhipsalis bartlettii	0	64	late	epiphyte
Cecropiaceae				
Cecropia obtusifolia	425	605	pioneer	tree
Cyperaceae				
Scleria pterota	4	2	ruderal	herb
Euphorbiaceae				
Tetrorchidium rotundatum	48	20	pioneer	tree
Fabaceae				
Senna papillosa	1	0	late	tree
Poaceae				
Brachiaria sp.	0	2	ruderal	herb
Lasiasis sp.	1	0	ruderal	herb
Melastomataceae				
Conostegia xalapensis	583	248	pioneer	shrub
Monimiaceae				
Siparuna andina	1	3	pioneer	shrub
Moraceae				
Ficus (*Urostigma*)	433	131	late	epiphyte tree
F. (*Pharmacosycea*)	11	59	late	tree
Coussapoa purpusi	5	11	late	epiphyte tree
Myrtaceae				
Eugenia capuli	14	3	pioneer	tree
Phytolaccaceae				
Phytolacca rivinoides	58	2	ruderal	herb
Piperaceae				
Peperomia sp.	1	1	late	epiphyte
Piper auritum	51	371	pioneer	tree/shrub
P. yzabalanum	3	12	pioneer	shrub
Sapindaceae				
Cupania glabra	15	0	pioneer/late	tree
Paullinia clavigera	0	1	late	vine
Solanaceae				
Solanum rudepanum	12	32	pioneer	shrub
S. diphylum	96	24	pioneer	shrub
Lycianthes heteroclita	0	1	pioneer	vine herb
Physalis sp.	5	14	pioneer	shrub
Ulmaceae				
Trema micrantha	5	4	pioneer	tree
Vitaceae				
Cissus microcarpa	12	3	late	vine
Total	1979	1699		

**The 32 unidentified morphospecies are not in the table (379 day seeds; 88 night seeds), but included 195 seeds (4.7% of the total number of seeds) from zoochorous species and 272 seeds (6.6% of total seeds) from nonzoochorous species. Successional categories and life form follow Guevara et al. (1997).*

Table 5. Main species (from seed rain) dispersed by bats (night) and birds (day) in pastures at Los Tuxtlas, Veracruz, Mexico.

	Seeds		*Contribution*			
Plant species	n	*percentage*	*night (%)*	*day (%)*	Z*	p*
Cecropia obtusifolia	1030	27.95	58.7	41.3	5.67	<0.0001
Conostegia xalapenis	831	22.57	29.8	70.2	11.55	<0.0001
Ficus (*Urostigma*)	564	15.33	23.2	76.8	12.72	<0.0001
Piper auritum	422	11.47	87.9	12.1	15.58	<0.0001
Solanum diphylum	120	3.26	20.0	80.0	6.57	<0.0001
Cordia spinescens	100	2.72	6.0	94.0	8.80	<0.0001
Ficus (*Pharmacosycea*)	70	1.90	84.3	15.7	5.74	<0.0001
Tetrorchidium rotundatum	68	1.85	29.4	70.6	3.39	0.0003
Rhipsalis bartlettii	64	1.74	100.0	0.0	10.00	<0.0001
Oreopanax obtusifolius	61	1.66	27.9	72.1	3.46	0.0003
Phytolacca rivinoides	60	1.63	3.3	96.7	7.23	<0.0001
Saurauia yasicae	47	1.28	76.6	23.4	3.65	0.0001
Solanum rudepanum	44	1.20	72.7	27.3	3.02	0.0013
Total	3478	94.56	43.88	50.68		

**Calculated with the normal approximation to the binomial test.*

cies of contrasting zoochorous syndrome (*Ficus yoponensis* [1985 seeds, 1.68 seeds/m^2/day-night] and *F. colubrinae* [1693 seeds, 1.44 seeds/m^2/day-night]) did not differ significantly ($F_{1,4} = 0.11$, $p = 0.76$; Table 6). A higher but not statistically significant ($F_{1,4} = 0.59$, $p = 0.48$) number of zoochorous seeds was collected during the day than during the night. As expected, the seed rain varied throughout the year ($F_{3,12} = 3.24$, $p = 0.06$): lower quantity and density in winter (486 seeds, 0.83 seeds/m^2/day-night) and higher quantity and density in fall (1258 seeds, 2.14 seeds/m^2/day-night; Bonferroni pairwise comparisons $t = 2.75$, $p < 0.05$). Because of interaction ($F_{3,12} = 3.69$, $p = 0.04$), variation was not consistent through the season. Birds dispersed a higher but not significant number of seeds than bats in dry, early wet, and wet season; but in the late wet season birds dispersed a lower number of seeds (134), which was significantly different from the number of seeds they dispersed in autumn (1053, the highest throughout the year).

