
Frog, Bat, and Dung Beetle Diversity in the Cloud Forest and Coffee Agroecosystems of Veracruz, Mexico

EDUARDO PINEDA,* ‡ CLAUDIA MORENO,† FEDERICO ESCOBAR,* AND GONZALO HALFFTER*

*Departamento de Biodiversidad y Comportamiento Animal, Instituto de Ecología, A. C. Apartado Postal 63, Xalapa 91000, Veracruz, Mexico

†Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Apartado Postal 69-1, Pachuca 42001, Hidalgo, Mexico

Abstract: We compared the species diversity of copronecrophagous beetles (Scarabaeinae), bats, and frogs in tropical montane cloud forest (original vegetation) and shaded coffee plantations (an agroecosystem common to the region) for a landscape in central Veracruz, Mexico. We sampled in three tropical montane cloud forest fragments and in three coffee plantations with traditional polyculture shade between 1998 and 2001. The three indicator groups responded differently to the transformation of tropical montane cloud forest into shaded coffee plantations. The species richness of frogs was one-fifth less in coffee plantations than in forest fragments, and only one-third of the frog species occurred in both forest fragments and coffee plantations. The number of beetle species and their abundance was significantly greater in coffee plantations than in the forest fragments, whereas species richness and species composition of bats were virtually the same in both habitats. The majority of the abundant species remained as such in both communities, but species that were less abundant were not scarce in both habitats. We attributed differences in the species assemblages to the differing degrees of penetrability of the borders of the two habitat types (especially for the coffee plantations) and to the differences in life-history traits among species. Shaded coffee plantations form a matrix that envelops the remaining fragments of cloud forest. Together they connect the forest fragments with the other habitats of the landscape and represent a highly functional resource for the preservation of biodiversity that serves as a complement to but not a substitute for cloud forest in this notably modified landscape.

Key Words: indicator groups, Mexico, shaded coffee plantations, tropical montane cloud forest

Diversidad de Ranas, Murciélagos y Escarabajos del Estiércol en el Bosque de Niebla y Agrosistemas de Café en Veracruz, México

Resumen: Comparamos la diversidad de especies de escarabajos copronecrófagos (Scarabaeinae), murciélagos y ranas en bosque tropical montano nublado (vegetación original) y en plantaciones de café de sombra (un agrosistema común en la región) en un paisaje en el centro de Veracruz, México. Entre 1998 y 2001 muestreamos en tres fragmentos de bosque tropical montano nublado y en tres plantaciones de café con sombra de policultivo tradicional. Los tres grupos indicadores tuvieron diferente respuesta a la transformación de bosque tropical montano nublado en plantaciones de café de sombra. La riqueza de especies de ranas fue una quinta parte menor en las plantaciones de café que en los fragmentos de bosque, y solo la tercera parte de las especies de ranas ocurrieron tanto en los fragmentos de bosque como en las plantaciones de café. El número de especies de escarabajos y su abundancia fue significativamente mayor en las plantaciones de

‡Current address: 6 Suffolk Walk, University of East Anglia, Norwich NR4 7TU, United Kingdom, email pinedaed05@hotmail.com
Paper submitted November 24, 2003; revised manuscript accepted July 21, 2004.

café que en los fragmentos de bosque, mientras que la riqueza y composición de especies de murciélagos fue casi igual en ambos hábitats. La mayoría de las especies abundantes lo fueron en ambas comunidades, pero especies que fueron menos abundantes no fueron las mismas en ambos hábitats. Atribuimos las diferencias en los ensambles de especies a los diferentes grados de penetrabilidad de los bordes de los dos tipos de hábitat (especialmente en las plantaciones de café) y a las diferencias en características de la historia de vida de las especies. Las plantaciones de café de sombra forman una matriz que rodea a los fragmentos remanentes de bosque de niebla. En conjunto, conectan a los fragmentos de bosque con los demás hábitats en el paisaje y representan un recurso altamente funcional para la preservación de biodiversidad que sirve como complemento, pero no sustituto, del bosque de niebla en este paisaje notablemente modificado.

Palabras Clave: bosque tropical montano nublado, café de sombra, grupos indicadores, México

Introduction

Coffee is one of the most important agricultural exports for many Latin American countries (Perfecto et al. 1996). In Veracruz, Mexico, as in many other mountainous tropical zones, farmers grow *Coffea arabica* L. beneath shade. The shade may be provided by one species—usually an arboreal legume—or by many species (polyspecific), including tree species of the tropical montane cloud forest (TMCF). The canopy creates an understory microclimate that provides the light intensity, humidity, and temperature required by coffee plants, particularly the *criolla* and Borbón varieties grown in the region. Shade trees also protect the soil from erosion and reduce the need for fertilizers and pesticides.

Given the similarities in the environment and the vegetation structure, shaded coffee plantations (SCP) possess a species richness similar to that of native forests, especially when the canopy is made up of a wide variety of trees. Furthermore, they have greater species richness than plantations where the canopy is composed of only a few different tree species (Perfecto et al. 1996; Moguel & Toledo 1999). The majority of studies on the species richness in SCP under different management regimes have been done with arthropods (Perfecto & Snelling 1995; Perfecto et al. 1997; Ibarra-Núñez & García-Ballinas 1998; Perfecto & Vandermeer 2002; Arellano & Halffter 2003) and birds (Greenberg et al. 1997; Daily et al. 2001). Other studies have been done with mammals (Estrada et al. 1993; Gallina et al. 1996), frogs (Pineda & Halffter 2004), and plants (Soto-Pinto et al. 2001). Few studies have simultaneously compared the species diversity of different taxa in coffee plantations and native forest under the same transformation scenario (Perfecto et al. 2003). There is a debate about whether SCP can provide sufficient refuge to preserve and maintain biodiversity as native tropical forests are cleared (Rappole et al. 2003).

In Mexico many areas dedicated to growing coffee with shade are in zones originally occupied by TMCF. Although TMCF covers <1% of Mexico, it is the richest vegetation type in species per unit area and boasts a high number of endemics (Rzedowski 1998). As the expan-

sion of coffee plantations has occurred at the expense of TMCF, the latter has been notably reduced in area and fragmented (Challenger 1998). In our study region, the relatively undisturbed fragments of TMCF together represent approximately 10% of the original area covered by this type of forest (Williams-Linera et al. 2002).

We tested a strategy for understanding the effects of habitat transformation on biodiversity in various landscapes, with an eye to evaluating the importance of conserved and managed areas in species maintenance and conservation. After Halffter (1998), our strategy was based on (1) the use of several indicator groups with different biological and ecological attributes, distinct evolutionary histories, and sensitivity to ecological disturbances; (2) an evaluation of alpha (species richness) and beta (species exchange) diversity for each group; and (3) a comparison of the responses of the different indicator groups.

Coproncrophagous beetles, bats, and frogs have been cited as useful indicators of the impact of habitat modification. We based our methods on the ecological indicators concept, which allows that particular taxa are highly sensitive to environmental changes and thus indicative of habitat alteration, fragmentation, and climate change (McGeoch 1998). A useful indicator group (1) is taxonomically diverse and well known, (2) has an abundance of natural history data available, (3) is easily sampled and sorted, (4) contains species that have high ecological fidelity and functional importance within the ecosystem, and (5) exhibits a rapid response to environmental changes.

