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Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico

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ABSTRACT. At Los Tuxtlas, Mexico, presence of dung and carrion beetles, were sampled using baited pitfall traps, at the following habitats: isolated forest fragments, forest edges, plantations (coffee, cacao, mixed, citrus and allspice), live fences and pastures. A total of 14,269 beetles representing 36 species were captured. *Onthophagus batesi*, *Canthon femoralis*, *Canthidium centrale*, *Copris laeviceps*, *O. rhinolophus* and *Deltochilium pseudoparile* accounted for 75% of the captures in the overall sample from 79 sites. Across forest fragments capture rates of species and individuals were associated positively to area and negatively to isolating distance. Rarefaction analysis showed that forest fragments were the most species-rich habitats followed by the mixed and cacao plantations, the forest edge, live fences and coffee, citrus and allspice plantations. Pastures were the least species-rich habitat. Horizontal and vertical diversity of the vegetation at the habitats studied influenced the species richness of dung and carrion beetles and the number of species in common between forest fragments and human-made habitats. A significant relationship existed between the number of non-flying mammals recorded at the study sites and the richness of species and individuals of dung beetles at the habitats investigated. The relevance of this information is discussed in the light of the ecological flexibility of dung and carrion beetle species and of possible conservation scenarios involving landscapes in which isolation of forest fragments is reduced by the presence in open areas of human-made vegetation such as plantations of cacao, coffee, cacao and coffee and live fences.

KEY WORDS: conservation, dung beetles, forest fragmentation, Los Tuxtlas, Mexico, Scarabaeidae, tropical rain forest

INTRODUCTION

Dung and carrion beetles are a conspicuous component of the diversity of insects in Neotropical rain forests (Gill 1991, Halffter & Matthews 1966;

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Hanski 1983, 1989; Howden & Nealis 1975, 1978; Howden & Young 1981). Depending on the locality 28 to 60 species may be represented (Hanski & Cambefort 1991, Klein 1989) and as many as 2000 beetles per ha may be found in forested areas (Peck & Forsyth 1982). Beetles use the dung produced by forest vertebrates, particularly herbivorous mammals such as primates, and occasionally that of birds and reptiles (Howden & Young 1981, Young 1981), as food and as a substrate for oviposition and further feeding by their larvae (Gill 1991, Halffter & Edmonds 1982, Hanski 1989). Carrion as well as decaying fruit and fungi are also used as sources of food (Halffter & Matthews 1966, Hanski 1989). 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 & Edmonds 1982, Hanski 1991). Resource partitioning, such as preference for soil and cover (Lumaret 1978, Nealis 1977), diel flight time and dung size (Peck & Howden 1984), perching heights (Howden & Nealis 1978) and dung removal methods (Halffter & Matthews 1966) have been suggested to diminish competition among members of the guild. Since the general abundance of mammals sets the level of resource availability to dung beetles (Hanski & Cambefort 1991) and non-flying mammals are strongly sensitive to forest loss, fragmentation and isolation (Estrada *et al.* 1994, Lovejoy *et al.* 1986) this may make dung beetles sensitive to deforestation (Klein 1989).

Dung beetles are ecologically important in the neotropical habitats in which they occur. By burying the dung and carrion as food for their offspring they may increase the rate of soil nutrient cycling (Bornemissa & Williams 1970, Halffter & Mathews 1966, Nealis 1977), they exert an important control over the egg and larvae 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 many tree species in neotropical forests thus participating in the natural process of forest regeneration (Estrada & Coates-Estrada 1991). Recently dung beetles have been suggested to be good indicators for measuring biodiversity in the tropics (Halffter & Favila 1993).

In spite of the ecological importance of dung beetles and of the important numerical contribution of populations of these insects to the richness of the insect community 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) and in Central and South America (Howden & Nealis 1975, Klein 1989, Peck & Forsyth 1982). These studies report important negative effects such as fewer species and sparser populations as a result of clear cutting and that isolated forest fragments are important barriers for movement and dispersal (Klein 1989).

In the mountain region of Los Tuxtlas, in southern Veracruz, Mexico, lowland tropical rain forests reach their northernmost distribution in the American continent and are notable for their high biological diversity (Estrada *et al.*

1985). About 50 species of dung beetles have been reported to exist in the region and constitute an important component of the biological richness of these forests (Halffter *et al*. 1992, Moron & Blackaller 1997). Currently, the remaining rain forests consist of collections of forest fragments of various sizes and with different histories of isolation that are found scattered throughout the region (Estrada & Coates-Estrada 1996).