Table 6. Repeated-measures analysis of variance of abundance of zoochorous seed rain trapped below isolated fig trees (*n* = 5) in pastures of Los Tuxtlas, Veracruz, Mexico.

*Source**	*df*	*MS*	F	p
Between subject				
syndrome (A)	1	1.56	0.11	0.76
subject (B)	4	49.53	3.36	0.13
A*B	4	14.73		
Within subject				
disperser (C)	1	6.03	0.59	0.48
B*C	4	10.20		
A*C	1	1.57	0.24	0.65
A*B*C	4	6.55		
season (D)	3	51.54	3.24	0.06
B*D	12	15.92		
A*D	3	0.73	0 04	>0. 99
A*B*D	12	18. 62		
C*D	3	13.52	3.69	0.04
B*C*D	12	3.67		
A*C*D	3	4.19	0.82	0.51
A*B*C*D	12	5.11		
Total	79			

**Syndrome,* Ficus yoponensis *and* F. colubrinae*; disperser, bats and birds (day vs. night); season, early wet, wet, late wet, and dry. Subject (B) is isolated fig tree.*

Seeds voided from bats were successfully germinated within 2 months (mean for all species, 44.6 seeds, SE ± 0.96; 89.2% of all seeds, SE ± 1.92). Seeds began to germinate within 8 days. *Piper auritum* and *Cecropia obtusifolia* were the species with the highest germination success (96% and 92%, respectively), followed by *Ficus* (*Urostigma*) (88%), *Solanum rudepanum* (86%), and *Ficus* (*Pharmacosycea*) (84%).

Bats and birds dispersed seeds of all growth forms of the tropical rainforest (trees, shrubs, herbs, epiphytes, and vines), but the majority were trees (64.8%) and shrubs (27.0%). Most plant species (70.5%) whose seeds were moved across pastures to isolated trees were pioneer species usually found in early successional stages, but an important proportion (24.6%) of species were characteristic of late-successional stages (Table 7).

Discussion

Frugivorous bats were abundant around isolated trees and in riparian corridors in pastures at Los Tuxtlas. We inferred from our data on seed dispersal that they transported seeds across the landscape through pastures and toward isolated trees. Birds have also been found to be abundant and to disperse seeds in the study pastures (Guevara & Laborde 1993). Both bats and birds disperse plant species of both early and late-successional stages, although in a slightly higher proportion in early stages (pioneer trees and shrubs). Although there is some overlap of seeds dispersed by birds and bats, a large proportion

Table 7. Classification of plant species whose seeds were found in seed traps or bat fecal samples according to successional stage habit and growth form.

	Successional category		
Growth form	*early ruderal*	*late*	*Total*
Tree	9	8	17
Shrub	8	0	8
Herb	5	0	5
Epiphyte[a]	0	6	6
Vine	2	2	4
Total[b]	24	16	40

[a]*Trees not included.*
[b]*Seeds of 32 unidentified morphospecies were not classified.*

of species is dispersed only by birds or only by bats. Some species (32%) were usually dispersed by bats, others usually by birds (47%), and a few of them (21%) indistinctly by birds or bats.

The zoochorous syndrome of isolated fig tree species had no effect on the total amount of seeds dispersed under their canopies, indicating that they function equally well as perches for bats or birds. This should be expected because isolated trees fructify asynchronously, and each tree presents no fruit during most of the year. Therefore, factors influencing isolated trees as disperser attractors probably do not include the dispersal syndrome.

Although frugivorous bats and birds visited pastures and isolated trees all year round (for birds, Guevara & Laborde 1993; for bats, Galindo-González 1999), there was a significant decrease in dispersed seeds to isolated fig trees in the late wet season. More studies on the seasonal movements of bats and birds from pastures to nearby forest fragments are needed to understand how they affect seed rain into isolated trees within pastures. Both groups of frugivores may play an important role in plant recovery in pastures. Native plant species regenerated rapidly after the abandonment of pasture surrounding isolated trees (Guevara et al. 1992, 1998). These trees functioned as nurse plants, facilitating the establishment of zoochorous species.