Coproncrophagous beetles (Coleoptera: Scarabaeidae: Scarabaeinae) have specialized feeding and nesting habits, particular habitat requirements, and a low dispersal capacity (Klein 1989; Halffter et al. 1992; Escobar & Chacón-Ulloa 2000). They are also known for their role in the recycling of nutrients and in seed dispersal (Mittal 1993). The various diets of bats include fruit, pollen, nectar, small vertebrates, insects, other arthropods, and mammalian blood. Their roles in the ecosystem are most notably pollination, seed dispersal, and seed predation (Fenton et al. 1992; Medellín et al. 2000; Moreno & Halffter 2000). Habitat transformation has caused the decline of many frog populations around the world (Blaustein et al.

1994), and because of their biphasic life cycle, permeable skin, variety of reproductive modes, limited vagility, and strong philopatry, they can be quite sensitive to small-scale environmental changes (Wake 1991; Lips 1998).

To examine the responses of copronecrophagous beetles, bats, and frogs to the transformation of TMCF into SCP, we analyzed the patterns of species diversity in these two habitats. Although the environmental characteristics of SCP are similar to those of the native forest, the habitat is altered. We expected that this transformation of the forest would reduce species richness in the three indicator groups and that the magnitude of the reduction would vary among the taxa as a result of specific characteristics of each group.

In this study, we (1) examined whether the transformation of TMCF into SCP reduces species richness (alpha diversity) of copronecrophagous beetles, bats, or frogs; (2) determined how many of the indicator-group species in TMCF are also present in SCP (beta diversity); (3) evaluated the abundance and evenness patterns for the three groups in both habitats; and (4) identified those guilds most affected by the transformation of TMCF to SCP.

We also evaluated the reliability and significance of the data we gathered on species diversity and its changes by indicator group. Finally, we examined how useful indicator groups are for monitoring biodiversity and its change in landscapes subject to anthropogenic activities.

Methods

Study Area

We examined three TMCF remnants and three SCP, all located in the highlands of the La Antigua River basin (1120–1590 m above sea level [asl]), west of Xalapa, Veracruz, Mexico. Mean annual temperature varies between 17 ° and 20° C, and total annual rainfall ranges from 1600 to 1900 mm, falling mostly between May and October. The terrain is rugged and the soils are mainly of volcanic origin. Most of the area was originally covered by TMCF (Williams-Linera et al. 2002), and coffee was introduced to the region at the beginning of the nineteenth century. Between the end of the nineteenth century and the middle of the twentieth century the forest underwent the most severe transformation (Challenger 1998). Currently, both TMCF remnants and SCP form part of a heterogeneous mosaic that also contains cattle pastures, sugarcane, corn fields, secondary vegetation, and human settlements (Williams-Linera et al. 2002).

A wide variety of tree species are found in the remnants of TMCF, notably oaks (*Quercus*), sweetgum (*Liquidambar*), elm (*Ulmus*), summersweet (*Clethra*), American hornbeam (*Carpinus*), jonote (*Heliocarpus*), haya (*Platanus*), and many epiphytes and lianas. The forest remnants we studied were 62 ha (TMCF-1), 72 ha (TMCF-

2) and 18 ha (TMCF-3), and had an average canopy cover of 89%, 92%, and 84%, respectively. Cattle pastures, secondary vegetation, and SCP surrounded the forest fragments. The area of TMCF remnants has been reduced by fragmentation, and species composition of the remaining patches of TMCF has been directly altered by human activity (Williams-Linera 2002). Trees, ferns, and epiphytes are selectively harvested in the area, and the greatest continual pressure is on large fauna.

The vegetation structure of the SCP is complex and similar to the SCP that Moguel and Toledo (1999) classified as traditional polyculture. Two arboreal strata comprised the canopy: an upper stratum with a height of 20–25 m, which was composed mainly of elms, jonotes, oaks, matapalos (*Ficus*), and Oreopanax, and a lower strata 5–15 m tall, which was composed of cultivated species such as chalahuite and jinicuil (*Inga*), orange, banana, avocado, and guava (*Psidium guajava* L.), among others. Epiphytes were notably abundant. The SCP we studied were 104 ha (SCP-1), 63 ha (SCP-2), and 41 ha (SCP-3), and had an average canopy cover of 52%, 68%, and 48%, respectively. Forest fragments, cattle pastures, secondary vegetation, and human settlements surrounded the three SCP.

All sample sites included at least one river or stream, and the minimum distance between sites was >2250 m. Both the forest fragments and the coffee plantations studied have existed as such for more than 20 years.

Copronecrophagous Beetle Sampling

From April to October 2001 we surveyed each forest remnant and each plantation three times. We laid 16 to 18 pitfall traps, separated by 25 m along one transect and alternately baited them with human excrement and decomposing squid. After the traps were deployed for 48 hours, we checked the contents and collected them in plastic bags. Later, we cleaned the collected specimens and counted the number of species.

Bat Sampling

We counted only Phyllostomidae and Mormoopidae because they belong to common taxonomic and biogeographic units and are easy to catch in a mist net (Moreno & Halffter 2000). We deployed seven mist nets at ground level (four 12-m-long and three 9-m-long, 38-mm nets, all 2.5 m high). We opened the 75 m of netting for 3 hours starting at nightfall. Each forest remnant or coffee plantation was sampled twice between June 1998 and May 1999, for a total of six sampling nights per habitat. This represents the minimum sampling effort required to record 90% of the total bat fauna in a homogeneous area (Moreno & Halffter 2000). Because the bat inventory for the forests did not appear to be complete after this effort, we conducted another 4 nights of sampling

between May and June of 2001. To avoid capture bias, and because of the bats' lunar phobia, we sampled on moonless nights. We checked nets every 30 minutes, identified bats captured to species level with field keys (Medellín et al. 1997), marked each with a plastic collar, and then freed them at the site of capture.

Frog Sampling

We sampled frogs between May and November of 1998 and 2000, visiting each forest fragment and coffee plantation 11 to 13 times. Using a time-constrained technique (Scott 1994), we collected frogs from all possible microhabitats at dusk, during the night, and at dawn. Capture effort was measured in person-hours (e.g., 1 visit of 1.5 hours \times 2 people = 3 person-hours). The first individual of each species captured was preserved in a 70% alcohol solution as a voucher specimen. After identification, we released the other frogs where they had been captured. We recorded incidence for each species.