At Los Tuxtlas, agricultural activities occur sporadically in time and space in a sea of pasture and occupy only *c*. 3% of the land. These human-made islands of vegetation consist of cultivation of arboreal crops such as citrus (*Citrus sinensis*, Rutaceae), allspice (*Pimienta dioica*, Myrtaceae) and cacao (*Theobroma cacao*, Sterculiaceae). Farmers also cultivate coffee (*Coffea arabica*, Rubiaceae) as a single crop. Less common is the cultivation of plots of mixed crops that include coffee and cacao. Rain forest trees left by farmers provide shade in the case of cacao, coffee and mixed plantations.

It is a common practice among farmers and ranchers of Los Tuxtlas to use live posts of *Bursera simaruba* (Burseraceae) and *Gliricidia sepium* (Leguminosae) to hold barbed wire fences to delimit boundaries of properties and to divide the pasture land into smaller plots for cattle rotation. Because these posts grow rapidly in height and trunk diameter and produce moderately foliated crowns, single mature rows of these live fences resemble corridors of vegetation criss-crossing the pasture lands.

Thus, at Los Tuxtlas, as in many parts of the Neotropics, a landscape mosaic includes different kinds of human-made systems with various levels of occupation and maintenance, interdigitated with rain forest fragments of various sizes, shapes and degrees of disturbance and isolation. The edges of the remaining forest fragments are an important component of the morphology of these habitat islands and represent an abrupt transition between rain forest vegetation and human-made pastures.

We present information in this paper on dung beetle presence at Los Tuxtlas, Veracruz, Mexico in pasture habitats, isolated forest fragments, human-made forest edges and at human-introduced vegetation represented by live fences, and five types of agricultural crops: citrus, allspice, coffee, cacao and mixed plantations (coffee and cacao). We also provide information derived from surveys of non-flying mammals at these habitats (Estrada *et al*. 1994) to assess the effects of variation in richness of species and individuals among species of this community on dung beetle richness at the habitats investigated. We hope to enrich our understanding of the ecological plasticity of dung beetles to transformation of the landscape by humans and to assess what kind of landscape mosaics might provide maximum diversity and minimum species loss.

METHODS

At Los Tuxtlas (95°00′W, 18°25′N) in southern Veracruz, Mexico, lowland tropical rain forest vegetation is present in the form of archipelagos of forest fragments that vary in size, years of isolation and isolating distance (Estrada &

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Coates-Estrada 1996). Mean annual rainfall is 4900 mm with a drier season (mean = 111.7; SD ± 11.7 mm mo^{-1}) from March to May and a wetter season (mean = 486.25; SD ± 87.0 mm mo^{-1}) from June to February and mean annual temperature is 27 °C; elevation ranges from sea level to 1600 m above sea level (Estrada *et al*. 1985).

Sampling of dung beetles

We sampled dung beetles with baited pitfall traps between April and September in 1996 and again in 1997 in 55 forest fragments and in 24 human-made habitats located in the north eastern area of the region. Forest sites ranged in elevation from sea level to *c*. 1200 m, but 80% were located at 800 m above sea level. The forest fragments studied varied in isolating distance (distance to edge of nearest forest fragment) from 0.5 to 1.0 km and in area (obtained by digitizing aerial photograph and by corroboration in the field) from 1 to *c*. 400 ha. For each forest fragment we estimated years since isolation (isolation being complete separation of forest from a major forested area) by examining vegetation maps for the period before 1967, aerial photographs taken in 1967 and 1979, satellite images taken in 1986, 1990 and 1993 and complemented this with information gathered through interviews with ranchers and farmers owning the land. Years since isolation ranged from 5 to 35 y.

The human-made forest edge sites consisted of *c*. 1000 m long edge in which the forest bordered the pasture at three forest sites >200 ha in size and located at *c*. 2 km from each other. We sampled three replicates of each of the agricultural habitats investigated (cacao, coffee, mixed, citrus and allspice plantations) which ranged in size from 2–10 ha and in age from 12–15 y. All of these habitats were fruit productive and isolated from other similar habitats and from forest habitats. Distance from these habitats to the nearest forest fragment, regardless of size, ranged from 200 to 2000 m; distance to the nearest plantation ranged from 200 to 1000 m. Elevation of these sites ranged from sea level to 300 m.

The three live fence sites, each 2 km long, were located across the pasture land and in the vicinity of the forest and agricultural habitats studied; each of these sites was at least 5 km away from the others. The three pasture habitats (grasses about 15–30 cm in height; 15 ha in size each) were totally devoid of the original forest vegetation and of other vegetation introduced by man, and at least 5 km apart from each other, but within a 5-km radius of the forest sites that we studied. We located the sampling area in the centre of each pasture plot.

To sample dung beetles we used baited pitfall traps (similar to those described in Howden & Nealis 1975) 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 cow, horse and dog dung. This bait grossly mimicked the excreta produced by mammalian herbivores and omnivores in the forest (Estrada *et al*. 1993a). In the interior of each site investigated we placed 50 pitfall traps at 10–15 m intervals. At the live fence sites, pitfall traps were placed at the same distance intervals under the shade of the row of trees constituting the live fence. Both at the pasture and human made forest edge sites, pitfall traps were placed at the same intervals along a sinuous route in the case of the former habitat, starting at least 100 m away from the forest edge, while at the latter habitat pitfall traps were placed following the contour of the edge of the forest.

Pitfall traps were baited at 18 h and retrieved 24 h later at all sites investigated. 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 through comparison with a reference collection at the biological research station Los Tuxtlas and released the next morning at the capture site. We carried out 80% of the sampling between April and September when dung beetle populations have been documented to be at their peaks in the study areas (Estrada *et al*. 1993a).

Sampling of non-flying mammals

We conducted census of non-flying mammals at each site during 2 d. We used existing trails or trails demarcated by us with a cotton thread (see Estrada *et al*. 1994). These trails were walked at a slow pace (*c*. 2 km h^{-1}) and both sides of trail were scanned visually. Census routes were chosen to minimise trail overlap within and between days and nights and thus the probability of viewing the same individual more than once. The census trails were at least 10 m from the edge of the vegetation patch under investigation. We recorded the number of individuals of each species detected. We conducted the censuses between 06h00 and 12h00 and between 16h00 and 18h00 and between 19h00 and 24h00. We used at night, in addition to flash lights, a night vision scope (Javelin Electronics, model 221) to minimise disturbance to detected animals in the nocturnal censuses. Complementary sampling using baited Sherman and Tomahawk traps was employed to sample small terrestrial rodents (200 g) and medium sized mammal species which are cryptic in their behaviour and difficult to detect by visual means. All mammals captured were released after species identification and marking (see Estrada *et al*. 1994 for details). Results of these censuses were compared to results on dung beetle trapping for the same sites and habitats.

Measures of vegetation

The vegetation at each site was censused by recording all trees ≥ 10 cm in circumference at breast height and at least 1.5 m in height in six 10-m × 10-m plots. Plots were located randomly within the area where beetles were sampled; the plots were at least 30–40 m from each other. For each tree, we recorded the species, maximum height and circumference. Vertical foliage density was measured at four randomly selected spots within each of the six plots by scoring vegetation intercepts along a vertical pole at the following intervals: 0–0.5, 0.51–1.0, 1.1–2, 2.1–3, 3.1–5, 5.1–8, 8.1–10, 10.1–15, >15 m (Schemske & Brokaw 1981). Intercepts at each height interval were expressed as the proportion of total intercepts recorded per site in each habitat and foliage vertical diversity was calculated using the Shannon-Wiener information index (H′) (Ludwig & Reynolds 1988). The same index was used to express horizontal tree diversity per habitat. Agricultural vegetation was divided into shaded (cacao, coffee and mixed crops) and not shaded (citrus and allspice) for some descriptions and comparisons.

Statistical treatment of data

We compared dung beetle individual and species captures across vegetation types using average (±SE) number of individuals and species captured per site in each habitat and used rarefaction to compare species richness among habitats where sample sizes differed (James & Rathburn 1981). We used Spearman's and Pearson's correlation coefficients and partial correlation analysis; and the Wilcoxon-test when contrasting groups of data (Fitch 1992, Ludwig & Reynolds 1988).

RESULTS

General aspects

Our sampling effort at the habitats investigated resulted in the capture of 14,269 dung beetles representing 36 species (Table 1). In the case of the forest fragments, 50% of the species were captured in the first 100 ha sampled and the total sample of 30 species were recorded at *c.* 300 ha (Figure 1). Further sampling of forest sites failed to detect more new species and only an additional six species were recorded when the agricultural habitats were sampled (Table 2).

Average number of individuals captured per site per species ranged from 0.007 (Sp. 1) to 49.6 (*Onthophagus batesi*) (Table 2). Six species (*Onthophagus batesi*, *Canthon femoralis*, *Canthidium centrale*, *Copris laeviceps*, *Onthophagus rhinolophus*, *Deltochilium pseudoparile*) accounted for 75% of the captures and had the highest average captures per site (>10.0 individuals per site) (Figure 2, Table 2). One introduced species of Indo-african origin, *Digitonthophagus gazella*, was also captured at four habitats, but had its highest mean captures per site at the pasture habitat (Table 2).

Forest sites

We captured 10,060 dung beetles representing 30 species at the 55 forest fragments. Average number of species captured per site at these habitats was 9.4 ± 0.6 and of individuals 127.4 ± 17.7 (Table 1). Three species, *Canthon femoralis*, *Copris laeviceps* and *Canthidium centrale*, accounted for 50% of individuals captured. Another 30% of the captures were contributed by *Deltochilum pseudoparile*, *Onthophagus rhinolophus*, *Canthon viridis vazquezae*, *Onthophagis batesi*

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Table 1. Number of dung and carrion beetle species and individuals captured at the study habitats. Sampling effort at each site consisted of 50 baited pitfall traps for a 24-h period. Also shown for each habitat are the number of non-flying mammal species and individuals recorded and diversity measures for the vegetation.

				Mean number of				Non-flying mammals		Vegetation H′	
Habitat	Number of sites	Species	N	Species per site	± SE	Individuals per site	± SE	Species	Individuals	Horizontal	Vertical
Forest	55	30	10 060	9.4	0.6	127.4	17.7	38	1518	5.5	1.5
Forest edge	3	14	864	13.0	0.5	96.0	18.3				
Cacao	3	21	1 309	10.6	3.6	145.4	127.1	16	144	3.5	1.2
Coffee	3	10	83	9.7	2.9	27.7	11.3	13	106	2.4	1.2
Mixed	3	21	428	12.3	1.7	107.0	40.2	13	145	3.8	1.3
Citrus	3	13	345	5.0	0.6	40.0	12.4	8	38	1.6	0.5
Allspice	3	11	84	8.3	2.3	28.0	4.4	7	42	1.6	0.6
Live fence	3	14	367	7.5	1.0	91.8	29.6	11	83	2.5	0.6
Pasture	3	9	729	4.8	0.5	81.0	31.7	4	93	0.29	0.09
Total	79	36	14 269								

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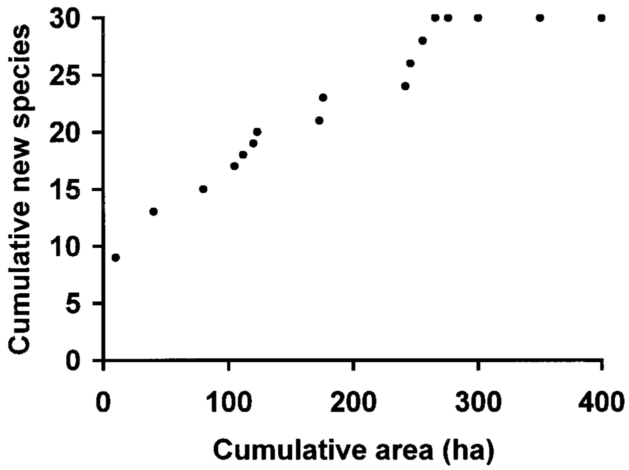

Figure 1. Cumulative number of dung beetles species detected and cumulative area of forest fragments sampled.

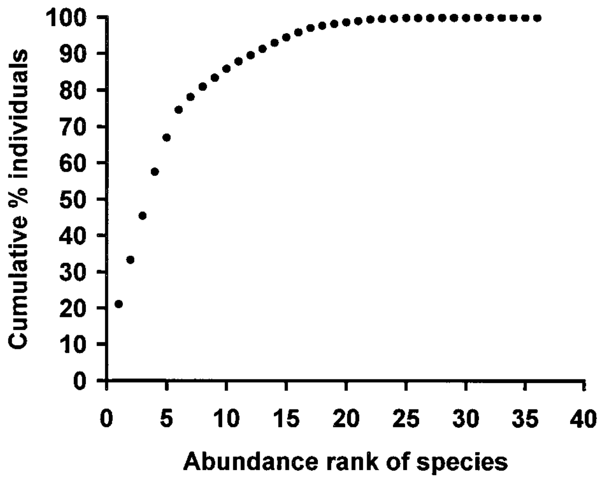

Figure 2. Dominance diversity curve for the dung and carrion beetles recorded. Note the relatively high dominance of first six species. (Species identities are given in Table 2).

and *Dichotomius satanas*. The rest of the species (73%) accounted for the rest of the individuals captured (20%) at these sites (Table 2). Both area and isolating distance of forest fragment were significantly correlated (df = 53 in all cases) with mean captures of dung beetle species (area $r_s = 0.74$, $P < 0.001$; isolating distance $r_s = -0.57$, $P < 0.001$) and individuals (area $r_s = 0.67$, $P < 0.001$; isolating distance $r_s = -0.50$, $P < 0.001$) per site. Partial correlation analysis showed, however, that average captures were better correlated with isolating distance (species $r = -0.57$, $P < 0.001$; individuals $r = -0.40$, $P < 0.001$) than with area (species $r = 0.38$, $P < 0.01$; individuals $r = 0.29$, $P < 0.05$) of forest sites.

Table 2. Mean numbers of captures per site for each species (55 forest sites and three sites for each of the other habitats) of dung and carrion beetle species captured at forest fragments and at human-made habitats studied. Also shown are the overall average number of individuals captured per species, the number of habitats in which a species was present and the percent of total individuals captured represented by each species in the total sample. Species are ranked by overall mean captures.