Based on seed rain, overlap of seed deposition between bats and birds was high, but the dispersal syndrome seems to be important for some species found in pastures. We suggest that bats and birds in pastures are in some way complementary in the seed-dispersal services they provide (Palmeirim et al. 1989; Whittaker & Jones 1994; Gorchov et al. 1995). Because of the differences in foraging behaviour between bats and birds, however, they produce different seed shadows: (birds deposit a majority of seeds from a perched position under the canopy whereas bats defecate in flight [Charles-Dominique 1986; Thomas et al. 1988; Gorchov et al. 1993]). In pastures, birds probably deposit more seeds under canopy trees, whereas bats frequent more open areas in pastures. Thus our day-night traps may underestimate the number of seeds dispersed by bats.

Bats and birds were important seed-dispersal agents in our study. Seed rain under isolated trees was clearly dominated by zoochorous species (88.6%). These frugivores dispersed seeds of a wide variety of growth forms, with trees and shrubs predominating. Dispersed seeds were mainly pioneer species (*Cecropia*, *Piper*, *Conostegia*, and *Solanum*), with an important component of late-successional species that allow secondary forest to develop rapidly. Guevara et al. (1998) found that 3 years after cattle were removed from pastures, vegetation recovered successfully under isolated trees. Microhabitat conditions allowed seedling establishment, and a closed canopy more than 4 m high developed. Woody secondary species and fast-growing pioneers dominated this canopy. Under this developing canopy, herbs and ruderal species were absent, whereas seedlings of primary rainforest species (such as *Ficus* spp., *Oreopanax*, and *Saurauia*) established themselves successfully. Although successional processes alone may not lead to the total recovery of an original forest structure, especially where natural disperser populations have declined or disappeared locally (Corlett & Turner 1997; Thébaud & Strasberg 1997), dispersers at our pasture sites are abundant and efficient (Guevara & Laborde 1993; this study).

From the standpoint of disperser effectiveness (Schupp 1993), *Sturnira lilium* was the most important seed-dispersing flying mammal at our site. In terms of the quantity of seeds dispersed, *S. lilium* dispersed most of the seeds (based on contents of fecal samples), mixed several plant species in droppings, and was present and abundant throughout the year. In terms of the quality of dispersal, seeds from bat feces were viable. Seeds deposited under the canopy of isolated trees in pastures were in favorable condition for germination and seedling establishment (Guevara et al. 1998). According to Fleming and Sosa (1994), *S. lilium* is a legitimate, efficient, and effective seed disperser in pastures.

Comparisons between the percentage of germinated seeds taken from mature fruits and those removed from bat feces show either no difference between the two treatments or else improved germination rates for seeds passing through the gut (Fleming & Heithaus 1981; Lieberman & Lieberman 1986; Figueiredo & Perin 1995; Bizerril & Raw 1998). These comparative studies show that germination rates are high for seeds of *Cecropia peltata*, *C. obtusifolia*, and *Solanum bazenii*, but that bat ingestion has no effect on seeds of *Piper amalago*, *P. friedrichsthalli*, *Chlorophora tinctoria*, and *Muntingia calabura* (Vázquez-Yanes & Orozco-Segovia 1986; Fleming 1988; Palmeirim et al. 1989; Fleming & Williams 1990). Thus, it seems that germination of seeds dispersed by bats is improved or unaffected by treatment in the gut.

Although seeds pass rapidly through the digestive tract of bats (28.7 ± 3.8 minutes; Morrison 1980; Bonaccorso & Gush 1987; Fleming 1988), they can provide relatively long-distance dispersal (e.g., 20 m to 8 km; Galindo-González 1998). This commonly occurs as the bats change feeding areas or return to their day roosts, defecating during flight along the way. Moreover, bats drop fecal clumps with a mix of two to five seed species, thus increasing species diversity at the microsite where seeds fall. Nevertheless, this seed mixing may increase seed and seedling competition.

