Biodiversity and Conservation **11:** 1903–1918, 2002.

Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas, Mexico

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Received 7 May 2001; accepted in revised form 23 November 2001

Key words: Conservation, Dung beetles, Forest fragmentation, Los Tuxtlas, Mexico, Tropical rain forest

Abstract. With the aim of determining what kind of landscape mosaics might sustain maximum diversity and minimum species loss, dung beetles were sampled with baited pitfall traps to compare species richness and species composition in a tract of continuous forest, forest fragments and a habitat island consisting of a mosaic of forest and arboreal crops in Los Tuxtlas, southern Mexico. We captured 7332 dung beetles representing 33 species. Similar numbers of species were captured in the three habitats. However, 56% of individuals were captured in the continuous forest, 29% in the mosaic habitat and 15% in the forest fragments. Eight species (*Canthon femoralis*, *Copris laeviceps*, *Canthidium centrale*, *Onthophagus batesi*, *Deltochilum pseudoparile*, *O. rhinolophus*, *Canthon viridis vazquezae and Dichotomius satanus*) accounted for 90% of the captures, but their relative dominance varied among habitats. A clear trend was evident in the number of dung beetles captured in the dung processing guilds (rollers/tunnelers) as well as in the diurnal and nocturnal guilds, with captures decreasing from the continuous forest to the mosaic habitat to the forest fragments. A similar trend was detected in detection rates for medium and small size dung producing mammals. Species richness of forest fragments and mosaic habitat did not differ from that found in the continuous forest, but these habitats differ significantly in species richness from isolated shaded and unshaded plantations, linear strips of vegetation, the forest–pasture edge and pastures according to rarefaction analysis. The co-occurrence of the continuous forest, the mosaic habitat and the cluster of forest fragments in close proximity seems to be preserving a diverse assemblage of dung beetle species in the local landscape.

Introduction

Dung and carrion beetles are a conspicuous component of the diversity of insects in Neotropical rain forests (Halffter and Mathews 1966; Howden and Nealis 1975, 1978; Howden and Young 1981; Hanski 1983, 1989; Gill 1991). Depending on locality, 28–60 species may be represented (Klein 1989; Hanski and Cambefort 1991) and as many as 2000 beetles per hectare may be found in forested areas (Peck and Forsyth 1982). Beetles use the dung produced by forest vertebrates, particularly mammals such as primates, and occasionally that of birds and reptiles (Howden and Young 1981; Young 1981) as food and as a substrate for oviposition and feeding by their larvae (Halffter and Edmonds 1982; Hanski 1989; Gill 1991). Carrion as well as decaying fruit and fungi are also used as sources of food (Halffter and Mathews 1966; Hanski 1989). Resource partitioning, such as preference for soil and cover (Nealis 1977; Lumaret 1978), diel flight time (diurnality versus nocturnality) and dung size (Peck and Howden 1984), perching heights (Howden and Nealis 1978) and dung removal methods (rollers versus tunnelers; Halffter and Mathews 1966) have been suggested to diminish competition among members of the guild.

By burying the dung and carrion as food for their offspring, dung beetles may increase the rate of soil nutrient cycling (Halffter and Mathews 1966; Bornemissa and Williams 1970; Nealis 1977), they exert important control over the egg and larva populations of parasitic flies present in the fresh dung of mammals (Bergstrom et al. 1976), and they also act as important secondary dispersal agents for the seeds of several tree species in Neotropical forests, thus participating in the natural process of forest regeneration (Estrada and Coates-Estrada 1991). Recently dung beetles have been suggested to be good indicators for measuring biodiversity as indicators of disturbance in the tropics (Halffter and Favila 1993; Davis et al. 2001).

Field studies have suggested that dung resources in the tropical rain forest are limited as a result of the general scarcity and patchy distribution of dung-producing mammals and dung and carrion beetles compete intensively for resources as attested by their competitive and combative behaviours (Halffter and Edmonds 1982; Hanski 1991). Since the general abundance of mammals sets the level of resource availability to dung beetles (Hanski and Cambefort 1991), and non-flying mammals are strongly sensitive to forest loss, fragmentation and isolation (Lovejoy et al. 1986; Estrada et al. 1994), this may make dung beetles sensitive to deforestation (Klein 1989; Estrada et al. 1998).

In spite of the ecological importance of dung beetles and of the important numerical contribution of populations of these insects to the richness of insect communities in Neotropical forests, reports on dung beetle species responses to destruction, fragmentation and isolation of tropical rain forests are still very rare in the literature and exist only for a few localities in Mexico (Halffter et al. 1992; Estrada et al. 1998) and in Central and South America (Howden and Nealis 1975; Peck and Forsyth 1982; Klein 1989). These studies report important negative effects, such as fewer species and sparser populations as a result of clear-cutting, and the fact that isolated forest fragments are important barriers for movement and dispersal (Klein 1989). Very few data are available as well on the value of different spatial arrangements of remnant forests and man-made vegetation for dung beetle persistence in modified Neotropical landscapes (Estrada et al. 1998). In line with this need, in this paper we describe species composition and relative abundance for the dung beetle assemblages present in a continuous tract of pristine lowland rain forest, in a cluster of forest fragments and in a forest-agricultural man-made mosaic of vegetation. These habitats form part of a landscape located in the northeastern section of Los Tuxtlas region, Veracruz, Mexico. This report attempts to infer what kind of landscape mosaics might sustain maximum diversity and minimum species loss and it expands on earlier work on dung beetle responses to fragmentation of their native habitat (Estrada et al. 1998, 1999).

Methods

Study area

The tropical rain forest of Los Tuxtlas, in southeastern Veracruz, Mexico, represents the most northern limit of the lowland rainforests on the American continent. About 50 species of dung beetles have been reported to exist in these forests and they constitute an important component of the biological richness found in this region (Halffter et al. 1992; Moron and Blackaller 1997). Weather monitoring stations indicate a mean annual temperature of 27 °C (range 20–28 °C). Average annual rainfall is 4900 mm, but from March to May average monthly rainfall is 111.7 ± 11.7 mm and from June to February this average equals 486.25 ± 87.0 mm.

Study habitats

The continuous tract of pristine lowland rain forest comprised the 700 ha property of the biological research station 'Los Tuxtlas' of UNAM (95°00′ W, 18°25′ N). The forest of this reserve is connected to about 3500 ha of pristine rain forest that forms part of the Los Tuxtlas Biosphere Reserve (Figure 1). The original lowland rain forest in a 126 km^2 area immediately north of the continuous forest was gradually converted to pasture lands between 1960 and 1970, but clusters of forest fragments have remained in this area due to difficult topography or in order to preserve water supplies. Sixteen of a group of 60 forest fragments present in this landscape were randomly selected to sample dung beetles (Figure 1). The average area of these sites was 13 ha (range 1–80 ha) and the total accumulated area of these fragments was 240 ha.

The mosaic of forest and fruit-productive man-made vegetation was located at about 1.2 km north of the research station and about 0.5–1.2 km west from the cluster of forest fragments mentioned above. The mosaic habitat is an 'island' of vegetation about 250 ha in size, surrounded by pastures. It consists of remnant rain forest and interdigitated 20–25-year old stands of coffee and cacao shaded by rain forest trees and of citrus and banana groves as well as patches of pineapple, avocado and papaya (Figure 1).

Dung beetle sampling

Between 1997 and 1999 dung beetles were sampled in 16 locations within 250 ha of the continuous forest site, in one location within each of the 16 forest fragments and in 16 locations within the mosaic of agricultural vegetation. In the latter habitat, four sampling locations were in forest and three locations were in each of the major agricultural habitats (coffee, cacao, citrus and banana) present at this site. The distance among sampling locations in the continuous forest and mosaic habitat ranged from 500 to 1000 m. At each location in the interior of the continuous forest, the mosaic site and the forest fragments, we set up 50 baited pitfall traps [similar to

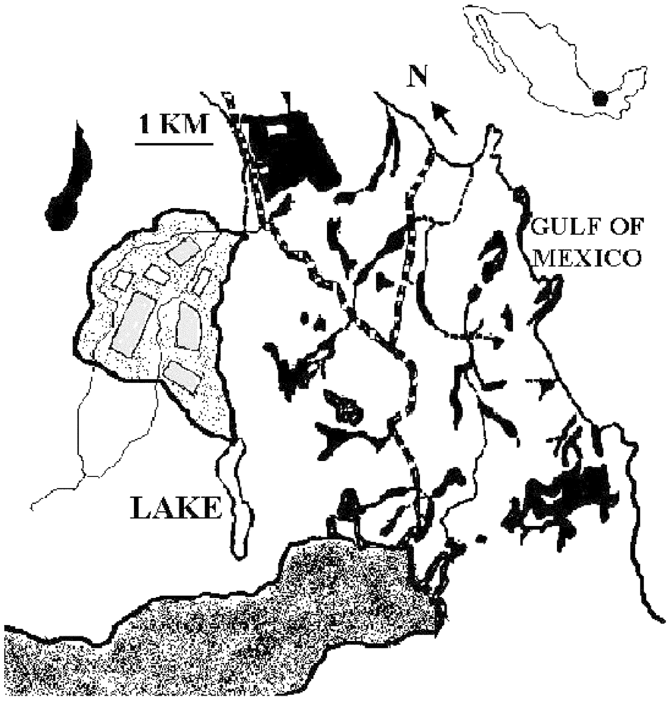

Figure 1. Study sites in the northeastern region of Los Tuxtlas in southern Veracruz, Mexico. The continuous forest site (about 4000 ha), partly shown, is the shaded area at the bottom of the figure. Forest fragments, to the right of the figure, are shown in black. Mosaic habitat is the lighter shaded area to the left. In this habitat, cacao and coffee groves shaded by forest trees are shown as gray rectangles. Open squares are citrus and banana groves. The broken line is a dirt road and continuous lines indicate streams. White areas are pastures.

those described by Howden and Nealis (1975)], at 10–15 m intervals, consisting of a cylinder-shaped plastic container with 15 cm of loose soil on top of which we placed the bait. We baited the pitfall traps with 60 g of a homogenised mixture of fresh howler monkey, cow, horse and dog dung. This bait grossly mimicked the excreta produced by mammalian herbivores and omnivores in the forest (Estrada et al. 1993).

Pitfall traps were baited at 18 h and retrieved 24 h later at all locations in the habitats investigated. Dung beetles were sampled in February–March, May–June, and September–October in the 3-year period for 288 24-h periods. Trapping was carried out under similar general climatic conditions, avoiding rainy or heavily overcast days. All dung beetles captured were kept overnight and each individual was identified to species level through comparison with a reference collection housed at the biological research station Los Tuxtlas and released the next morning at the capture site.

Sampling of mammals excluding bats

All mammals except bats were surveyed along three 4.0 km long sinuous transects in the continuous forest and in mosaic habitat. In the forest fragments the transects ran the length of the fragment. The transects were walked at a slow pace (ca. 2 km h^{-1}) and we visually scanned the sides of the transect searching for non-flying mammals. Counts were conducted between 06.00 and 12.00 hours and between 19.00 and 24.00 hours. A total of 18 h of diurnal surveys and 15 h of nocturnal surveys were completed in the continuous forest and in the mosaic habitat. In each of the forest fragments we completed 5 h of diurnal (80 h in total) and 5 h of nocturnal surveys (80 h in total). For each mammal sighted we recorded the species and the number of individuals observed. To sample small terrestrial rodents (<200 g), we used Sherman traps placed at 50 m intervals in each habitat. In the continuous forest and mosaic habitats we used 20 Sherman traps. These traps were operated during three different nights for a total of 60 trap nights per habitat. In each forest fragment we set up 10 Sherman traps. A total of 160 trap nights were completed at these sites. Rodents captured were released after species identification. Results of these counts were compared to results on dung beetle trapping in the same habitats.

Data analysis

Since sampling effort (number of pitfall traps and 24-h trapping periods) was the same across sampling locations and habitats, we compared dung beetle species counts across vegetation types using totals, averages and percentages. Rarefaction curves were used to compare species richness among habitats. This statistical method estimates the number of species that can be expected in a sample of n individuals [denoted by $E(S_n)$] drawn from a population of N total individuals distributed among S species (Ludwig and Reynolds 1988). For each sample, rarefaction algorithms generate expected species richness based on random subsamples of individuals for each abundance level. Iteration generates a mean and a variance of species richness for each abundance, allowing a statistical comparison of expected species richness of two or more samples that differ in abundance of individuals (Gotelli and Entsminger 2001). Published data on dung beetle species richness documented at isolated shaded plantations (cacao and coffee) and unshaded plantations (citrus and allspice), live fences (live posts of *Bursera simaruba*, Burseraceae, used by ranchers to hold barbed wire), the forest–pasture edge and pastures are included here for comparative purposes (Estrada et al. 1998). Shannon's diversity index (H') was used to compare habitats in species diversity. Non-parametric tests were used for statistical comparisons (Fitch 1992). Mean and standard deviations (±SD) or averages and standard errors (±SE) are given throughout the paper. The term dung beetle is used in the text to refer to both dung and carrion beetles.

Table 1. Summary of captures of dung and carrion beetles at the habitats investigated.

	Continuous forest	Mosaic habitat	Forest fragments
Dung beetles			
Total number of species	25	24	25
Total number of individuals	4110	2140	1082
Mean (±SD) number of species captured per location	12.1 ± 5.5	10.6 ± 4.0	8.5 ± 4.4
Mean (±SD) number of individuals captured per location	257.0 ± 236.9	134.0 ± 131.0	64.0 ± 52.6
Mammals			
Number of species	27	18	18
Number of individuals	171	121	187
Mean rate for diurnal per individual	0.31 ± 0.48	0.15 ± 0.06	0.06 ± 0.05
Mean rate for nocturnal per individual	0.33 ± 0.42	0.41 ± 0.46	0.16 ± 0.16
Howler monkeys, troops/h	1.00	1.94	0.28
Small rodents, ind/trap/night	0.18 ± 0.13	0.07 ± 10.08	0.05 ± 0.05

Sampling of dung beetles based on 50 baited pitfall traps at 16 locations in each habitat for one 24-h period. Also shown are the results of surveys of non-flying mammals at each habitat. Rates for howler monkeys are troops/h.

Results

General aspects

Our trapping efforts resulted in the capture of 7332 dung beetles representing 33 species. Seventy-six percent of the species recorded in the pitfall traps were captured in the continuous forest habitat, 73% in the mosaic habitat and 76% in the forest fragments. The mean number of species captured per location in the three habitats was 12.1 (±5.5) in the continuous forest, 10.6 (±4.0) in the mosaic habitat and 8.5 (±4.4) in the forest fragments. These values were not significantly different between the continuous forest and the mosaic habitat, but the differences between the continuous forest and the forest fragments were significant ($z = 1.75$, $P = 0.03$). No significant differences were found between the mosaic habitat and the forest fragments ($z = 1.39$, $P = 0.08$).

The largest proportion of dung beetles was captured in the continuous forest (56%), followed by the mosaic habitat (29%) and the forest fragments (15%) (Table 1). The mean number of dung beetles captured per location in the three habitats was 257 (±236.9) for the continuous forest, 134 (±131.7) for the mosaic habitat and 64 (±52.6) for the forest fragments. The differences between the continuous forest and the mosaic habitat in these numbers were not significant ($z = -1.49$, $P = 0.06$), but those between the continuous forest and the forest fragments and between the mosaic habitat and the forest fragments were statistically significant ($z = -2.63$, $P = 0.004$; $z = 1.96$, $P = 0.02$, respectively).

Species diversity and species richness

Species diversity, measured by Shannon's function (H'), was 2.28 in the mosaic habitat, 2.17 in the continuous forest, and 2.12 in the forest fragments. Rarefaction analysis showed that at $n = 1000$, the continuous forest was the richest habitat in accumulated species, followed by the forest fragments and the mosaic habitat (Figure 2). The same analysis showed that the sample for the forest fragments and for the mosaic habitat fell within the 95% confidence interval of the rarefaction curve for the continuous forest sample, suggesting that species richness among these three habitats did not differ. Isolated shaded plantations approached the species richness of the mosaic habitat at $n = 500$, but at $n = 1000$ the mosaic habitat had a higher species richness than the isolated shaded plantation. The continuous forest, the forest fragments and the mosaic habitat differed significantly in species richness from the forest–pasture edge, the isolated unshaded plantations, the live fences and the pasture habitats (Figure 2).

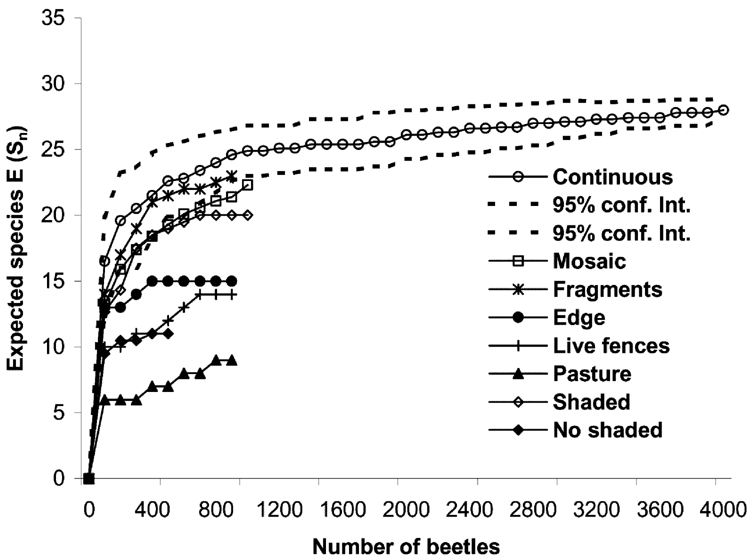

Figure 2. Rarefaction curves for the three habitats investigated. $E(S_n)$ refers to the number of species that can be expected in a sample of n individuals drawn from a population of N total individuals distributed among S species. For comparative purposes we also show data from other studies (Estrada et al. 1998) on dung beetle species richness for the forest–pasture edge, isolated shaded (cacao and coffee plantations) and unshaded (citrus and allspice) plantations, for a linear strip of live posts of *Bursera simaruba* (Burseraceae), and for pasture habitats also sampled in the area. Comparisons for the three habitats reported in this study were made at $n = 500$. Note that the forest fragments and the mosaic habitat fall within the 95% confidence interval for the continuous forest at $n = 500$.

Species ranking

The total sample of dung beetles captured was dominated by three species, *Canthon femoralis*, *Copris laeviceps*, and *Canthidium centrale*, which accounted for 50% of the captures. Another five species (*Onthophagus batesi*, *Deltochilum pseudoparile*, *Onthophagus rhinolophus*, *Canthon viridis vazquezae*, *Dichotomius satanas*) accounted for an additional 40% of dung beetle captures. All these species, except for *Di. satanas*, dominated the sample in each of the habitats investigated (Table 2). Dung beetle species overall rank abundance was correlated with the number of habitats in which a species was present ($r_s = 0.85$, $P < 0.0001$, $N = 33$).

A small subset of dung beetle species dominated the assemblages. In the continuous forest, species such as *Canth. femoralis*, *O. batesi*, *De. pseudoparile* and *Co. laeviceps* accounted for 70% of the records. In the mosaic habitat, species such as *O. rhinolophus*, *Canthi. centrale*, *Co. laeviceps*, *Canth. femoralis* and *De. pseudoparile* accounted for 75% of the records. In the forest fragments, species such as *Canth. femoralis*, *Co. laeviceps*, *Canthi. centrale* and *De. pseudoparile* accounted for 75% of the records (Table 1).

Species ranking varied among habitats and significantly different values in Kendall's coefficient of concordance between the overall abundance rank of each dung beetle species and their abundance rank in each habitat indicated that, in general, dung beetle assemblages were similarly structured, but the mosaic habitat was closer to the continuous forest in this measure (continuous forest $r_t = 0.83$, $P < 0.001$; mosaic $r_t = 0.74$, $P < 0.001$; forest fragments $r_t = 0.66$, $P < 0.001$).

On average, 60% of the recorded dung beetle species were common among the three habitats. The continuous forest and mosaic habitat had 21 dung beetle species in common and 20 species of dung beetles were common between continuous forest and the forest fragments (Table 1).

Dung beetle guilds

The number of dung beetle species captured in the roller and tunneler dung processing guilds as well as those for the diurnal and nocturnal guilds were similar among the three habitats investigated (Table 3). However, the number of dung beetle individuals captured in each guild differed significantly among habitats. In the tunneler guild, the proportion of dung beetles captured diminished from the forest (51%), to the mosaic habitat (33%) to the forest fragments (16%). Similar results were obtained for the roller guild, with the continuous forest accounting for 64% of individuals captured, the mosaic habitat for 23% and the forest fragments for 13%. In the case of the diurnal guild, 62% of dung beetles were captured in the continuous forest, 26% in the mosaic habitat and 12% in the forest fragments. A similar trend was found for the nocturnal guild, with the continuous forest accounting for 50% of individuals captured, the mosaic habitat for 33% and the forest fragments for 18% (Table 3).

Table 2. Species and number of dung beetles captured in each habitat investigated.

	Continuous forest	Mosaic habitat	Forest fragments	Total
Canthon femoralis Chevrolat	1200	248	258	1706
Copris laeviceps Harold	451	349	247	1047
Canthidium centrale Boucomont	379	381	192	952
Onthophagus batesi Howden & Cartwright	721	142	37	900
Deltochilum pseudoparile Paglian	530	199	110	839
Onthophagus rhinolophus Harold	243	429	106	778
Canthon (*G.*) *viridis vazquezae* Martinez, Halffter & Halffter	114	147	10	271
Dichotomius satanas Harold	117	19	28	164
Canthon cyanellus cyaneilus Harold	43	53	14	110
Dichotomius carolinus colonicus Say	104	4	1	109
Phanaeus endymion Harold	46	29	10	85
Uroxys boneti Pereira & Halmer	15	32	10	57
Eurysternus mexicanus Harold	14	35	6	55
Deltochilum gibbosum sublaeve Bates	14	23	2	39
Canthon (*C.*) *morsei* Harold	16	17	2	35
Sulcophanaeus chryseicollis Harold	26	3	4	33
Coprophanaeus telamon corythus Harold	21	9	2	32
Eurysternus caribaeus Herbst	13	4	13	30
Canthon (*Gl.*) *subhyalinus* Harold	19	4	1	24
Copris lugubris Bohemen	3	3	12	18
Eurysternus angustulatus Harold	9	1		10
Digitonthophagus gazella Fabricius			7	7
Bdelyropsis newtoni Howden	6			6
Canthon (*Gl.*) *sp.*		6		6
Onthophagus landolti Harold			5	5
Ateuchus illaesum Harold	4			4
Canthon (*C.*) *indagaceus chiapas* Robinson			3	3
Onthophagus nasicornis Harold		2		2
Anaides laticollis Harold		1		1
Canthidium sp.	1			1
Ontherus mexicanus Erichson	1			1
Onthophagus crinitus Harold			1	1
Uroxys sp.			1	1
Total	4110	2140	1082	7332
Number of species	25	24	25	33

Species are ranked according to their total abundance. Note the predominance of the first eight species, which accounted for 90% of the individuals captured.

Table 3. Number of species and of individuals captured in each of the dung processing guilds and in the diurnal and nocturnal guilds.

	Continuous forest		Mosaic habitat		Forest fragments	
	Species	N	Species	N	Species	N
Tunnelers	15	2144	13	1403	15	663
Rollers	10	1972	11	731	10	419
Diurnal	11	2345	13	973	13	460
Nocturnal	14	1760	11	1167	12	627

Mammal species except bats

While the habitat richest in non-flying mammal species was the continuous forest, the mosaic habitat harboured as many species of non-flying mammals as the forest fragments. A clear tendency was evident for average detection rates of individual mammals to decrease from the continuous forest to the mosaic habitat to the forest fragments. The same was true in the case of howler monkeys (Table 1).

Discussion

General aspects

Our results showed that the continuous forest was the richest habitat in dung beetle species and forest fragments were less diverse than the continuous forest. Interestingly, the mosaic habitat island was significantly richer in species than isolated arboreal plantations, linear strips of vegetation, the forest–pasture edge and pastures. Earlier studies have reported that conversion of forest to pastures results in significant decreases of dung beetle species and numbers (Howden and Nealis 1975; Klein 1989; Montes de Oca and Halffter 1995). Other studies indicated that in fragmented landscapes clusters of small forest fragments and linear strips of vegetation may help sustain dung and carrion beetle species and populations by acting as stepping stones or as temporary habitats (Estrada et al. 1998). Our study suggests that in fragmented landscapes there might be other and sometimes complementary land management alternatives that may also contribute to sustaining dung beetle species numbers and populations. These alternatives may include areas of forest managed to produce cash crops such as, among others, cacao, coffee, citrus and bananas, as in the mosaic habitat investigated.

Species dominance among habitats

Data showed that a few species dominated the samples in each habitat investigated. Species such as *O. batesi* and *Co. laeviceps* have been reported to occupy a variety of habitats ranging from forest fragments to shaded and unshaded arboreal plantations to pastures; other species such as *Canth. femoralis* and *Canthi. centrale* tend to be predominant in forest habitats (Estrada et al. 1998). Our results seemed to be consistent with the above, with species such as *Canth. femoralis* strongly dominating the sample in the continuous forest and in the forest fragments (29 and 24% of the records, respectively) and species such as *O. rhinolophus* and *Co. laeviceps* accounting for 20 and 23% of the samples in the mosaic habitat and in forest fragments, respectively.

While we lack information on the mobility of each of the dung beetle species recorded, distances of up to 1.0 km have been reported to be traversed by these beetles in 2d in other tropical localities (Peck and Forsyth 1982). Dung beetle species capable of reaching forest habitats outside of the patch in which they reside may encounter a greater variety of habitats in which to find resources and meet survival requirements. Such diversity of opportunities will increase significantly if a species can make use of human-managed habitat islands in the landscape. This could result in less concentration of mobile elements of the biota in the forest remnants, avoiding over-exploitation of resources, increased competition and predation (Offerman et al. 1995). In this scenario, some species (e.g. *O. batesi*, *Co. laeviceps*) may be able to sustain their numbers as a result of their capacity to exist in a greater diversity of habitats in the landscape. Other species (e.g. *Canth. femoralis)*, restricted to movement and dispersal in their original habitat (e.g. rain forest), may depend more closely on resources produced by forest interior mammals such as howler monkeys (Halffter et al. 1992; Estrada et al. 1999), but may be able to persist in plantations shaded by forest vegetation.

Dung beetle guilds

While the numbers of species of the roller and tunneler and of the diurnal and nocturnal dung beetle guilds were similar among habitats, numbers of beetles captured in each guild were consistently lower in the forest fragments than in the mosaic habitat and in the continuous forest. This may suggest that the small size of each forest fragment and its isolation from other habitat islands and from the continuous forest may result in important declines in the size of dung beetle populations composing each guild. Studies of dung beetles in Central and South America suggest that fragmentation may result in sparser populations and that isolated forest fragments are important barriers for movement and dispersal (Howden and Nealis 1975; Peck and Forsyth 1982; Klein 1989; Gill 1991). In general, the forest fragments were particularly poor in dung beetle captures, accounting for only 15% of the records. The small size of the forest fragments coupled to the sparse vegetation and large edge-to-area ratio, a continued edge effect resulting in deterioration of ecological conditions (Laurance et al. 1997) and their isolation may preclude the existence of many dung beetle species and possibly of large populations of dung beetles in these habitats (Klein 1989; Estrada et al. 1998).

The mosaic habitat island and forest fragments

The presence of rain forest vegetation and of shaded and unshaded plantations in the mosaic habitat may provide a great variety of microhabitats for dung and carrion beetles, possibly allowing many dung beetles of many species to co-occur in these types of habitat. The lack of statistical difference in species capture rates per location between the continuous forest and the mosaic habitat seems to support this idea. The mosaic habitat may include suitable perching sites important for locating food odours and cover from predators such as staphylinid beetles, spiders and even bats (Gill 1991). The presence of the mosaic habitat in conjunction with the nearby continuous forest may allow the persistence in fragmented landscapes of many dung beetle species that differ in ecological requirements (Hanski 1989; Gill 1991; Estrada et al. 1994). Other land management practices in which pastures dominate the landscape may have important consequences for dung beetle population sustenance, including the replacement of a rich assemblage of native species by introduced species such as *Digithonthophagus gazella*, a savanna specialist of African origin, that has been expanding its range southward from southern United States, partly as a result of conversion of large extensions of rain forest to pastures (Montes de Oca and Halffter 1995).

Non-flying mammal richness

Detection rates of medium size mammals in the mosaic habitat were as high as those found in the continuous forests and in the forest fragments, suggesting a relationship between dung beetle relative abundance and the presence of dung-producing mammals in this habitat. The presence of dung-producing mammals may constitute an important contribution to dung beetle relative abundance and diversity in the habitats investigated (Cambefort and Walter 1991; Hanski 1991; Estrada et al. 1999). The forest vegetation in the mosaic habitat harboured medium size diurnal mammals such as the howler monkey (*Alouatta palliata*) and coati (*Nasua narica*), and nocturnal species such as the kinkajou (*Potos flavus)*, the ringtailed cat (*Bassariscus sumichrasti*) and several opossums (e.g. *Didelphis marsupialis*, *Philander opossum*, *Caluromys derbianus*), among others (Estrada et al. 1994). These mammals display different degrees of arboreality and feeding habits, adding opportunities for the coexistence of various dung beetle species.

The low number of howler monkeys detected in the forest fragments was consistent with the poorness of dung beetle individuals captured in these sites. In contrast, in the continuous forest and in the mosaic habitat the higher number of dung beetles captured corresponded with a higher number of howler monkeys found in these habitats than in the forest fragments. About 16 species of dung beetles have been documented to display an affinity for howler monkey dung (Estrada et al. 1993), and other studies have reported an important relationship between howler monkey absence in forest fragments and the poorness of dung beetles (Estrada et al. 1999). The existence in the mosaic habitat of a rich assemblage of mammals and of rain forest vegetation with fruiting trees of Moraceae (e.g. *Ficus* spp., *Brosimum alicastrum*, *Pseudolmedia oxyphyllaria*), Lauraceae (e.g. *Nectandra ambigens*, *Ocotea* spp.), Anacardiaceae (e.g. *Spondias mombin*), and Sapotaceae (*Pouteria zapota*) plant families, among others, results in dung and mature and rotting fruit availability for dung beetles, features that may explain the richness of dung beetles in these habitats.

General implications

Our study is limited because of the use of pitfall traps, the few sites sampled and the few points in time sampled. The efficacy of baited pitfall traps relies on the attractiveness of the baits used and not all dung beetle species respond to such bait (Davis and Sutton 1997; Davis et al. 2001). For example, we did not capture about 17 additional species reported to exist in the area (Moron and Blackaller 1997).

These species may be rare, restricted to other altitudes or habitats or to the forest interior, or may not be attracted to the bait we used. The use of flight intercept traps and light traps may be necessary to ensure a more complete sampling of the dung beetle assemblages in the habitats studied (Hill 1996).

With the above limitations in mind, we may take the present study as a diagnostic survey of how land management practices are affecting the conservation of dung beetle species assemblages. Our study suggests that conservation planning of isolated forest fragments in pasture-dominated landscapes is incomplete, unless we also assess the conservation value of other types of human-introduced vegetation present in Neotropical landscapes. Some of these may be valuable in reducing isolating distances among forest fragments and between these and continuous forest or may provide habitat not only for common generalist dung beetle species, but also for those species that are moderately common (e.g. *U. bonetti*, *D. gibbosum*) or rare (e.g. *O. nasiricornis*) or that may display a tendency to prefer the dung of particular mammal species such as howler monkeys (e.g. *Canthi. centrale*, *Canth. femoralis*, *Co. laeviceps*, *De. Pseudoparile*; Estrada et al. 1993). Consistent with this idea, our study showed the presence of a high number of dung beetles and a rich species assemblage in the mosaic habitat. It also showed that species of the roller, burrower, diurnal and nocturnal guilds were present in this habitat.

The data presented suggest that the preservation of landscapes containing clusters of forest fragments is incomplete unless we consider the conservation value of other vegetation types present in such landscapes [see Davis et al. (2001) for an example in Borneo]. These vegetation types may also provide dung beetles with increased area of vegetation, increased diversity of resources and habitats available and reduction of isolating distances among habitat islands. The close proximity of these habitats to forest fragments and to continuous forest may support ecological sustainability (*sensu* Recher et al. 1987) by providing increased opportunities for dung beetle persistence, reduced isolation, and facilitation of contact among conspecifics.

Scenarios such as the above would help sustain common, rare, generalist and specialist dung beetle species, increasing the number of species preserved. Economic dividends resulting from the marketing of cash crops obtained from mosaic-type habitats may help strengthen the subsistence economy of local inhabitants (Gleissman et al. 1981; Morowitz 1991; Ricker et al. 1999). Other added benefits derived from the presence of mosaic-type habitats and the conservation of forest fragments may be soil, nutrient and water retention, as well as sources of wood, firewood and of medicinal, ornamental and edible plants (Myers 1988; Orr 1991). Such benefits may outweigh the benefits obtained from turning fragmented landscapes into pasturelands (Beier and Noss 1988; Saunders and De Rebeira 1991; Pimentel et al. 1992; Lindemayer and Nix 1993; Turner and Corlett 1996). Further important consequences for forest conservation resulting from preservation of remaining dung beetle assemblages would be continued soil aeration and removal through their burrowing activities, rapid dispersal and burying of animal dung, control of parasitic flies and secondary dispersal of seeds of rain forest plants that are sources of fruit to fruit-eating mammals (Halffter and Mathews 1966; Nealis 1977; Estrada and Coates-Estrada 1991).

Acknowledgements

We are grateful to the Cleveland Zoo Scott Neotropic Fund for their encouragement and support. Universidad Nacional Autónoma de México provided logistical aid.

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