Species	Forest	Forest edge	Cacao	Coffee	Mixed	Citrus	All-spice	Live fence	Pasture	Overall mean	No. of habitats	%
Onthophagus bates Howden & Cartwright	7.7	42.0	24.3	3.7	25.3	73.7	11.0	86.3	172.7	49.6	9	12.2
Canthon femoralis Chevrolat	43.5	120.0	70.0	0.7	9.0			2.3		40.9	6	21.0
Canthidium centrale Boucomont	21.9	36.0	104.7	7.3	17.7	0.7	3.3	2.3		24.2	8	12.0
Copris laeviceps Harold	23.6	31.0	85.7	8.0	15.3	2.0	1.0	6.7		21.7	8	12.3
Onthophagus rhinolophus Harold	13.9	2.0	58.7	1.7	46.3		0.3	1.0		17.7	7	7.7
Detochilium pseudoparile Paglian	20.9	22.0	36.3	3.0	2.0					16.8	5	9.4
Canthon (G.) viridis vazquezae Martinez, Halffter & Halffter	4.5		0.3		4.7	6.0		24.3		8.0	5	2.5
Canthon (C.) eurycelis Bates			1.0		1.0	0.7	0.3		26.7	5.9	5	0.6
Phanaeus endymion Harold	4.2	14.0	8.0	1.7	2.3	1.0	1.0	12.7		5.6	8	2.5
Canthon cyanellus cyaneilus Harold	3.5		15.3	0.7	4.0	0.3	9.0			5.5	6	2.0
Copris lugubris Bohemen	2.9	1.0				20.3	0.7	3.3	4.0	5.4	6	1.7
Dichotomius satanas Harold	6.4	8.0	3.3		2.7					5.1	4	2.8
Digitonthophagus gazella Fabricius	0.1				6.0			1.0	11.0	4.5	4	0.4
Canthon (C.) morsei Harold	8.4		7.7		3.0	0.3	0.7	0.7		3.5	6	3.5
Uroxys boneti Pereira & Halmer	4.1		4.0		0.7					2.9	3	1.7
Eurysternus mexicanus Harold	3.0		5.3	0.7	5.3	0.3		2.0		2.8	6	1.5
Coprophanaeus telamon corythus Harold	2.0	3.0	2.7		0.3	2.0		3.0	3.0	2.4	7	1.4
Deltochilium gibbosum sublaeve Bates	2.8	2.0	6.0	0.3	0.7					2.4	5	1.3
Dichotomius carolinus colonicus Say	4.2		0.7		0.3	1.7	0.3	0.3	0.7	1.2	7	1.7
Canthon (GI.) subhyalinus Harold	0.7	3.0	0.3		0.3					1.1	4	0.4
Onthophagus landolti Harold		1.0								1.0	1	0.02
Coprophanaeus sp.		1.0								1.0	1	0.02
Sulcophanaeus chryseicollis Harold	1.0	2.0	0.3		0.7			0.3		0.9	5	0.4
Eurysternus caribaeus Herbst	1.2		1.0				0.3			0.8	3	0.5
Eurysternus angustulatus Harold	0.5		0.7					0.3		0.5	3	0.2
Onthophagus nasicornis Harold	0.3				0.7					0.5	2	0.1
Anaides laticollis Harold					0.3					0.3	1	0.007
Phanaeus sallei Harold									0.3	0.3	1	0.007
Sp. 1									0.3	0.3	1	0.007
Canthidium sp.	0.3									0.3	1	0.1
Canthon (C.) indagaceus chiapas Robinson	0.1									0.1	1	0.04
Ateuchus illaesum Harold	0.1									0.1	1	0.03
Onthophagus crinitus Harold	0.1									0.1	1	0.03
Bdelyropsis newtoni Howden	0.1									0.1	1	0.02
Uroxys sp.	0.04									0.04	0.01	
Sp. 2	0.02									0.02	1	0.007
Total	10 060	864	1309	83	428	345	84	367	729	14 269		
Species	30	15	21	10	21	13	11	14	8	36		

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Human-made forest edge

At the three human-made forest edge sites, we captured 864 dung beetles of 15 species. Average number of species captured per site at this habitat were 13.0 and individuals 96.0 (Table 1). Four species (*Canthon femoralis*, *Onthophagus batesi, Canthidium centrale* and *Copris laeviceps)* accounted for 80% of the records and mean number of captures per species per site ranged from 1.0 (e.g., *Onthophagus landolti*) to 120.0 (*Canthon femoralis*) (Table 2).

Agricultural habitats

Pitfall traps at the 15 agricultural habitats investigated (pastures not included) yielded 2249 dung beetles of 25 species. Average number of species captured per site per habitat ranged from 5.0 (citrus) to 12.3 (mixed plantation) and individuals from 27.7 (coffee) to 145.4 (cacao) (Table 1). At these habitats, five species (*Canthidium centrale, Onthophagus batesi, Copris laeviceps, Canthon femoralis, Onthophagus rhinolophus* and *Deltochilum pseudoparile*) accounted for 76% of the records and also had the highest records for mean number of individuals captured per site (Table 2). At the shaded plantations (cacao, coffee and mixed) we captured 1820 beetles representing 23 species and average number of species captured per site was 10.9 and individuals 113.8. In the non-shaded plantations (citrus and allspice) 439 beetles were captured representing 13 species and average number of species captured per site was 6.1 and individuals 36.0. Shaded plantations differed significantly from non-shaded ones in having higher numbers of dung beetles captured per site ($z = 2.3$, $P = 0.02$). In the shaded plantations *Canthidium centrale*, *Onthophagus rhinolophus*, *Copris laeviceps* and *Canthon femoralis* contributed 70% of the captures and had the highest average captures at these habitats (Table 2). In contrast, in the non-shaded plantations *Onthophagus batesi* contributed 59% of the captures, followed by *Copris lugubris* with 18% and *Digitonthophagus gazella* and *Canthon* (G.) *viridis vazquezae* with 6% each. These species had the highest average captures per site at these habitats (Table 2).

Live fences

At the three live fence habitats we captured 367 beetles representing 14 species. Average number of species captured per site was 7.5 and individuals 91.8 (Table 1). One species, *Onthophagus batesi* accounted for 71% of the records and had the highest average capture of individuals (83 per site) at these habitats followed by *Phanaeus endymion* with 12.7 individuals per site (Table 2).

Pastures

Sampling of dung beetles at the three pasture sites yielded 729 individuals of nine species. Average captures of species per site was 4.8 and individuals 81.0 (Table 1). At these habitats *Onthophagus batesi* accounted for 71% of the individuals and had the highest mean capture of individuals per site followed by *Canthon eurycelis* and *Canthon* (G.) *viridis vazquezae* (Table 2).

Forest fragments and human-made habitats

While dung beetles were detected at all habitats examined, species varied in the number of habitats in which they were present. The number of habitats occupied by a single species ranged from one (e.g., *Onthophagus crinitus*) to nine (*Onthophagus batesi*) (average 4.0). Three other species *Canthidium centrale, Copris laeviceps* and *Phanaeus endymion* were present at eight and *Onthophagus rhinolophus* at seven habitats. The rest of the species were present in fewer habitats (Table 2). The number of habitats in which a species was present was correlated with the mean number of individuals captured per site per species ($r_s = 0.88$, $df = 36$, $P < 0.001$). Seven species, with the lowest captures, were recorded only in forest fragments and six species were captured only at the human-made habitats (Table 2).

Rarefaction analysis indicated that at N = 500 the richest habitats in dung beetle species were the forests fragments followed by the shaded plantations (cacao, coffee and mixed). The poorest habitats were pastures. The human-made forest edge occupied an intermediate position relative to pastures and to forest fragments, while live fences and unshaded plantations (citrus and allspice) were intermediate between pastures and the human-made forest edge (Figure 3).

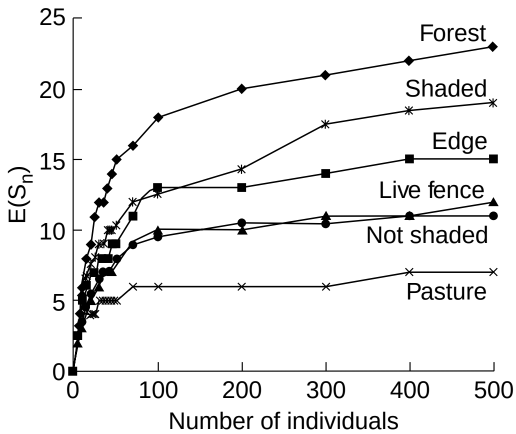

Figure 3. Rarefaction curves for all habitats examined. $E(S_n)$ is the expected number of species in a random sample of size n where S is the sum of the probabilities that each species will be included in the sample. Comparisons can be made of the expected number of species at different sample sizes. Comparison made at N = 500.

At the habitats investigated horizontal and vertical diversity of the vegetation were strongly correlated ($r_s = 0.91$, $df = 8$, $P = 0.0001$). The forest fragments and the cacao, mixed and coffee plantations attained the highest and pastures the lowest H′ values for both measures of the vegetation (Table 1). Both horizontal and vertical plant diversity (H′) were correlated with mean number of species of dung beetles captured per site for each habitat (horizontal H′ $r_s = 0.74$, $df = 8$, $P = 0.01$; vertical H′ $r_s = 0.82$, $df = 8$, $P < 0.01$).

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Partial correlation showed that the number of dung beetle species in common between forest sites and agricultural habitats including live fences were correlated with both horizontal ($r = 0.74$, $P = 0.02$) and vertical diversity ($r = 0.71$, $P = 0.03$) of the vegetation at these habitats.