Isolated trees in pastures might guide the movements of dispersers, determining the spatial deposition pattern of seeds in the landscape and developing "nuclei of regeneration" (or recruitment foci) under isolated trees (Yarranton & Morrison 1974; McDonnell & Stiles 1983; Guevara et al. 1986; McClanahan & Wolfe 1987; Belsky et al. 1989; McClanahan 1993; Nepstad et al. 1996). Through seed dispersal, frugivorous bats and birds may connect forest remnants, enhance and maintain plant diversity in pastures, and facilitate the recovery of vegetational structure and composition, provided that grazers are excluded. Frugivorous bats and birds might thus play a paramount role in connecting landscape elements—forest fragments, regeneration nuclei, riparian vegetation, isolated trees, and pastures—and could be considered taxa critical to the recovery of fragmented landscapes. Both groups of frugivores are essential in the regeneration of Neotropical rainforest at clear-cut strips (Gorchov et al. 1995), abandoned cornfields and other disturbed habitats (Medellín & Gaona 1999), and pastures under isolated trees (this study). Therefore, bats and birds should be considered in the management of transformed and fragmented landscapes, in the restorations of ecosystems, and in the study of vegetation regeneration. Isolated trees and "live fences" should also be considered in the management of the fragmented landscape of the tropics because they can provide food and cover for frugivores that fly through pastures (for birds, Guevara & Laborde 1993; for bats, Galindo-González 1999).

Acknowledgments

We thank J. Laborde, O. Muñoz, O. Barrera, G. Sánchez, and F. Martínez for their help in the field. C. Escobar and L. Juan allowed us to use their pastures. Valuable comments and suggestions from V. Rico-Gray, R. A. Medellín, J. Laborde, A. G. Chiarello, E. Main, D. Bennack, and two anonymous reviewers improved the manuscript. J. M. García helped us with seed-trap work. A. Cuarón exerted great effort on the editing of this special section. This study was partially supported by a Consejo Nacional de Ciencia y Tecnología (CONACyT) doctoral grant to J. Galindo-González. European Union no. B7-8110/95/D4, CONACyT no. 4127P-N9607, Departamentos de Ecología Vegetal (902-16) and Ecosistemas Templados (902-19) from Instituto de Ecología, A. C. provided fieldwork support. J. Laborde facilitated seed collection, W. C. Hanson donated mist nets, and S. Casados provided bat necklaces. A. M. González, C. Pulido, and L. Gómez provided unconditional and valuable support.

Literature Cited

Aide, T. M., and J. Cavelier. 1994. Barriers to lowland tropical forest restoration in the Sierra Nevada de Santa Marta, Colombia. Restoration Ecology **2**:219–229.

Belsky, A. J., R. G. Amundson, J. M. Duxbury, S. J. Riha, A. R. Ali, and S. M. Mwonga. 1989. The effect of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology **26**:1005–1024.

Bizerril, M. X. A., and A. Raw. 1998. Feeding behaviour of bats and the dispersal of *Piper arboreum* seeds in Brazil. Journal of Tropical Ecology **14**:109–114.

Bonaccorso, F. J., and T. J. Gush. 1987. Feeding behaviour and foraging strategies of captive Phyllostomid fruit bats: an experimental study. Journal of Animal Ecology **56**:907–920.

Bongers, F., J. Popma, J. Meave del Castillo, and J. Carabias. 1988. Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico. Vegetatio **74**:55–80.

Brown, S., and A. E. Lugo. 1990. Tropical secondary forests. Journal of Tropical Ecology **6**:1–32.

Charles-Dominique, P. 1986. Inter-relations between frugivorous vertebrates and pioneer plants: *Cecropia*, birds and bats in French Guyana. Pages 119–135 in A. Estrada and T. H. Fleming, editors. Frugivores and seed dispersal. Dr W. Junk, Dordrecht, The Netherlands.

Corlett, R. T., and I. M. Turner. 1997. Long-term survival in tropical forest remnants in Singapore and Hong Kong. Pages 333–345 in W. F. Laurance and R. O. Bierregaard Jr., editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago.

Crome, S. H. J. 1997. Researching tropical forest fragmentation: shall we keep on doing what we're doing? Pages 485–501 in W. F. Laurance and R. O. Bierregaard Jr., editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago.

da Silva, J. M. C., C. Uhl, and G. Murray. 1996. Plant succession, landscape management, and the ecology of frugivorous birds in abandoned Amazonian pastures. Conservation Biology **10**:491–503.