Data Analysis

For each of the indicator groups, we evaluated alpha diversity (within habitat) in both habitats with species accumulation curves and species richness estimates. We obtained smoothed accumulation curves through repeated random reordering (50 repetitions) of the samples in the program EstimateS (Colwell 2000). To determine the inventory completeness for each group, we used four species estimates: two parametric (Clench's model and the linear dependence model [Soberón & Llorente-Bousquets 1993]), and two nonparametric (Chao 2 and bootstrap [Colwell & Coddington 1995; Colwell 2000]). For each group, beta diversity (between habitats) was calculated with a complementarity index (Colwell & Coddington 1995) that expressed the difference in the lists of species of two habitats as a percentage:

$$C = \frac{S_j + S_k - 2V_{jk}}{S_j + S_k - V_{jk}} \times 100,$$

where S_j and S_k are the number of species in habitats j and k , respectively, and V_{jk} is the number of species found in both habitats. The minimum value of C is zero, when the species lists are identical for the two habitats. A maximum value of 100 indicates that the lists are completely different.

To compare abundance or frequency patterns and species evenness between habitats and among the indicator groups, we used dominance-diversity graphs, also known as Whittaker curves or abundance-range graphs (Feinsinger 2001). We analyzed abundance patterns for beetles and bats and observation frequency patterns for frogs (the number of occasions on which a given species was observed at each site).

To detect whether the proportion of guilds for each taxa is habitat dependent, we grouped species into dif-

ferent categories according to their natural-history attributes. We characterized beetles (after Hanski & Cambefort 1991) by size (total length) as large (>10 mm) or small (≤ 10 mm), and by feeding habit as (1) coprophages if more than 75% of the individuals were captured in traps baited with excrement, (2) necrophages if more than 75% of the individuals were captured in traps baited with squid, or (3) generalists or copronecrophages if a species did not fall into either of the other two groups. We classified collected bat species by size (forearm length) as large (>50 mm) or small (≤ 50 mm), and by feeding habit as frugivores, insectivores, nectarivores, or hematophages. Frog species were classified according to criteria set by Duellman (1970), Crump (1974), and Campbell (1999a) by size (snout-vent length) as large (>40 mm) or small (≤ 40 mm). We also classified frog species by reproductive mode: (1) eggs and larvae develop in water, (2) eggs develop out of water and larvae develop in water, or (3) eggs and larvae develop out of water.

We used a G test for contingency tables (having done a Yates correction): 2×6 for the bats and frogs and 2×5 for the beetles (because one of beetle guilds was not represented). To specifically detect those guilds whose proportional size depended on habitat type, we subdivided the contingency tables and submitted the data to the same test (Zar 1996).

Results

Estimate of Species Richness and Beta Diversity

Seventeen species of beetles were collected: 8 from TMCF and 16 from SCP (Table 1). The species accumulation curve for TMCF reached an asymptote and that of the SCP nearly did (Fig. 1a). Richness estimates indicated that in TMCF more than 94% of the species present were captured, whereas more than 90% were captured in SCP (Table 2). The estimates predict that as many as 18 species could be recorded for the group of sites studied. The complementarity value (59%) was determined by the 9 species recorded exclusively in SCP and the lone species that was exclusive to TMCF (Table 1). Seven species occurred in both TMCF and SCP.

Eleven bat species occurred in the habitats studied. The same number of species (10) was found in each habitat type, with only one species differing between them (Table 1). The species accumulation curves did not reach an asymptote (Fig. 1b). The richness estimates indicated that the inventory levels in TMCF and in SCP were above 76% and 86%, respectively (Table 2), even though the sampling effort was greater in the forest than in SCP. The highest species richness expected for the two habitats, according to the Chao 2 estimator, was 13 species—2 more than we recorded here. Because only 1 species (*Desmodus rotundus*) was recorded exclusively in TMCF and one

Table 1. Beetle, bat, and frog species recorded in tropical montane cloud forest (TMCF) and shaded coffee plantations (SCP), and their abundance and natural history traits.^a

Code	Species	TMCF			SCP			Natural history	
		1	2	3	1	2	3	feeding	size
A	<i>Dichotomius satanas</i>	64	36	46	79	113	381	C	L
B	<i>Ontobopbagus cyanellus</i>	9	12	12	5	47	75	G	S
C	<i>Deltochilum mexicanum</i>	16	114	1		1		C	L
D	<i>Ontobopbagus rbinolphus</i>				49	39	25	G	S
F	<i>Ontobopbagus incensus</i>	2	1	1	2	16	62	C	S
G	<i>Coprophanæus telamon</i>				36	10	15	N	L
H	<i>Ontobopbagus subcancer</i>	59	1					C	S
I	<i>Ontiberus mexicanus</i>	14	11		2			C	S
J	<i>Phanaeus endymion</i>						18	G	L
K	<i>Copris incertus</i>	3		1	1	6	3	C	L
L	<i>Eurysternus magnus</i>		6	2		1	1	C	L
M	<i>Ontobopbagus boepfneri</i>						4	C	S
N	<i>Dichotomius colonicus</i>				2	1		C	L
O	<i>Eurysternus mexicanus</i>				1	1		G	L
P	<i>Ontobopbagus nasicornis</i>					2		G	S
Q	<i>Ontobopbagus mextexus</i>					1		G	S
R	<i>Scatimus ovatus</i>					1		C	S
	total	167	181	63	177	239	584		
	bats							feeding	size
A	<i>Sturnira ludovici</i>	12	64	24	22	90	9	F	S
B	<i>Artibeus jamaicensis</i>		1		2	54	3	F	L
C	<i>Carollia brevicauda</i>	2	12	1	1	7		F	S
D	<i>Artibeus lituratus</i>		1			2	7	F	L
E	<i>Glossophaga soricina</i>		1	1	1	5		Ne	S
F	<i>Artibeus intermedius</i>		1		3	1	1	F	L
G	<i>Anoura geoffroyi</i>	3				1	1	Ne	S
H	<i>Dermanura phaeotis</i>		2	2		1		F	S
I	<i>Pteronotus davyi</i>		2				1	I	S
J	<i>Mormoops megalophylla</i>				1			I	L
K	<i>Desmodus rotundus</i>	1						H	L
	total	18	84	28	30	161	22		
	frogs ^b							RM	size
A	<i>Hyla miotympanum</i>	8	9	9	2	8	4	1	S
B	<i>Rana berlandieri</i>	7	8	6	6	8	4	1	L
C	<i>Eleutherodactylus rbodopis</i>		7	8	6	4	3	3	S
D	<i>Eleutherodactylus pygmaeus</i>	4	4	6	6		5	3	S
E	<i>Eleutherodactylus cystignathoides</i>	4	5		5	3	5	3	S
F	<i>Hyalinobatrachium fleischmanni</i>				5	6	5	2	S
G	<i>Bufo valliceps</i>		2		4	3	4	1	L
H	<i>Eleutherodactylus mexicanus</i>	4		3		6		3	S
I	<i>Eleutherodactylus decoratus</i>		4	6				3	S
J	<i>Eleutherodactylus berkenbuschi</i>	4		4				3	L
K	<i>Hyla taeniopus</i>	3		4				2	L
L	<i>Bufo cristatus</i>	2		4				1	L
M	<i>Hyla picta</i>		1	2		2		2	S
N	<i>Leptodactylus fragilis</i>	1		3				2	S
O	<i>Hyla arborescens</i>			3				2	L
P	<i>Eleutherodactylus alfredi</i>				3			3	S
P	<i>Eleutherodactylus spatulatus</i>	2		1				3	S
R	<i>Gastrophryne usta</i>				1	2		1	S
S	<i>Hyla mixomaculata</i>	2						2	S
T	<i>Smilisca baudini</i>				2			1	S
U	<i>Scinax staufferi</i>					2		1	L
	total	41	40	59	40	44	30		

^aAbbreviations: 1, eggs and larvae in water; 2, eggs outside water and larvae in water; 3, eggs and larvae outside water; S, small; L, large; C, coprophage; N, necrophage; G, generalist; F, frugivore; I, insectivore; H, hematophagous; Ne, nectarivore; RM, reproductive mode.