We discovered a significant positive relationship between the average number of dung beetle species and individuals recorded per site ($df = 8$ in each case) for each habitat and the number of non-flying mammal species detected at the habitats investigated (species $r_s = 0.74$, $P = 0.01$; individuals $r_s = 0.69$, $P = 0.02$) (Table 1). A similar relationship existed with number of non-flying mammals recorded at each of these habitats (species $r_s = 0.61$, $P = 0.05$; individuals $r_s = 0.64$, $P = 0.04$).

DISCUSSION

Our study showed the existence of a rich pool of forest dung beetles species still existing in the fragmented landscape at Los Tuxtlas, but the majority of the species were present in low numbers. Forest habitats were the richest and pastures the poorest habitats in dung beetle species (19% of those recorded in the forest fragments) compared to the other habitats investigated suggesting that conversion of forest to pastures results in significant decrements of dung and carrion beetle species (Howden & Nealis 1975, Klein 1989, Montes de Oca & Halffter 1995). Forest habitats and the cacao and mixed plantations surpassed pastures in mean captures of species and individuals per site, attesting to the value of forest fragments and the above plantations for sustaining dung beetle species and numbers.

Species such as *Onthophagus batesi* had the highest mean captures of individuals per site in the overall sample and it was predominantly present at the non-forest habitats, especially at the pasture sites. In contrast, *Canthon femoralis*, *Copris laeviceps* and *Deltochilum pseudoparile* had the highest mean captures at the forest fragments. Our sampling at the edge of the forest indicated the absence of 57% of the dung and carrion beetle species detected in the interior of the forest fragments, suggesting that the abrupt transition of forest to pastures coupled to a high exposure to wind and solar radiation may result in temperature and humidity conditions not suitable for all dung and carrion beetle species subsistence (Gill 1991, Hanski 1989).

Area and particularly isolating distance were important variables influencing dung beetle species richness in the forest fragments. Smaller distances between patches of native vegetation seem to favour richer assemblages of species, probably the result of greater dispersal by dung beetle. Small areas and large isolating distances of forest fragments coincide with poor mammal species assemblages and numbers (Estrada *et al.* 1994) and species of dung beetles may also be sensitive to these effects.

Although, the use of all habitats examined seemingly applied only to a few of the species detected,(e.g., *Onthophagus batesi*, *Copris laeviceps*, *Canthidium centrale*, and *Phanaeus endymion)*, 77% of the species were present in at least one habitat other than forest, suggesting the existence of variable plasticity among dung beetle species. Hence, in the landscape investigated at Los Tuxtlas, we have dung beetle species that can occupy a large variety of human-made habitats (e.g. *Onthophagis batesi*, *Phanaeus endymion*, *Copris laeviceps*) and species that were predominant at forest fragments (e.g. *Canthon femoralis*, *Canthidium centrale*) were also common at those human-made habitats that grossly resembled the forest because of the shade provided by rain forest trees. These species, however, were less common at more open plantations such as citrus and allspice and were not recorded at the pasture habitat. Inversely, species that were common at pastures (e.g. *Onthophagus batesi*, *Canthon eurycelis*) were poorly represented in the forest fragments. Other species recorded at forest fragments may display less flexibility and may thus exist in a truly fragmented landscape (e.g., *Uroxys* sp., *Onthophagus crinitus*).

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 transverse by these beetles in 2 d in other tropical localities (Peck & 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 also make use of the human-made islands of vegetation available 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). However, extremes in isolating distance may impose limits on the accessibility of these opportunities for dung beetles.

Thus, it is possible that the use by dung beetles of small forest patches, agricultural islands and live fences as stepping stones may reduce isolation and ease crowding effects resulting from forest loss and fragmentation. In this scenario, some species (e.g., *Onthophagus batesi*, *Copris 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. *Canthon femoralis)* may be restricted to movement and dispersal in their original habitat (e.g. rain forest) and may depend more closely on resources produced by arboreal mammalian herbivores such as howler monkeys (Halffter *et al*. 1992).

The greater diversity of the vegetation along vertical and horizontal dimensions at the shaded plantations resulting from the combination of the cultivated plants and the rain forest trees left by farmers to provide shade for the cacao and coffee plants, may provide suitable perching sites important for locating food odours and cover from predators such as staphylinid beetles, spiders and even bats for dung beetles (Gill 1991). Moreover, these shaded human-made habitats possess temperature and humidity conditions similar to that of the forest interior favourable for dung beetle presence and activity (Moron 1987). The complexity of the vegetation along vertical and horizontal dimensions possibly allows more dung beetle species to co-occur at these plantations than at the citrus and allspice habitats which lack such shade. The wide inter-row space and the sparse vegetation at these latter habitats may explain also the low number of species and individuals captured at these sites. Only species such as *Onthophagus batesi*, *Canthon cyanellus* and *Canthon lugubris* predominated at these more open habitats, These species have been reported to have generalist feeding habits and seem to prefer the forest edge and open areas (Halffter *et al*. 1992, Montes de Oca & Halffter, 1995).

The presence of arboreal agricultural habitats and live fences in the landscape may compensate in part not only the loss of area of rain forest vegetation for dung beetles, but also the lost heterogeneity of the landscape when the forest was converted to pasture. This situation may allow remaining mobile forest dung beetles species that differ in ecological requirements to persist longer in time and space than if such heterogeneous collection of human-made habitats were not existing (Estrada *et al*.1994, Johns 1991). Changes in land management practices in which pastures replace arboreal crops as a result of changes in commercial demands may have, like disappearance of the forest, important consequences for dung beetle sustenance in the wet tropics, including the replacement of a rich assemblage of native species by introduced species such as *Digithonthophagus gazella*, a savanna specialist, that has been expanding its range southward from the United States in part as a result of conversion of large extension of rain forest to pastures (Montes de Oca & Halffter 1995).

At Los Tuxtlas, the conservation value for dung beetles of arboreal agricultural islands as stepping stones could be enhanced by the presence of live fences. Our study showed that these habitats were inhabited by a significant number (47%) of dung beetles species detected in the total forest sample. In contrast to the rectangular or square shape of agricultural habitats, the hundreds or thousands of linear metres of vegetation in the form of live fences across the landscape are available to dung beetles inhabiting the many forest fragments in the region. Some of these live fences end at the edge of forest patches or interconnect with the forest vegetation remaining along streams and rivers, thus enhancing biotic connectivity in the area (Estrada & Coates-Estrada 1996).

The trees forming the live fences not only provide perching sites and cover for dung beetles, but also constitute a rich set of macro- and micro-habitats in which not only these insects become established, but also small and medium sized mammals, birds and reptiles may temporarily reside in them (Estrada *et al*. 1993b, 1994). In those live fences where the vegetation has been allowed to regenerate under the trees, the presence of high concentrations of plant species of the genera *Piper* (Piperaceae) *Solanum* (Solanaceae), *Cecropia*

(Moraceae), *Siparuna* (Mominaceae), *Eugenia* (Myrtaceae), *Psychotria* (Rubiaceae) and occasional strangler figs (*Ficus* spp) suggests the occurrence of food resources for dung beetles that complement their diet with important amounts of mature and rotting fruit (Gill 1991, Hanski 1989).

Surely the presence of dung producing mammals was an important determinant of dung beetle richness at the habitats investigated (Cambefort & Walter 1991). Habitats such as cacao, coffee and mixed plantations were structurally more complex in the measures of vegetation than the pastures, a feature which allows the existence of medium sized diurnal mammals such as howler monkeys (*Alouatta palliata*), coati (*Nasua narica*) and nocturnal species such as the kinkajou (*Potos flavus)*, the ringtailed cat (*Bassariscus sumichrasti)*, the common gray four-eyed opossum (*Philander opossum)*, the central American woolly opossum (*Caluromys derbianus*) among others (Estrada *et al*. 1994). These mammals display different degrees of arboreality occupying various heights in the canopy of the plantations thus adding more opportunities for the coexistence of various dung beetle species. The existence of rain forest vegetation with fruiting trees of the 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*) among others, at the shaded plantations, means presence of mature and rotting fruit availability for dung beetles.

Clearly, we need long-term observations and basic ecological studies to assess the impact of land management practices on the survival of each of the various dung beetle species detected in our study. The limitation of our study is that we used a small number of traps per site and that it provides information only at one or two points in time on species presence. In addition, pitfall traps may not capture all species present at the sites investigated. For example, we did not capture the *c*. 14 additional species reported to exist in the area (Moron & Blackaller 1997). These species may be rare, may be restricted to other altitudes or habitats, 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 community (Hill 1996). While 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 & Sutton 1997), the objective of the present study was to sample those components of the dung beetle community displaying a general and specific attraction to feacal material produced by mammals (Estrada *et al*. 1994) that still exist in the landscape investigated, With the above limitations in mind, the present study when taken as a diagnostic survey of how land management practices are affecting the conservation of species, we can derive some guidelines to ascertain the value of modifying such practices.

Thus, our study suggests that in certain landscapes at Los Tuxtlas the presence of arboreal crops interdigitated in the landscape may help reduce physical and biotic isolation thus sustaining dung beetles populations and species present in the remaining forest fragments. A heterogeneous landscape matrix in which forest fragments and shaded and unshaded human-made arboreal habitats separated by short distances from one another and from live fences against a background of pastureland seems to be a more benign arrangement of the land for the spatial and temporal persistence of segments of the remaining rain forest dung beetle fauna than pasturelands alone. In this scenario, the study of the dynamics of sources and sinks (*sensu* Pulliam 1988) and their impact on the regulation of populations of remaining dung beetle species, might be an adequate step to take to further improve the precision of conservation models.

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