Dirzo, R., and M. C. García. 1992. Rates of deforestation in Los Tuxtlas, a Neotropical area in Southeast Mexico. Conservation Biology **6**: 84–90.

Figueiredo, R. A. De, and E. Perin. 1995. Germination ecology of *Ficus luschnathiana* drupelets after bird and bat ingestion. Acta Oecologica **16**:71–75.

Fleming, T. H. 1988. The short-tailed fruit bat: a study in plant-animal interactions. University of Chicago Press, Chicago.

Fleming, T. H., and E. R. Heithaus. 1981. Frugivorous bats, seed shadows, and the structure of the tropical forest. Biotropica **13(supplement)**:45–53.

Fleming, T. H., and V. J. Sosa. 1994. Effects of nectarivorous and frugivorous mammals on the reproductive success of plants. Journal of Mammalogy **75**:845–851.

Fleming, T. H., and C. F. Williams. 1990. Phenology, seed dispersal, and recruitment in *Cecropia peltata* (Moraceae) in Costa Rican tropical dry forest. Journal of Tropical Ecology **6**:163–178.

Forman, R. T. T., and M. Godron. 1986. Landscape ecology. Wiley, New York.

Galindo-González, J. 1998. Dispersión de semillas por murciélagos: su importancia en la conservación y regeneración del bosque tropical. Acta Zoológica Mexicana (nueva serie) **73**:57–74.

Galindo-González, J. 1999. Los murciélagos frugívoros en la regneración de la vegetación del paisaje pastizal-selva de los Tuxtlas, Veracruz. Ph.D. thesis. Instituto de Ecología, A. C., Xalapa, Veracruz, México.

Gorchov, D. L., F. Cornejo, C. Ascorra, and M. Jaramillo. 1993. The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. Pages 339–349 in T. H. Fleming and A. Estrada, editors. Frugivory and seed dispersal: ecological and evolutionary aspects. Kluwer Academic, Dordrecht, The Netherlands.

Gorchov, D. L., F. Cornejo, C. Ascorra, and M. Jaramillo. 1995. Dietary overlap between frugivorous birds and bats in the Peruvian Amazon. Oikos **74:**235–250.

Guevara, S., and J. Laborde. 1993. Monitoring seed dispersal at isolated standing trees in tropical pastures: consequences for local species availability. Pages 319–338 in T. H. Fleming and A. Estrada, editors. Frugivory and seed dispersal: ecological and evolutionary aspects. Kluwer Academic, Dordrecht, The Netherlands.

Guevara, S., S. Purata, and E. van der Maarel. 1986. The role of remnant trees in tropical secondary succession. Vegetatio **66:**74–84.

Guevara, S., J. Meave, P. Moreno-Casasola, and J. Laborde. 1992. Floristic composition and structure of vegetation under isolated trees in Neotropical pastures. Journal of Vegetation Science **3:**655–664.

Guevara, S., J. Laborde, D. Liesenfeld, and O. Barrera. 1997. Potreros y ganadería. Pages 43–58 in E. González-Soriano, R. Dirzo, and R. Vogt editors. Historia natural de los Tuxtlas. Instituto de Biología, Instituto de Ecología, Universidad Nacional Autónoma de México, México, D. F.

Guevara, S., J. Laborde, and G. Sánchez. 1998. Are isolated remnant trees in pastures a fragmented canopy? Selbyana **19:**34–43.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics **13:**201–228.

Ibarra-Manríquez, G., M. Martínez-Ramos, R. Dirzo, and J. Núñes-Farfán. 1997. La vegetación. Pages 61–85 in E. González-Soriano, R. Dirzo, and R. Vogt editors. Historia natural de los Tuxtlas. Instituto de Biología, Instituto de Ecología, Universidad Nacional Autónoma de México, México, D. F.

Janzen, D. H. 1978. A bat-generated fig seed shadow in rain–forest. Biotropica **10:**121.

Janzen, D. H., G. A. Miller, J. Hackforth-Jones, C. M. Pond, K. Hooper, and D. P. Janos. 1976. Two Costa Rican bat-generated seed shadows of *Andira inermis* (Leguminosae). Ecology **57:**1068–1075.

Laurance, W. F., and R. O. Bierregaard Jr., editors. 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago.