^bThe numbers in columns 3 to 8 denote the number of times the species was observed at each site.

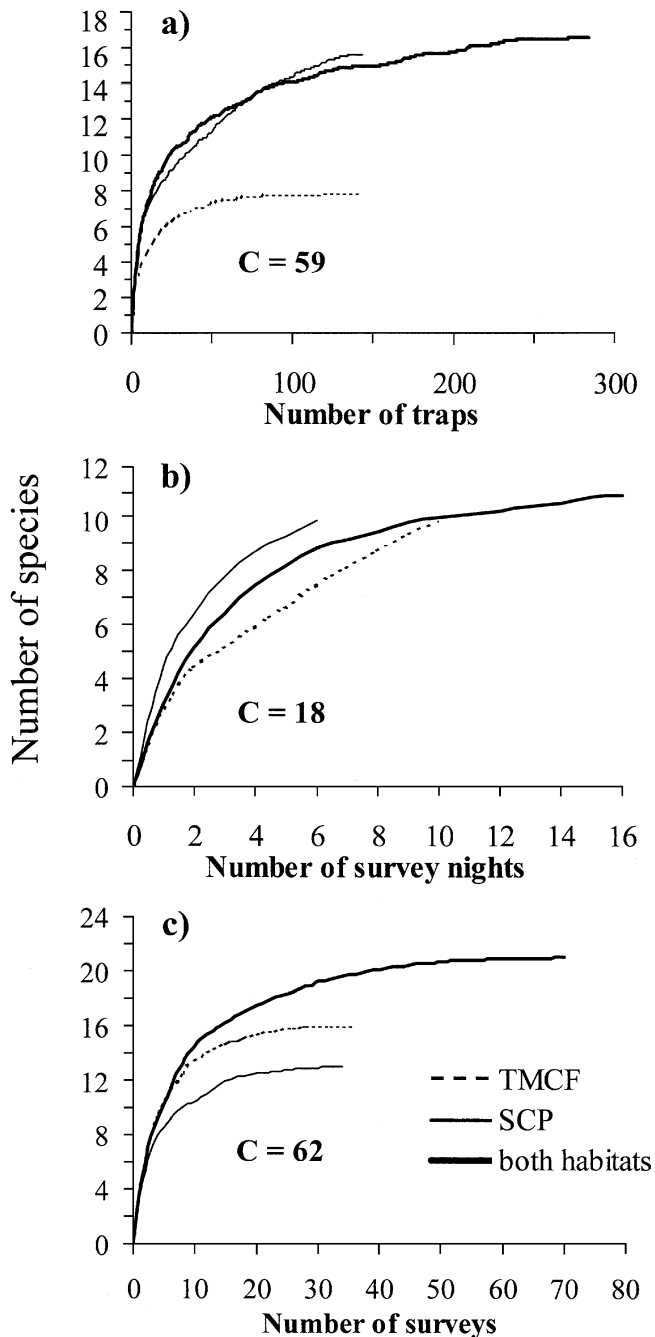


Figure 1. Species accumulation curves for the three indicator groups in tropical montane cloud forest (TMCF), shaded coffee plantations (SCP), and in both habitats (C is complementarity index [see Methods]): (a) dung beetles, (b) bats, and (c) frogs.

in SCP (*Mormoops megalophylla*), the complementarity value (18%) was the lowest obtained for the three groups studied.

Twenty-one frog species occurred in the two habitats. Of these, 16 were collected in TMCF and 13 in SCP. The species accumulation curves reached asymptotes for both

Table 2. Observed and estimated species richness in tropical montane cloud forest (TMCF), shaded coffee plantations (SCP), and both habitats of beetles, bats, and frogs based on parametric and nonparametric methods.

Species richness estimator*	Both habitats	TMCF	SCP
Beetles			
species observed	17	8	16
Clench model	17.6	8.5	17.8
Chao 2	17.8	8.0	17.1
bootstrap	18.1	8.1	17.7
completeness	94-97	94-100	90-94
Bats			
species observed	11	10	10
linear-dependence model	10.7	10.8	10.2
Chao 2	13.0	13.1	11.6
bootstrap	11.8	11.9	11.2
completeness	85-100	76-93	86-99
Frogs			
species observed	21	16	13
Clench model	23.0	17.9	14.5
Chao 2	21.0	16.0	13.0
bootstrap	21.6	16.4	13.5
completeness	91-100	89-100	90-100

*Completeness is a percentage of estimated richness (minimum-maximum).

habitats (Fig. 1c). Species richness estimates indicated that the inventory level was >89% in both habitats (Table 2). According to the Clench model, the highest expected richness for the two sites is 23 species. The complementarity value for frogs (62%) was the highest of the values obtained for the three groups studied. Of the 21 species collected, 8 were exclusive to TMCF and 5 to SCP (Table 1).

Abundance Patterns

We collected a total of 1411 copronecrophagous beetles: 71% in SCP and 29% in TMCF (Table 1). In the dominance-diversity graphs for the beetles in these habitats (Fig. 2a) the slopes are similar, although neither the abundance distribution pattern nor the hierarchical order of the species was similar. In TMCF two beetles were dominant, four were moderately high in abundance, and two were moderately low in abundance. There were no rare species or species with low abundance (one or two individuals). In SCP only one species was notably abundant, four were moderately high in abundance, another four were of moderately low abundance, and seven were rare (Fig. 2a). *Dichotomius satanas* was the most abundant species in both habitats and the only one that maintained the same hierarchical position. This species represented 50% of all the individuals captured in both habitats. *Deltochilum mexicanum* was the second most abundant beetle in the forest but was practically absent from the coffee plantations. There was a marked increase in the number of beetle species in SCP, and several species had very few individuals.

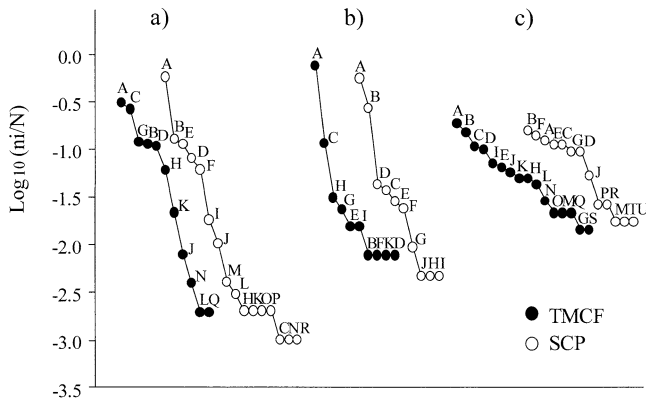


Figure 2. Dominance-diversity graphs for the three indicator groups in tropical montane cloud forest (TMCF) and shaded coffee plantations (SCP): (a) dung beetles, (b) bats, and (c) frogs. Species codes (capital letters) are defined in Table 1, *ni* is the number of individuals of each species, and *N* is the number of individuals of all species.

In all, we collected 343 phyllostomid and mormoopid bats: 62% in SCP and 38% in TMCF (Table 1). The dominance-diversity graphs had similar slopes and the same distribution pattern for two dominant species, four species of intermediate abundance, and four rare species. Although we found 9 of the 10 species in both habitats, only 2 species occupied the same hierarchical position: *Sturnira ludovici* and *Glossophaga soricina* (Fig. 2b). *S. ludovici* was the most abundant species both in TMCF and in SCP (77% and 57% of the total number of individuals, respectively; Table 1). The second most abundant species was *Carollia brevicauda* in TMCF and *Artibeus jamaicensis* in SCP. None of the four species that were rare in one habitat were also rare in the other habitat.

Of 254 frogs that we captured, 54% were caught in TMCF and 46% in SCP (Table 1). The slopes of the dominance-diversity graphs were similar for both habitats and were not as steep as those of the bats or the copronecrophagous beetles. The dominance-diversity patterns were also less defined than those of the other two groups (Fig. 2c). No one species was clearly dominant in terms of observation frequency, and no species maintained the same hierarchical position in the two habitats. *Hyla picta* was the only rare species in both habitats. With the exception of *Bufo valliceps*, which was moderately abundant in the SCP and rare in TMCF, the other rare species were exclusive to one habitat or the other.

Guilds and Habitat Modification

The 17 species of beetles fell into five of the six possible guilds. The missing guild was small necrophages. Five guilds were registered for SCP, and only three were recorded for TMCF, where both large necrophages (*Co-*

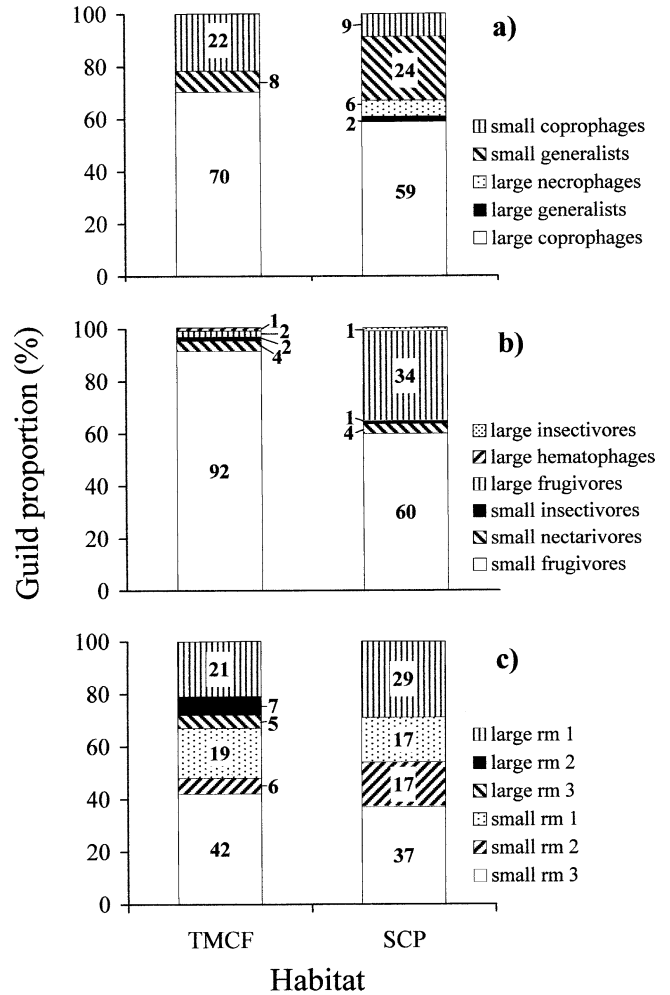


Figure 3. Proportion of guilds of the three indicator groups in tropical montane cloud forest (TMCF) and shaded coffee plantations (SCP): (a) dung beetles, (b) bats, and (c) frogs. In (c) *rm1*, *rm2*, and *rm3* refer to reproductive modes 1, 2, and 3 (see Methods). Numbers in bars denote the proportion (%) of individuals that belonged to each guild.

prophanaeus telamon) and large generalists (*Phanaeus endymion* and *Eurysternus mexicanus*) were absent. In both habitats the large coprophage guild was the most abundant (Fig. 3a), representing 70% of the individuals collected in TMCF and 59% of the individuals collected in SCP. The proportion of individuals belonging to each guild depended on habitat type ($\chi^2 = 135.41, p < 0.001$). All guilds were habitat dependent: large coprophages ($\chi^2 = 15.99, p < 0.01$); large generalists ($\chi^2 = 10.08, p < 0.01$); large necrophages ($\chi^2 = 38.15, p < 0.001$); small coprophages ($\chi^2 = 40.15, p < 0.001$); and small generalists ($\chi^2 = 54.72, p < 0.001$; Fig. 3a).

The 11 bat species recorded fell into six guilds, of which four were recorded in TMCF and four in SCP. The only hematophage (*Desmodus rotundus*) was found only in the forest, and the only large insectivore (*Mormoops*

megalophylla) was found only in SCP. In both habitats the small frugivore guild was the most abundant (92% and 61% of the total number of individuals collected in the TMCF and SCP, respectively; Fig. 3b). The proportion of individuals belonging to each guild depended on habitat type ($\chi^2 = 57.58$, $p < 0.001$). Small frugivores ($\chi^2 = 40.75$, $p < 0.001$), and large frugivores ($\chi^2 = 57.43$, $p < 0.001$; Fig. 3b) were dependent on habitat transformation.

The 21 frog species recorded fell into six guilds. All six were recorded in TMCF, with only four in the SCP. In the plantation, we did not find any large species whose eggs develop out of the water and larvae develop in water (reproductive mode 2, *Hyla arborescandens* and *H. taeniopus*). We also did not find the only large species whose eggs and larvae develop out of water (reproductive mode 3, *Eleutherodactylus berkenbuschi*; Fig. 3c). The most abundant guild in the forest and the plantation was the small species with reproductive mode 3 (42% and 37%, respectively). As observed for beetles and bats, the proportion of individuals belonging to each guild was habitat dependent ($\chi^2 = 18.87$, $p < 0.005$). The guilds with the greatest degree of dependence were large species with reproductive mode 2 ($\chi^2 = 7.98$, $p < 0.005$), large species with reproductive mode 3 ($\chi^2 = 4.77$, $p < 0.05$), and small species with reproductive mode 2 ($\chi^2 = 5.55$, $p < 0.025$; Fig. 3c).

Discussion

Our results indicated that the three groups of fauna responded to the same scenario of habitat transformation in different ways. For the copronecrophagous beetles, SCP appeared to allow for greater species diversity, given that both the number and abundance of individuals was notably greater than in the TMCF fragments. The differences in habitats did not appear to affect bats because the number and identity of species was virtually the same in both habitats. For the frogs, SCP was a less amenable habitat than TMCF because, in addition to a 20% reduction in species richness, there was 62% dissimilarity in the composition of the frog species assemblages.

Species Richness, Beta Diversity, and Guilds

COPRONECROPHAGOUS BEETLES

Of the total number of species captured in both habitats, 94% and a high proportion of individuals for the majority of the species were caught in SCP. Only 3 of the 17 species captured (*Deltochilum mexicanum*, *Onthophagus subcancer*, and *Ontherus mexicanus*) were more abundant in TMCF than in SCP. Arellano and Halffter (2003) reported 18 species, found between 1990 and 1996, for a group of TMCF remnants and SCP in the same landscape.

We found 1 species (*Eurysternus mexicanus*) that Arellano and Halffter (2003) did not, although they did find it at the next lowest elevational level (<1000 m asl).

The cumulative list of species obtained over several years of sampling in the same study region has 19 species of Scarabaeinae, two more than the number of species we recorded in this study. During 1 year of sampling in the TMCF-1, however, Arellano and Halffter (2003) found 5 more species (*Onthophagus hœpfneri*, *Onthophagus nasicornis*, *Onthophagus mexicanus*, *Scatimus ovatus*, and *Eurysternus mexicanus*) than we found (7 species) in the same site. Each of these 5 species, however, had a low abundance (one or two individuals). It is possible that increased sampling time allows species with low population densities to be detected in environments, such as TMCF, that are structurally more complex or where yearly variation in their presence is notable. In SCP we collected the 5 species in equally low abundances (Table 1).

The abundance of *Dichotomius satanas*, a large coprophage beetle, in SCP was almost four times its abundance in TMCF. This could be because there is more human excrement available in SCP. Hanski and Cambefort (1991) proposed that greater resource availability results in an increase in the abundance of coprophagous beetles and allows species with larger body sizes to prosper. We found dramatically more *Deltochilum mexicanum*, another large coprophage, in TMCF (131 individuals) than in SCP (1 individual). This suggests that this species is highly sensitive to the microenvironmental changes resulting from the transformation of forest into coffee plantation. Arellano et al. (2005) also found that *Deltochilum mexicanum* occurred in the forest but not in SCP or other habitats. Similarly, there were notably fewer *Onthophagus subcancer* and *Ontherus mexicanus*, coprophages of small and medium size, respectively, in coffee plantations. *Onthophagus subcancer* was not even recorded for SCP, suggesting that these species are also highly sensitive to the transformation of the forest.

The high permeability of the habitat edges to Scarabaeinae is noteworthy and occurred under the environmental conditions of the landscape we studied. The opposite (i.e., decreased habitat permeability) occurs in the majority of tropical landscapes (Halffter & Arellano 2002). The reason for this may lie in the climatic characteristics of the landscape being studied (ample cloud cover, frequent rains, and high environmental humidity, for example), but it may also be a result of the disturbance of the TMCF fragments and the peculiar arboreal composition of the SCP—two elements that dilute the ecotone between both types of community.

BATS

The ability of bats to fly several kilometers in a single night and the arboreal cover of the SCP gives the landscape uniformity, reducing the structural and microenvironmental

differences between TMCF and SCP. This may explain the similar species richness and composition between the two habitats. Differences in the hierarchy of the majority of bat species in each habitat (except *Sturnira ludovici* and *G. soricina*), could be related to variable resource availability. Understory turnover and the introduction of cultivated plants into the SCP appear to create differences in food availability for some species. In the SCP of this region, fruit trees of banana, guava, and *Ficus* are often planted. Because these provide food for large frugivorous bats, this guild is favored in SCP (see also Estrada et al. 1993).

For bat fauna, SCP can clearly function as a landscape reservoir, furnishing both roosting sites and food. The similarity in the species diversity of the SCP and the natural habitats notwithstanding, the long-term conservation of this fauna may depend in large measure on the fragments of forest in the landscape mosaic, as has been suggested for other Neotropical regions that have undergone extensive transformation (Estrada & Coates-Estrada 2001). In addition, other published evidence suggests that in the study landscape, SCP can function as reservoir for other biological groups such as soil macrofauna and mesofauna (Juárez 2000).

FROGS

Frogs were the only group we studied for which the results approach the proposed explanation: that differences caused by the transformation of the forest would be reflected in a reduction in species richness. In SCP there were 20% fewer species (13) than in TMCF (16), and as such, SCP alone could not maintain all the frog species of native TMCF. Although we found only half the 16 frog species recorded for the forest in SCP, it was a suitable environment for 5 other species not found in our patches of TMCF.

In a study carried out in the same area, Pineda and Halffter (2004) collected 21 frog species for the entire landscape. Thirteen species were recorded for the SCP, none of which were exclusive. We also collected 21 species, of which only 8 were found exclusively in the TMCF and 5 in SCP. This gives a high value (63%) of beta diversity between these two habitat types. Of the 8 species found exclusively in the forest, 5 (*Bufo cristatus*, *Hyla arboreoscandens*, *H. mixomaculata*, *H. taeniopus* and *Eleutherodactylus berkenbuschi*) have been recorded exclusively in other locations in well-conserved TMCF (Duellman 1970; Mendelson 1997; Campbell 1999b), suggesting that they are particularly sensitive to the transformation of TMCF. The other three species (*Hyla picta*, *Eleutherodactylus spatulatus*, and *Leptodactylus fragilis*) have been caught in different types of vegetation or in disturbed habitats (Lee 1996; Campbell 1999b).

Similarly, the five species found exclusively in SCP have also been registered in small fragments of TMCF in the

same landscape (Pineda & Halffter 2004). The microenvironmental characteristics of small forest fragments and those of SCP are probably similar enough that similar species are found in both types of habitat. The variability in the frog species exclusive to the two habitats can probably, as for the beetles, be attributed to the degree of permeability of the limits between communities.

Because none of the frog species maintained the same hierarchical position in both habitats, all species were probably affected to some degree by the transformation of the forest. The decrease in canopy cover could be one of the main factors affecting the presence and abundance of frogs because a reduction in canopy cover leads to an increase in temperature and a decrease in relative humidity and soil moisture content (Murcia 1995). Frogs need to keep their skin moist for gaseous exchange and rely on external heat to regulate their body temperature. A warmer, drier environment would negatively affect several species, especially those that lay their eggs out of the water and have aquatic larval development because their clutches would be more vulnerable to atmospheric desiccation. This would also be true of large species because their greater surface area would result in a greater loss of water through evapotranspiration. The importance of the canopy as a determinant of the presence and abundance of several frog species coincides with the findings of Toral et al. (2002) in that arboreal cover is the most important variable with respect to the presence of Leptodactylid frogs in a cloud forest in Ecuador.

Frog species respond strongly but differently to the degree of landscape fragmentation. Two of the coffee plantations studied by Pineda and Halffter (2004) were as rich as or richer in species than some individual fragments of TMCF. The dissimilarity in the composition of the species assemblages between both habitat types, however, was >50%. These plantations had 23% to 36% less canopy cover than the TMCF but were notably larger (2 to 7 times) than the forest fragments we studied.

Whether the patterns of species diversity we found would hold if the comparison were between SCP or TMCF fragments and larger, well-conserved TMCF is an interesting question. Unfortunately there is no site with such characteristics in the study area. To have a point of reference for the species diversity in the study landscape, we compared our results with information from several studies (including other, more disturbed land covers). Surveys covering a span of 100 years in this landscape (Flores-Villela 1998; Pineda & Halffter 2004) have reported 24 species of frogs, whereas we recorded 21 (88%) of those species. For copronecrophagous beetles, we recorded 17 (89%) of the 19 species recorded in the same landscape by others (Arellano & Halffter 2003; Arellano et al. 2005). For bats there were no data to compare with our findings. Overall, our data suggest that SCP and TMCF fragments altogether maintain an important proportion of species diversity in the study landscape.

Conclusion

The changes in species diversity for the two habitats surveyed occurred most notably in species with few individuals, revealing the high degree of instability of species with low abundances in assemblages that, for various reasons, are poorly consolidated. This seems to be related to the permeability of the limits between habitats (between coffee plantations and the rest of the landscape) that allow for the occasional presence of tourist species. For the frogs and particularly for the beetles, the composition of the fauna of the SCP (an agroecosystem that preserves many species of the original forest) is unstable. This fauna is composed of elements originally from the TMCF and a notable but variable number of species that are more heliophilic from other habitats of the landscape.

As for the relative usefulness of the indicator groups, bats were not useful at the landscape scale we examined, beetles and frogs clearly reflected landscape differences, and frogs had greater sensitivity to habitat modification. Even the evidence provided by good indicator groups, however, should be considered with caution. Changes in the number of species where the species are represented only by a few individuals could be the result of the random capture of truly rare species. But these changes could also be the outcome of capturing transient species, whose presence within a habitat is purely occasional. The presence of many transient species reduces the diagnostic value of the total number of species recorded for a given habitat. More comparative studies of different indicator groups in different landscapes are needed to determine whether species represented by only a few individuals (<3) should be included in calculations. Their exclusion might be a way to avoid the bias introduced when transient species are numerous.

Our results demonstrate the importance of agroecosystems such as SCP for the conservation of biodiversity in this type of landscape. This result is supported by Perfecto et al. (2003), who found that butterflies and foraging ants, but not birds, are affected when TMCF is converted to coffee plantations in Chiapas (southeast Mexico). Coffee plantations, then, are probably more important for the conservation of birds than for other groups.

Shaded coffee plantations form a matrix that surrounds and connects TMCF fragments. This matrix is relatively permeable to the occasional entry of species (transients) common to treeless environments. In a landscape where other agroecosystems offer less or no tree cover and have much lower species richness, however, SCP provides a highly functional resource for the preservation of biodiversity in a relatively hostile environment.

Acknowledgments

We thank L. Arellano for helping to identify beetles. C. L. Sampieri, A. Guerrero, A. Rizo, G. Sánchez, G. Gil, J.

Bueno, M. Valle, and S. Cárcamo provided indispensable field assistance. J. F. Ornelas and G. Williams-Linera made useful suggestions on early versions of this manuscript. We thank B. Delfosse for translating the manuscript into English from the original in Spanish and for offering valuable suggestions. This study was funded by the Mexican National Science and Technology Council (Consejo Nacional de Ciencia y Tecnología [CONACYT], project 37514-V); the National Commission for the Knowledge and Use of Biodiversity (Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, projects FB733/U030/00 and FB904/BE012/03); the International Foundation for Science; and ORCYT-UNESCO (contract 883.612.2). E.P. gratefully acknowledges the graduate scholarship from CONACYT. This paper was written in partial fulfillment of the requirements for E. P. as a doctoral candidate of the Graduate Studies Division, Instituto de Ecología, A.C., Xalapa, Veracruz, Mexico.

Literature Cited

- Arellano, L., and G. Halffter. 2003. Gamma diversity: derived from and a determinant of alpha diversity and beta diversity. An analysis of three tropical landscapes. *Acta Zoológica Mexicana* 90:27-76.
- Arellano, L., M. E. Favila, and C. Huerta. 2005. Diversity of dung and carrion beetles in a disturbed Mexican tropical montane cloud forest and on shade coffee plantations. *Biodiversity and Conservation*: in press.
- Blaustein, A. R., D. B. Wake, and W. P. Sousa. 1994. Amphibians decline: judging stability, persistence, and susceptibility of populations to local and global extinctions. *Conservation Biology* 8:60-71.
- Campbell, J. A. 1999a. Amphibians and reptiles of Northern Guatemala, the Yucatan and Belize. University of Oklahoma Press, Norman.
- Campbell, J. A. 1999b. Distribution patterns of amphibians in Middle America. Pages 111-210 in W. E. Duellman, editor. *Patterns of distribution of amphibians: a global perspective*. The Johns Hopkins University Press, Baltimore, Maryland.
- Challenger, A. 1998. Utilización y conservación de los ecosistemas terrestres de México. Pasado, presente y futuro. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Universidad Nacional Autónoma de México, Agrupación Sierra Madre, S.C., México, D.F. (in Spanish).
- Colwell, R. K. 2000. EstimateS 6.0b1: statistical estimation of species richness and shared species from samples. Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs. Available from <http://viceroy.eeb.uconn.edu/estimates> (accessed September 2002).
- Colwell, R. K., and J. A. Coddington. 1995. Estimating terrestrial biodiversity through extrapolation. Pages 101-118 in D. L. Hawksworth, editor. *Biodiversity measurement and estimation*. Chapman & Hall, New York.
- Crump, M. L. 1974. Reproductive strategies in a tropical anuran community. Miscellaneous publication. Museum of Natural History, University of Kansas 61:1-68.
- Daily, G. L., P. R. Ehrlich, and A. Sánchez-Azofeifa. 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecological Applications* 11:1-13.
- Duellman, W. E. 1970. The hylid frogs of Middle America. Monograph. Museum of Natural History, University of Kansas, Kansas City.
- Escobar, F., and P. Chacón-Ulloa. 2000. Distribución espacial y temporal en un gradiente de perturbación de la fauna de coleópteros coprófagos (Scarabaeidae, Aphodiinae) en la Reserva Natural La Planada, Nariño, Colombia. *Revista de Biología Tropical* 48:961-975 (in Spanish).

- Estrada, A., R. Coates-Estrada, and D. M. Merritt Jr. 1993. Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. *Ecography* **16**:309–318.
- Estrada, A., and R. Coates-Estrada. 2001. Species composition and reproductive phenology of bats in a tropical landscape at Los Tuxtlas, Mexico. *Journal of Tropical Ecology* **17**:627–646.
- Feinsinger, P. 2001. Designing field studies for biodiversity conservation. *The Nature Conservancy and Island Press*, Washington, D.C.
- Fenton, M. B., L. Acharya, D. Audet, M. B. C. Hickey, C. Merriman, M. K. Obrist, and D. M. Syme. 1992. Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. *Biotropica* **24**:440–446.
- Flores-Villela, O. 1998. Herpetología del Estado de Veracruz: data base. Report project A27. Sistema Nacional de Inventarios Biológicos—Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. México, D.F. (in Spanish).
- Gallina, S., S. Mandujano, and A. González-Romero. 1996. Conservation of mammalian biodiversity in coffee plantations of central Veracruz, Mexico. *Agroforestry Systems* **2**:11–17.
- Greenberg R., P. Bichier, A. Cruz-Angon, and R. Reitsma. 1997. Bird populations in shade and sun coffee plantations in Central Guatemala. *Conservation Biology* **11**:448–459.
- Halffter, G. 1998. A strategy for measuring landscape biodiversity. *Biology International* **36**: 3–17.
- Halffter, G., and L. Arellano. 2002. Response of dung beetle diversity to human-induced changes in a tropical landscape. *Biotropica* **34**:144–154.
- Halffter, G., M. E. Favila, and V. Halffter. 1992. A comparative study of the structure of the scarab guild in Mexican tropical rain forest and derived ecosystems. *Folia Entomológica Mexicana* **84**:131–156.
- Hanski, I., and Y. Cambefort. 1991. Resource partitioning. Pages 331–349 in I. Hanski and Y. Cambefort, editors. *Dung beetles ecology*. Princeton University, Princeton, New Jersey.
- Ibarra-Núñez, G., and J. A. García-Ballina. 1998. Diversidad de tres familias de arañas tejedoras (Araneae: Araneidae, Tetragnathidae, Theridiidae) en cafetales del Soconusco, Chiapas, México. *Folia Entomológica Mexicana* **102**:11–20 (in Spanish).
- Juárez, R. D. 2000. Patrones de la macro y meso-fauna edáfica en agroecosistemas cafetaleros con distinto grado de intensificación. M.S. thesis. Instituto de Ecología, A.C. Xalapa, México (in Spanish).
- Klein, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* **70**:1715–1725.
- Lee, J. C. 1996. *The amphibians and reptiles of the Yucatán Peninsula*. Cornell University Press, Ithaca, New York.
- Lips, K. R. 1998. Decline of a tropical montane amphibian fauna. *Conservation Biology* **12**:106–117.
- McGeoch, M. D. 1998. The selection, testing and applications of terrestrial insects as bioindicators. *Biological Reviews of the Cambridge Philosophical Transactions* **73**:181–201.
- Medellín, R. A., H. T. Arita, and O. Sánchez. 1997. Identificación de los murciélagos de México: clave de campo. *Publicaciones especiales no. 2 Asociación Mexicana de Mastozoología Asociación Civil*, México, D.F. (in Spanish)
- Medellín, R. A., M. Equihua, and M. A. Amin. 2000. Bat diversity and abundance as indicators of disturbance in Neotropical rainforests. *Conservation Biology* **14**:1666–1675.
- Mendelson, J. R., III. 1997. A new species of toad (Anura: Bufonidae) from Oaxaca, México with comments on the status of *Bufo cavifrons* and *Bufo cristatus*. *Herpetologica* **53**:268–286.
- Mittal, I. C. 1993. Natural manuring and soil conditioning by dung beetles. *Tropical Ecology* **34**:150–159.
- Moguel, P., and V. M. Toledo. 1999. Biodiversity conservation in traditional coffee systems of Mexico. *Conservation Biology* **13**:11–21.
- Moreno, C. E., and G. Halffter. 2000. Assessing the completeness of bat biodiversity inventories using species accumulation curves. *Journal of Applied Ecology* **37**:149–158.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology & Evolution* **10**:58–62.
- Perfecto, I., and R. Snelling. 1995. Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. *Ecological Applications* **5**:1084–1097.
- Perfecto, I., R. A. Rice, R. Greenberg, and M. E. Vander Voort. 1996. Shade coffee: a disappearing refuge for biodiversity. *Bio Science* **46**:598–608.
- Perfecto, I., J. H. Vandermeer, P. Hanson, and V. Cartín. 1997. Arthropod biodiversity loss and the transformation of a tropical agro-ecosystem. *Biodiversity and Conservation* **6**:935–945.
- Perfecto, I., and J. Vandermeer. 2002. The quality of the agricultural matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conservation Biology* **16**:174–182.
- Perfecto, I., A. Mas, T. Diestch, and J. Vandermeer. 2003. Conservation of biodiversity in coffee agroecosystems: a tri taxa comparison in southern Mexico. *Biodiversity and Conservation* **12**:1239–1252.
- Pineda, E., and G. Halffter. 2004. Species diversity and habitat fragmentation: frogs in a tropical montane landscape in Mexico. *Biological Conservation* **117**:499–508.
- Rappole, J. H., D. I. King, and J. H. Rivera-Vega. 2003. Coffee and conservation. *Conservation Biology* **17**:334–336.
- Rzedowski, J. 1998. Diversidad y orígenes de la flora fanerogámica de México. Pages 129–145 in T. P. Ramamoorthy, R. Bye, A. Lot and J. Fa, editors. *Diversidad biológica de México: orígenes y distribución*. Universidad Nacional Autónoma de México, México, D.F. (in Spanish).
- Scott, N. J. 1994. Complete species inventories. Pages 84–92 in W. R. Heyer, M. A. Donnelly, R. W. McDiarmid, L. A. C. Hayek, and M. S. Foster, editors. *Measuring and monitoring biological diversity. Standard methods for amphibians*. Smithsonian Institution Press, Washington, D.C.
- Soberón, J. M., and J. E. Llorente-Bousquets. 1993. The use of species accumulation functions for the prediction of species richness. *Conservation Biology* **7**:480–488.
- Soto-Pinto, L., Y. Romero-Alvarado, J. Caballero-Nieto, and G. S. Warnholtz. 2001. Woody plant diversity and structure of shade-grown-coffee plantations in Northern Chiapas, Mexico. *Revista de Biología Tropical* **49**:977–987.
- Toral, E., P. Feinsinger, and M. Crump. 2002. Frogs and a cloud forest edge in Ecuador. *Conservation Biology* **16**:735–744.
- Wake, D. B. 1991. Declining amphibian populations. *Science* **253**:860.
- Williams-Linera, G. 2002. Tree species richness complementary, disturbance and fragmentation in a Mexican tropical montane cloud forest. *Biodiversity and Conservation* **11**:1825–1843.
- Williams-Linera, G., R. H. Manson, and E. V. Isunza. 2002. La fragmentación del bosque mesófilo de montaña y patrones de uso del suelo en la región oeste de Xalapa, Veracruz, México. *Madera y Bosques* **8**:73–89 (in Spanish).
- Zar, J. 1996. *Biostatistical analysis*. 4th edition. Prentice Hall, Upper Saddle River, New Jersey.

