Response of Dung Beetle Diversity to Human-induced Changes in a Tropical Landscape[1]

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ABSTRACT

This paper examines dung beetle communities in remnant patches of tropical deciduous forest at Veracruz, Mexico, as a case study of the effects of tropical deforestation on biodiversity. The two study areas have a common biogeographic history and similar macroclimatic conditions and have been modified by human activities to different extents. The main difference between them is that cattle, which provide the dung beetle's food supply, are present in only one of the areas. Comparison of the dung beetle faunas sheds light on the relative importance of forest cover versus food supply as the principal factor determining the structure and diversity of the fauna. This comparison, which we broaden through an examination of data from other localities in central Veracruz, permits us to speculate about what happens to biodiversity when a tropical deciduous forest undergoes modification of varying type and intensity. Where tree cover has been most modified, native forest species undergo local extinction and are replaced by open area species. On the whole, there has not been a net reduction in species richness (gamma diversity) in the fragmented landscape of central Veracruz, although local species richness (alpha diversity) has diminished.

RESUMEN

En este trabajo se presenta una aproximación de lo que ocurre con la biodiversidad estudiada a través de un grupo indicador (los escarabajos del estiércol) en dos remanentes de bosque tropical caducifolio del estado de Veracruz, México. Los dos sitios comparten la misma historia biogeográfica, condiciones macroclimáticas semejantes, y ser bosques parcialmente modificados por la actividad humana. La diferencia principal está en la oferta de alimento para los Scarabaeinae, porque solamente en uno de los lugares hay ganado vacuno. La comparación de la fauna de Scarabaeinae de los dos lugares nos permite señalar que la cubierta forestal, y no la oferta de alimento, es el principal elemento conformador de la estructura y diversidad del gremio. Esta comparación, ampliada con datos de otros puntos de Veracruz centro nos permite especular lo que ocurre con la biodiversidad (representada por los Scarabaeinae) al modificarse el bosque tropical caducifolio en distintas formas e intensidades. Es relevante la sobrevivencia de las especies propias del bosque a nivel paisaje (diversidad gama), aunque puedan desaparecer en parte a escala puntual. Así como su reemplazo por especies heliófilas en los puntos en que la vegetación arbórea ha sido más modificada. En conjunto el paisaje fragmentado y diverso de Veracruz centro no señala una pérdida de especies, aunque puntualmente (diversidad alfa) sí ocurra.

FEW PUBLICATIONS MEASURE BIODIVERSITY LOSS IN DIFFERENT TAXA, especially in the tropics, despite the fact that much has been published about loss of species due to human activities (Murphy 1989, Brown & Brown 1992, Santos Filho 1995). Almost all studies have aimed at determining the local effects of habitat destruction (*e.g.,* for arthropods, see Klein 1989, Shure & Phillips 1991, Holloway *et al.* 1992, Majer & Beeston 1996). The conclusions of these studies are alarming: few species from the original communities survive and there is an important loss of biodiversity. There is no doubt that this view (which has led to much speculation about the extinction of species) is realistic at the small spatial and temporal scales at which the changes take place. These conclusions, however, may not be directly extrapolated to the landscape level, which is the scale at which extinction and survival generally occur (except in the case of restricted-range endemics).

There are two main reasons why the conclusions of small-scale studies cannot be extrapolated directly to the much larger scale of landscapes. First, the physical matrix may be heterogeneous, especially in landscapes with complex topography. This heterogeneity (orographic, edaphologic) does not permit human activities to occur uniformly

throughout the landscape. Second, not all human activities cause radical changes to natural communities. In the tropics, a forest may be destroyed over a large area to provide land for plantations or for livestock, but remnant patches are often left relatively unmodified. In such cases, human activities produce very heterogeneous landscapes in which natural communities are fragmented but do not disappear completely. These landscapes provide a challenge to biodiversity studies, because at intermediate levels of disturbance, diversity may actually increase (Connell 1975, 1978).

In this paper, we examine how biodiversity responds to habitat fragmentation at the local and landscape levels using dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) as an indicator group (Forsyth *et al.* 1998 and references therein; Halffter 1998). We studied dung beetle communities in two areas of central Veracruz that were once covered continuously by tropical deciduous forest and subjected to different types of human disturbance. We compared them with each other and to other dung beetle communities in central Veracruz.

Veracruz is one of three states in Mexico that have extremely high biodiversity (a megadiverse area); however, it is also a region with one of the highest amounts of habitat destruction. Contrary to what might be expected, and partly due to the complex orography of central Veracruz (with a gradient of 0 to 4250 m elev. over 80 km), the landscape has not been affected in a uniform way by human activities as would have occurred if the land were flat. The main consequence has been that habitats persist as patches in the least accessible areas and the landscape is extremely heterogeneous. These patches, some of them quite extensive, have been influenced by human activities to varying degrees, making Veracruz an appropriate location to study the effects of fragmentation on biological diversity.

Our working hypothesis was that the amount and quality of the food supply is the main factor determining species richness and trophic structure in dung beetle communities. To test this hypothesis, we compared one area with and one without cattle (large human-induced change in food supply), other environmental conditions being similar. We expected to find a large difference in the species composition and trophic structure of the two areas. We did not expect to find significant differences in necrophagous beetles; among coprophagous beetles, we expected the area with cattle to have a much larger number of species, higher abundances

of large species and burrowers, greater total biomass, and lower equitability.

METHODS

STUDY AREAS.—The two study areas Jalcomulco and Rancho Real Minero (RRM) are located (19°19′39″–19°26′39″N, 96°44′08″–96°35′18″W) 20 km apart in the lower foothills of central Veracruz (Fig. 1). The original vegetation of both areas was tropical deciduous forest (Castillo-Campos 1995). Jalcomulco has a remnant of original vegetation with patches of different successional stages. The patch we studied (which covers *ca* 500 ha) was on a southward-facing slope and had an average density of 12 trees and 8 shrubs per 100 m². There were no cattle on this slope, although cattle were present in small numbers in the flat valley bottom. RRM measures 300 ha and contains patches of forest with an average density of 5 trees and 15 shrubs per 100 m² interspersed with pastureland containing species introduced 28 years ago (*e.g., Sorghum halapanse* and *Cynodon plectostachyus*). On average, 40 head of cattle fed on a rotational basis in the pasture as well as in the forest patches.

SAMPLING METHODS.—Four different trap types were used to sample beetles. (1) The surface excrement trap consisted of a 1-liter plastic container buried in the soil so that its rim was at ground level. Each trap contained 150 g of fresh cow manure placed in a nylon stocking in the upper part of the container, and the bottom of the container was filled with 250 ml of water containing detergent. We placed 40 traps in each study area for a 24-hour interval and 168 for periods of 12 hours in order to distinguish between diurnal (0600–1800 h) and nocturnal (1800–0600 h) activities. (2) The surface carrion trap was constructed from a container similar to the preceding trap but was baited with 150 g of squid meat. The number of traps and the sampling periods were the same as with the previous traps. (3) The bottom excrement, or bottom carrion trap, was baited with 150 g of human excrement or 150 g of squid but was placed on a layer of soil in the bottom of the plastic container. In this case, 20 traps of each type were left for a 24-hour period. (4) The permanent necrotrap (NTP 80; Morón & Terrón 1984), which was designed to remain functional for long periods, had bait consisting of 150 g of squid meat and was left it in the field for 30 days. There were four traps per study area. We protected the first three types from rain by covering them with a plastic plate at

1. Cerro El Metate
2. Laguna Verde
3. Los Velázquez
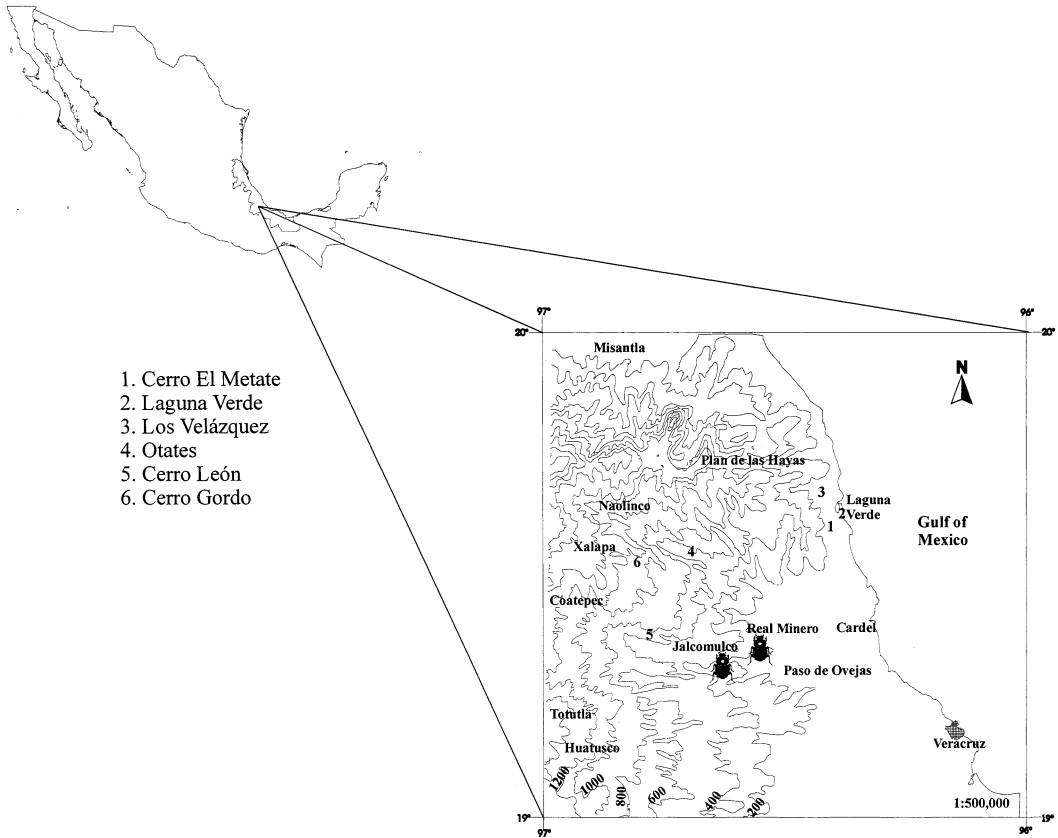4. Otates
5. Cerro León
6. Cerro Gordo

FIGURE 1.   Location of the study areas. Beetles represent sampling sites; arabic numbers: points of comparison used in Table 2.

10 cm height from the rim of the trap. Finally, and as a complementary method, we placed on two (RRM) and three (Jalcomulco) days in July 1996, two baits of human excrement and two of squid on a sheet of paper; in each, we counted the number of dung beetle individuals arriving on an hourly basis. All captures were made in the rainy season (June–October) of 1994, 1995, and 1996, when numbers of species and individuals were highest.

We carried out two independent experiments to account for the effect of light and that of cattle on the amount of dung beetles captured. To test for the effect of light, we laid out ten cow pats under the shade and ten cow pats under direct solar radiation. To test for the effect of cattle presence, we laid out ten cow pats in each of two sites, one with and the other without cattle. We found no significant differences in the amount of captured specimens in relation to cattle presence ($t = 137.0$, $P = 0.511$), but the number of captured individ-

uals was significantly different in relation to light intensity ($t = 132$, $P = 0.044$).

To determine the degree of completeness of our samples, we calculated species accumulation curves using the logarithmic and exponential or linear dependence models of Soberón and Llorente (1993), and estimated the true species richness of each study area using the software SIGMA-STAT 2.0 (Jandel Corporation 1995; Fig. 2). The species accumulation curves accounted for 96.5 and 97.2 percent of the variance in sampling performance at RRM ($P < 0.001$) and estimated that we collected 87.5 and 95 percent of the true species richness (Fig. 2a). For Jalcomulco, the models explained 90.8 and 96.1 percent of the variance ($P < 0.001$) and estimated that we collected 100 and 105 percent of the true species richness (the latter obviously an error of the model; Fig. 2b). Additional species of dung beetles are found in the flat agricultural lands near our Jalcomulco study area; how-
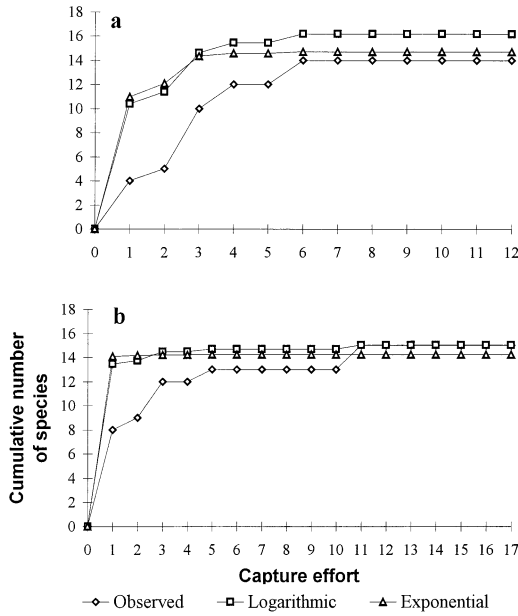
FIGURE 2.   Species accumulation curves. Capture units express total sampling effort and were calculated considering both the sampling effort invested in the different traps and direct sampling effort. (a) Rancho Real Minero: logarithmic model R^2 = 96.5, P < 0.0001; exponential model R^2 = 97.2, P < 0.001. (b) Jalcomulco: logarithmic model R^2 = 90.8, P < 0.001; exponential model R^2 = 96.1, P < 0.0001.

ever, we believe that our samples represented point diversities (alpha diversities) for the conditions sampled.

DATA ANALYSIS.—For each study area, we recorded the observed number of species (S), number of individuals (N), and biomass per species (based on weight of ten individuals dried at 120°C for 48 h). We graphed the dominance–diversity curves for each study area. With the software Statistical Ecology (Ludwig & Reynolds 1988), we calculated the Jaccard similarity index between study areas; for each study area, we calculated the Simpson dominance index, the Hill numbers, and the modified Hill ratio (Magurran 1988), in all cases using biomass instead of number of individuals. Using the software Statistica (StatSoft 1991), we estimated Kendall's coefficient of concordance W (Siegel & Castellan 1995) among the abundances of the ten most abundant species shared by the study areas. We used a χ^2 contingency table (species × study area) to analyze the standardized residuals of the above test. We compared the trophic structure of dung beetle communities following Halffter and

Favila (1993), considering: (1) foraging niche width: the proportion of generalists (species in which at least 80% of the individuals were collected in both copro- and necrotraps) to specialists (species in which more than 80% of the individuals were collected in either copro- or necrotraps); (2) foraging tactics: the proportion of burrowers to rollers; (3) temporal segregation: the proportion of nocturnal to diurnal species; (4) spatial segregation: the proportion of forest specialists to non-forest (heliophilous) species; and (5) size segregation: the proportion of large species (18–28 mm), medium-sized species (9–17.99 mm), and small species (<9 mm).

To compare equitability between study areas, we performed jackknifing (Magurran 1988) on the modified Hill ratio. A Kolmogorov–Smirnov test (Siegel & Castellan 1995) was then performed to test for normality. The mean values of this test were a much better estimate of equitability than the raw values (Magurran 1988).

RESULTS

In total, we collected 3493 individuals of 19 dung beetle species (1314 individuals of 15 species in Jalcomulco and 2179 individuals of 14 species in RRM). The total biomass in Jalcomulco was nearly six times lower than in RRM (Table 1). Considering only species presence or absence, we found a 75.86 percent similarity between the study areas, a rather high similarity value. In contrast, Halffter et al. (1992) had found that similarity values among three tropical rain forests of eastern Mexico ranged between 62.96 and 68.80 percent.

Although the dominance value was lower in Jalcomulco (Table 2), dominance–diversity curves showed similar biomass distribution between the study areas (Fig. 3). In contrast, Kadiri et al. (1997) had found that a significant increase in food resources increased diversity and equitability in European forests and pastures.

In terms of their frequencies, there were four dominant species in Jalcomulco (N_2 = 3.99): Canthon (Glaphyrocanthon) leechi (38.81%), Canthon cyanellus (28.84%), Deltochilum gibbosum (7.46%), and Canthon (Glaphyrocanthon) zuninoi (6.77%); there were three dominant species in RRM (N_2 = 3.09): C. cyanellus (47.59%), Deltochilum lobipes (29.6%), and Canthon (Glaphyrocanthon) leechi (6.42%). In Jalcomulco, the dominant species accounted for 81.88 percent of the total frequency and in RRM, 83.61 percent. In terms of biomass, two species dominated in Jalco-

TABLE 1. *Comparison of the abundance and biomass of dung beetle species in the two study areas.*

Locality	Jalcomulco		Real Minero	
Species	No. of ind.	Biomass (mg)	No. of ind.	Biomass (mg)
Onthophagus batesi	3	48.60	13	210.60
O. hoefneri	75	159.75	64	136.32
Dichotomius amplicollis	19	3344.00	89	15,664.00
Uroxys boneti	74	86.58	32	37.44
Canthidium puncticolle	0	0	13	250.90
Phanaeus tridens	0	0	23	3611.00
P. endymion	6	768.00	0	0
Coprophanaeus pluto	0	0	23	8533.00
C. telamon	1	381.00	3	1143.00
Sisyphus mexicanus	31	750.20	0	0
Canthon cyanellus	379	8451.70	1037	23,125.10
C. indigaeus chevrolati	1	36.20	1	36.2
C. (Glaphyrocanthon) zuninoi	89	445.98	0	0
C. (G.) moroni	1	5.05	0	0
C. (G.) leechi	510	2565.30	140	704.20
C. (G.) femoralis	13	274.30	1	21.10
Deltochilum gibbosum	98	41,748.00	0	0
D. lobipes	0	0	645	274,770.00
D. scabriusculum	14	4648.00	95	31,540.00
Total	1314	63,712.57	2179	359,782.86

mulco (N_2 = 2.18): *D. gibbosum* (65.52%) and *C. cyanellus* (13.26%); two also dominated in RRM (N_2 = 1.67): *D. lobipes* (76.37%) and *Deltochilum scabriusculum* (8.77%). In the former, the dominant species accounted for 78.78 percent of the total biomass and in the latter, 85.14 percent. The

dominant species, both in terms of frequency and in terms of biomass, were all rollers.

With respect to ecological structure, Jalcomulco had a larger proportion of forest species and non-digging species (Fig. 4). These differences, however, were not statistically significant (number of forest-restricted species: χ^2 = 0.4505, P = 0.5938; biomass: t = 41.5, P = 0.165; frequency: t = 44.5, P = 0.318; Fig. 4a). In RRM, 57.14 percent of the species were diggers, and in Jalcomulco, only 40 percent were diggers (Fig. 4b); however, the difference between diggers and rollers was not significant (number of species: χ^2 = 0.4505, P = 0.5814; frequencies: t = 90, P = 0.273; biomass: t = 86.5, P = 0.174).

With respect to feeding preferences, in Jalcomulco 46.66 percent of the species were coproph-

TABLE 2. *Comparison of diversity measures obtained in the two study areas.*

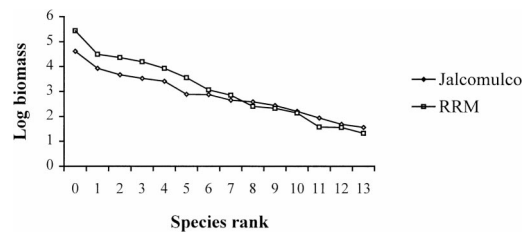|	Jalcomulco	Real Minero
Based on abundances		
N_0	15.000	14.000
R_1	1.950	1.691
R_2	0.414	0.299
H'	1.726	1.496
χ	0.251	0.323
N_1	5.618	4.647
N_2	3.986	3.097
E_5	0.647	0.605
Based on biomass		
N_0	15.000	14.000
R_1	1.266	1.016
R_2	0.594	0.233
H'	1.249	0.912
χ	0.457	0.598
N_1	3.486	2.490
N_2	2.188	1.673
E_5	0.478	0.452

FIGURE 3. Dominance–diversity curves based on biomass in the two study areas.
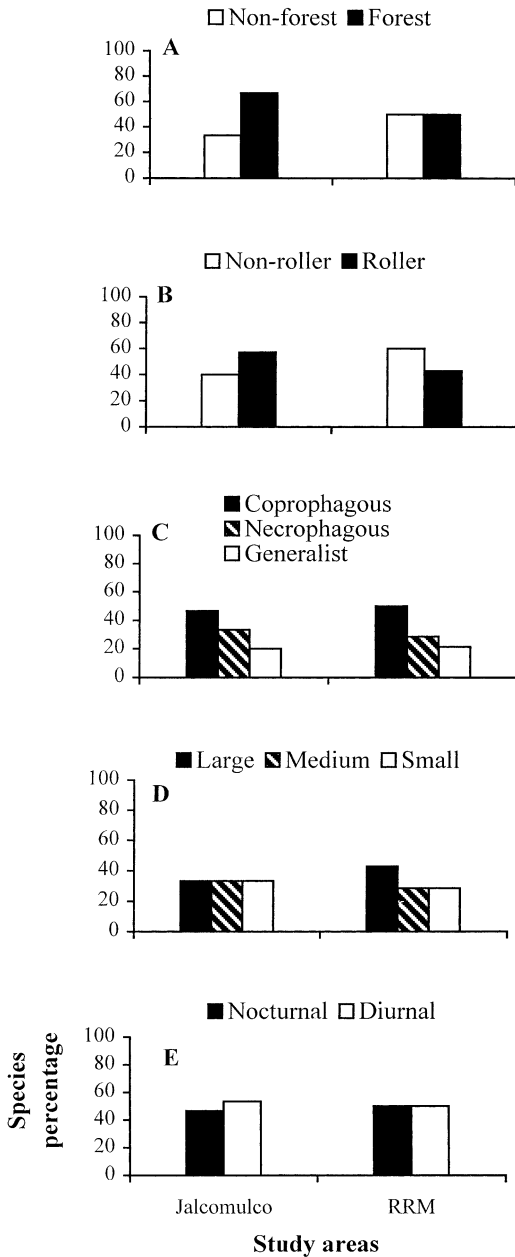
FIGURE 4.   Structure of the Scarabaeinae group in the two study areas: (a) spatial segregation; (b) food relocation; (c) segregation by food source; (d) segregation by size; and (e) temporal segregation.

agous, 33.33 percent were necrophagous, and 20 percent were generalists. In RRM, 50 percent of the species were coprophagous, 28.57 percent were necrophagous, and 21.43 percent were generalists (Fig. 4c). We had hypothesized that the increased

food supply for coprophagous beetles in RRM would not affect the number and frequency of necrophagous beetles. Our results were consistent with this hypothesis because we captured five species of necrophagous beetles in Jalcomulco and four in RRM, and there were no significant differences between their frequency ($t = 36.5$, $P = 0.699$) or biomass ($t = 37.0$, $P = 0.818$).

We found the three size categories to be equally represented in Jalcomulco (33.33%) but there was a higher percent of large species in RRM (42.86%; Fig. 4d). In Jalcomulco, we found only one species of large, digging coprophages, *Dichotomius amplicollis* (1.5%); in RRM, there were two, *D. amplicollis* (4.08%) and *Phanaeus tridens* (1.055%), the two adding up to 5.13 percent of the total. There was a larger number of diurnal species in Jalcomulco, whereas there was a similar proportion of nocturnal and diurnal species in RRM (Fig. 4e).

We expected to find greater biomass and a lower number of species in RRM. The total biomass in Jalcomulco was 63,712.57 mg and in RRM, 359,782.9 mg, with 83.61 percent of the biomass accounted for by only three species. In terms of capture frequencies, we found greater equitability in Jalcomulco (Table 2). The following estimates of equitability (in terms of biomass) were derived from the jackknife analysis: Jalcomulco = 0.6567 and RRM = 0.7154, with no significant differences between them ($T_t = 238.0$, $P = 0.228$).

In contrast to the previous tests, in which we did not find significant differences between the study areas, Kendall's coefficient of concordance among the ten most abundant species shared by the study areas revealed significant differences (Kendall's $W = 0.0031$, $P = 0.049$). Analysis of the residuals of the contingency table revealed that *Uroxys boneti*, *C. cyanellus*, *Canthon* (*Glaphyrocanthon*) *femoralis*, *D. gibbosum*, *D. lobipes*, and *D. scabriusculum* were significantly associated with forest patches and that *Onthophagus hoepfneri*, *D. amplicollis*, and *C.* (*G.*) *leechi* were associated with open areas containing cattle manure.

The cow pats monitored in 1996 attracted 49 individuals of six species (including the three non-forest species in the above table) in the open areas and only 3 individuals of two species under tree cover. In Table 3, we compare these results with six additional areas in central Veracruz that were originally covered with tropical deciduous forest. We conclude from this comparison that, on one hand, a larger number of open area species is associated with cattle, especially when most or all of tree cover has been removed. On the other hand, there is a

TABLE 3. *Principal characteristics of localities sampled in central Veracruz.*

Localities	Elevation (m)	Vegetation	Disturbance			Livestock		Scarabaeinae species	
			Low	Medium	High	Yes	No	Non-forest	Forest
Jalcomulco	450	Tropical Deciduous Forest	×				×	4	11
Rancho Real Minero	240	Tropical Deciduous Forest		×		×		6	8
Otates	480	Tropical Subperennifolious Forest		×			×	3	7
Cerro del Metate	30	Tropical Deciduous Forest			×		×	5	5
Cerro León	700	Tropical Deciduous Forest		×			×	3	5
Cerro Gordo	900	Tropical Deciduous Forest			×		×	5	4
Laguna Verde	20	Wooded Pasture			×	×		13	5
Rancho Los Velázquez	60	Pasture			×	×		8	0

greater number of forest-restricted species in the better-preserved forest fragments, independently of cattle presence or absence.

DISCUSSION

Both the qualitative and quantitative analyses revealed that there were more similarities than differences in the diversities and guild structure of dung beetles in Jalcomulco and RRM. The persistence of tropical deciduous forest in both was more important than the considerable difference in food supply, consistent with the assertion of Halffter and Matthews (1966) that tree cover was the most influential factor determining dung beetle community composition in the tropics (particularly in the New World). This leads us to speculate that most of the dung beetles of the New World tropics evolved in forests. Therefore, this group is an ideal indicator of degree of forest destruction and modification.

Thirty species of dung beetles have been found in the patchwork landscape of pastures and remnant tropical deciduous and semi-deciduous forest of central Veracruz (Table 4; see an analysis of biogeographic origin and composition in Halffter *et al.* 1995). Point (alpha) diversities in central Veracruz range between 8 and 18 ($\bar{x}$ = 11.5 ± 3.7; Table 3). Jalcomulco with 15 species and RRM with 14, are among the most species-rich patchwork landscape areas. The number of species in this landscape is much lower than the number in the nearest tropical rain forest and associated communities, Los Tuxtlas, which has 32 described (Morón & Blackaller 1997) and at least 5 still undescribed species. The alpha number of species of four tropical forests at Colombia (18–22 spp.; Escobar 1997) is similar to the alpha value found at the central Veracruz landscape. On the other hand, Amazonia *sensu lato* landscapes have a much larger number of species: 60 in Leticia, Colombia (Howden & Nealis 1975); 54 in Ecuadoran landscape; 64 in Vaupés, Colombia; 74 in Tambopata, Perú; and 97 in Parque Nacional Noel Kempff Mercado, Bolivia, with a maximum point (alpha) diversity of 64 species (Forsyth *et al.* 1998).

It is clear that species composition changes with cattle presence in open areas, and more so if a significant amount of the original tree cover has been removed (Table 3): forest-restricted species give way to heliophilous species as tree cover diminishes. On the other hand, the number of forest-restricted species is larger where there has been less forest de-

TABLE 4.   *Species of dung beetles in central Veracruz (0–900 m elev.).*

1. *Onthophagus batesi* Howden & Cartwright 1963
2. *O. hoepfneri* Harold 1869
3. *O. igualensis* Bates 1887
4. *O. schaefferi* Schaeffer 1914
5. *Digitonthophagus gazella* (Fabricius) 1787
6. *Copris incertus* (Say) 1835
7. *C. lugubris* Boheman 1858
8. *Dichotomius amplicollis* (Harold) 1869
9. *D. colonicus* (Say) 1835
10. *Uroxys boneti* Pereira & Halffter 1961
11. *Canthidium puncticolle* Harold 1868
12. *Phanaeus endymion* Harold 1863
13. *P. tridens tridens* Laporte 1840
14. *P. scutifer* Bates 1887
15. *Coprophanaeus telamon corythus* Harold 1863
16. *C. pluto* (Harold) 1863
17. *Euoniticellus intermedius* (Reiche) 1849
18. *Sisyphus mexicanus* Harold 1863
19. *Eurysternus mexicanus* Harold 1869
20. *Canthon (Glaphyrocanthon) femoralis* Chevrolat 1834
21. *C. (G.) antoniomartinezi* Rivera & Halffter 1999
22. *C. (G.) leechi* (Martinez, Halffter & Halffter) 1964
23. *C. (G.) zuninoi* Rivera & Halffter 1999
24. *C. (G.) moroni* Rivera & Halffter 1999
25. *C. (G.) circulatus* Harold 1868
26. *C. cyanellus cyanellus* Le Conte 1859
27. *C. indigaceus chevrolati* Harold 1868
28. *Deltochilum gibbosum sublaeve* Bates 1887
29. *D. scabriusculum scabriusculum* Bates 1887
30. *D. lobipes* Bates 1887

struction, independent of the presence or absence of cattle.

To further contrast the effect of tree cover versus food supply, we compared the dung beetle community of RRM with that of Laguna Verde (described in Halffter *et al.* 1992). The two are adjacent to each other and have similar biogeographic histories and macroclimatic conditions, but much more forest has been replaced by cattle pastures in Laguna Verde. Only isolated trees and a few very small patches of forest remain. In other words, whereas tree cover was similar and food supply was different between Jalcomulco and RRM, tree cover was distinctly different and the food supply was similar between RRM and Laguna Verde (although there are more cattle in Laguna Verde). In Laguna Verde, there are 21 species of dung beetles (18 cited in Halffter *et al.* 1992, and 2 recent invaders; see below) and in RRM there are 14. Some forest-restricted species have disappeared from Laguna Verde, while the numbers of species of open areas have increased.

In Laguna Verde, a number of coprophagous species are dominant in terms of numbers and bio-

mass, especially species of open areas. Many of these do not occur in RRM: *Digitonthophagus gazella* and *Euoniticellus intermedius* (Montes de Oca & Halffter 1998), *Copris lugubris, Copris incertus, Dichotomius colonicus,* and *Phanaeus scutifer.* In 1994, *E. intermedius* invaded RRM, but is found only along wide roads.

Two forest-restricted species occur in RRM that are not found in Laguna Verde, *U. boneti* and *C. (G.) femoralis.* These differences reveal the importance of tree cover, rather than food supply, in determining the composition of dung beetle communities. A detailed analysis of dung beetle distribution within RRM further revealed the importance of tree cover. *Canthidium puncticolle, P. tridens,* and *Canthon indigaceus chevrolati* were found in places where sunlight bathes the ground but very few or no specimens were found under tree cover. The first two species were not found in Jalcomulco and the last was very scarce there, as were other species of open areas (Table 1). These marked differences associated with degree of tree cover occur as well in the Department of Tolima, Colombia, also a heavily fragmented tropical forest landscape with pastures and cattle. Escobar (1997) found 22 species in Tolima; 20 were found in the forested patches, 12 of these being restricted to the forested patches. Many rollers of the forested patches disappear from the open areas. In a lower montane rain forest in another part of Colombia, Escobar and Medina (1996) found 17 species of dung beetles, 13 of which were found in pastureland but only 3 of which were restricted to that habitat.

Hanski (1989) synthesized the published information available and concluded that small isolated forest patches have lower dung beetle species richness and lack large species. Neither of these effects occurred in our study areas. The differences between the conclusions of Hanski (1989) and our study may be due to the following reasons: (1) Hanski (1989) referred to patches of rain forest in which dung beetle fauna (and perhaps other taxa) are more strongly affected by forest clearance than that of tropical deciduous forests; (2) despite area reduction, the central Veracruz forest patches remain interconnected; and (3) in central Veracruz, there is landscape invasion by many species of open areas. Our results separating the effect of tree cover from that of food availability are comparable to studies in southern France by Dr. Jean-Pierre Lumaret and collaborators (University of Montpellier; synthesis in Kadiri *et al.* 1997). In contrast to central Veracruz, in southern France, there are fewer

species of dung beetles in forest and many in open areas with livestock (cattle and sheep).

According to Kadiri *et al.* (1997), tree cover acts as a filter to prevent invasion by most species that live mainly in open areas, so that forests harbor an impoverished subset of open area species. Under these conditions, increasing food availability in the forest tends to cause rapid increases in the number of individuals and total biomass and a slower increase in the number of species. In contrast, in central Veracruz and other parts of the New World tropics, the forest fauna and open-area fauna are distinct and the former is richer. Under these conditions, an increase in food availability in the forest will cause an increase in the number of individuals, but almost no change in species composition. Reduction in tree cover has the opposite effect of altering species composition. Thus, in the tropics it is tree cover and not food availability, as in France, that determines community composition (see comments on colonization of novel resources in pastures by tropical forest species in Hanski and Cambefort 1991: 359).

The major influence of human activities on dung beetle communities works through the effect of these activities on the vegetative cover. These findings are consistent with the conclusion of Lobo *et al.* (1998) that solar radiation is the most influential factor determining dung beetle activity. In tropical regions formerly covered by forests, human-induced changes influence dung beetles (and probably other taxa as well) by deleteriously affecting the survival of forest-restricted species and by allowing forest invasion by native and introduced species of open areas. More forest-restricted species persist where more tree cover remains. There is a gradient of decreasing richness of forest-restricted species and increasing richness of open area species between Jalcomulco–Rancho Real Minero–Laguna Verde. An increase in food availability due to the presence of livestock produces an increase in the number of individuals and biomass (the major difference between Jalcomulco and RRM), but has a small effect on species composition.

Where fragmentation (as opposed to complete destruction) of forest is as old as in central Veracruz, it is difficult to find an area in which we can be sure that the habitat has not been disturbed by human activities. Complete forest clearance to develop pastures for raising livestock is a 20th century situation, but livestock raising arose in the 16th century. Before the Spaniards arrived in Mexico, central Veracruz had a large human population that performed slash-and-burn agriculture. Therefore,

Veracruz has probably had an extremely heterogeneous and dynamic landscape of patches for at least several hundred years. For an analysis on the evolution of landscapes in Veracruz, see Guevara *et al.* (1997) and Guevara *et al.* (1998); for an analysis on the development of cattle raising, see Barrera-Bassols (1992) and Skerritt (1992). This history explains two strange features of this study: the large number of native species in open areas and the survival of a large number of forest-restricted species in the landscape. Both situations lead us to an interesting conclusion: as expected, a fragmented landscape has a partially different species composition than the one of an unmodified tropical forest landscape, but the fragmented landscape unit (not specific sites) has more species than the unmodified landscape. We show this for the Scarabaeinae, but this may also be occurring with other organisms. To reach general conclusions, we need both to develop more studies using different organisms and to take into account two considerations: the original vegetation type and the period of time since the beginning of the fragmentation process.

Species of open areas are much more prevalent in central Veracruz (where human-induced habitat changes are very ancient) than in the large expanses of tropical rain forest. Clearance of tropical rain forest has had a drastic effect because the community of dung beetles then is made up almost exclusively of forest-restricted species (Howden & Nealis 1975, Klein 1989). Even so, a few species of open areas that did not occur previously in the forest interior have appeared in response to new conditions (Halffter *et al.* 1992, Escobar & Medina 1996, Escobar 1997). In central Veracruz, the dung beetle communities of open areas are unsaturated, as revealed by the ease with which these communities are invaded by species of open areas (*e.g., D. gazella* and *E. intermedius*; Montes de Oca & Halffter 1998) as well as the rapid population increase in native species of open areas. In contrast, the communities of tropical forests in Veracruz, as in the rest of the New World tropics, are saturated (Hanski 1989).

The abundance of three species of rolling necrophagous dung beetles, *C. cyanellus* and *D. gibbosum* in Jalcomulco and *C. cyanellus* and *D. lobipes* in RRM, is interesting (Table 1). *Coprophanaeus pluto*, a digging necrophagous species, is characteristic of RRM. These abundances cannot be associated with the presence of cattle. According to Hanski (1989: 489), tropical forests have a much higher mammal species richness than temperate forests. Where there are more vertebrates, there will

be more carrion. On the other hand, the abundance of small mammals (and their excrements) may explain the existence of small dung beetles in Jalcomulco (Table 1).

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