Lieberman, M., and D. Lieberman. 1986. An experimental study of seed ingestion and germination in a plant-animal assemblage in Ghana. Journal of Tropical Ecology **2:**113–126.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey.

McClanahan, T. R. 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. Conservation Biology **7:**279–288.

McClanahan, T. R., and R. W. Wolfe. 1987. Dispersal of ornithochorous seeds from forest edges in Central Florida. Vegetatio **71:**107–112

McDonnell, M. J., and E. W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. Oecologia **56:**109–116.

Medellín, R. A., and O. Gaona. 1999. Seed dispersal by bats and birds in forest and disturbed habitats in Chiapas, Mexico. Biotropica **31:** 478–485.

Medellín, R. A., H. T. Arita, and O. Sánchez. 1997. Identificación de los murciélagos de México, clave de campo. Publicaciones especiales 2. Asociación Mexicana de Mastozoología, A. C., México D. F.

Morrison, D. W. 1980. Efficiency of food utilization by fruit bats. Oecologia **45:**270–273.

Murray, K. G. 1988. Avian seed dispersal of three neotropical gap-dependant plants. Ecological Monographs **58:**271–298.

Nepstad, D. C., C Uhl, C. A. Pereira, and J. M. Cardoso da Silva. 1996. A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. Oikos **76:**25–39.

Palmeirim, J. M., D. L. Gorchov, and S. Stoleson. 1989. Trophic structure of a Neotropical frugivore community: is there competition between birds and bats? Oecologia **79:**403–411.

Ramírez-Pulido, J., A. Castro-Campillo, J. Arroyo-Cabrales, and F. A. Cervantes. 1996. Lista taxonómica de los mamíferos terrestres de México. Occasional Papers, 158. The Museum, Texas Tech University, Lubbock, Texas.

Robinson, G. R., and S. N. Handel. 1993. Forest restoration on a closed landfill: rapid addition of new species by bird dispersal. Conservation Biology **7:**271–278.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Pages 15–29 in T. H. Fleming and A. Estrada, editors. Frugivory and seed dispersal: ecological and evolutionary aspects. Kluwer Academic, Dordrecht, The Netherlands.

Stiles, E. W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. The American Naturalist **116:**670–688.

Thébaud, C., and D. Strasberg. 1997. Plant dispersal in fragmented landscapes: a field study of woody colonization in rainforest remnants of the Mascarene Archipelago. Pages 321–332 in W. F. Laurance and R. O. Bierregaard Jr., editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago.

Thomas, D. W., D. Cloutier, M. Provencher, and C. Houle. 1988. The shape of bird- and bat-generated seed shadows around a tropical fruiting tree. Biotropica **20:**347–348.

Turner, M. I. 1996. Species loss in fragments of tropical rainforest: a review of the evidence. Journal of Applied Ecology **33**:200–209.

van der Pijl, L. 1957. The dispersal of plants by bats (Chiropterochory). Acta Botanica Neerlandica **6:**291–315.

van Dorp, D. 1985. Frugivoría y dispersión de semillas por aves. Pages 333-363 in A. Gómez-Pompa and S. del Amo, editors. Investigaciones sobre regeneración de Selvas Altas en Veracruz, México. Instituto Nacional de Investigaciones sobre Recursos Bióticos-Alhambra, México.

Vázquez-Yanes, C., and A. Orozco-Segovia. 1986. Dispersal of seeds by animals: effect on light controlled dormancy in *Cecropia obtusifolia.* Pages 71–77 in A. Estrada and T. H. Fleming, editors. Frugivores and seed dispersal. Dr W. Junk, Dordrecht, The Netherlands.

von Ende, N. C. 1993. Repeated-measures analysis: growth and other time-dependent measures. Pages 113–137 in S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman & Hall, New York.

Whitmore, T. C. 1997. Tropical forest disturbance, disappearance and species loss. Pages 3–12 in W. F. Laurance and R. O. Bierregaard Jr., editors. Tropical forest remnants: ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago.

Whittaker, R. J., and S. H. Jones. 1994. The role of frugivorous bats and birds in the rebuilding of a tropical forest ecosystem, Krakatau, Indonesia. Journal of Biogeography **21:**245–258.

Yarranton, G. A., and R. G. Morrison. 1974. Spatial dynamics of a primary succession: nucleation. Journal of Ecology **62:**417–428.

Zar, J. H. 1996. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersey.