Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia

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Abstract: Anthropogenic disturbance in Amazonian forests has increased dramatically since the early 1980s and forest disturbance is expected to continue in the early twenty-first century. Logging and conversion to pasture for cattle are two of the largest causes of forest disturbance and destruction. This study examined the distribution and diversity of dung beetles (Coleoptera: Scarabaeidae) in intact forest and under three disturbance regimes (selective logging, clear-cutting and pasture) in a forest tract in southern Pará state, Brazil. Dung beetles were collected using faeces-baited pitfall traps, then identified, measured and weighed. Principal Components Analyses and the Sørensen's Index indicated that the intact and selectively logged areas were similar in terms of species composition but that the pasture areas and clear-cut areas had substantially different groups of species. Beetle size and diversity (as measured by species richness, Shannon index and Simpson's index) were lower in clear-cuts and pasture than in intact forest. The selectively logged forest was no less diverse than intact forest, and beetles were the same size or larger than those in intact forest. Total beetle biomass, however, was highest in the pasture due to the abundance of small-bodied beetles in this habitat. While the fact that selective logging has a relatively minor impact on the dung beetle community is heartening, the projected increase in the amount of highly disturbed landscape in Amazonia is expected to have a severe impact on dung beetle biodiversity in the region.

Key Words: Anthropogenic disturbance, biodiversity, Brazil, clear-cutting, dung beetles, pasture, pitfall traps, Scarabaeidae, selective logging

INTRODUCTION

Since the mid-1970s, damage to forests in the Brazilian Amazon has increased dramatically. In the Brazilian state of Pará where 93% of the area was originally in forest, the change is particularly striking: by 1988, 18% of all forested land had been affected by deforestation, fragmentation or edge effects (a 40% increase in 10 y) (Skole & Tucker 1993). In the following decade (1988–1998), forest damage continued, although the rate of deforestation decreased (Fearnside 1999). At present, 14% of the total Brazilian Amazon forest cover has been cleared, an additional 2–7% is expected to be removed over the next 25–35 y (Peres 2001). Estimates of overall damage by 2020 suggest that 72–95% of the forest may

be subject to modification by human activity (Laurance *et al.* 2001).

Much of the damage is due to conversion of forest to pasture and by logging. Conversion of forest to pasture in the Brazilian Amazon peaked in the 1980s with government-sponsored development programmes (Anderson 1990, Moran 1993). Large-scale logging began more recently, and is expected to increase as worldwide demand grows and Asian wood stocks decline (Fearnside 1999). Forest conversion to pasture creates obvious and immediate changes to all aspects of the ecology of the area. Biodiversity declines (Nepstad *et al.* 1992), not only for the obvious groups such as plants and vertebrate animals (Neill *et al.* 1995), but also for insects (Halffter *et al.* 1992, Klein 1989).

The damage caused by logging is dependent upon the intensity of the logging operation. High-intensity logging is known to have a negative effect on dung beetles and other insect groups (Davis *et al.* 2001, Hill 1999). In areas far from sawmills or without roads

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transportation costs are high and most of the logging currently conducted is selective extraction of high-value timber such as mahogany (*Swietenia macrophylla* King) (Uhl *et al.* 1997). Despite the prevalence of selective logging practices, there have been few studies conducted that examine how this type of logging affects local biodiversity (Scheffler 2002). In those instances where the effect of selective logging on biodiversity has been studied, the results have been mixed: in some cases biodiversity declines (Fredericksen *et al.* 1999, Ocha G. 2000, Thiollay 1992), in others it remains stable (Fredericksen *et al.* 1999, Laurance & Laurance 1996, Willott 1999), and in others it increases (Willott *et al.* 2000). The high incidence of selective logging in remote areas of the tropics and the call by some biologists to incorporate selective logging in forest conservation measures (Rice *et al.* 1997) increases the importance of understanding its effects on biodiversity.

This study seeks to understand the differences in diversity and community structure of dung beetles (Coleoptera: Scarabaeidae) in intact forest and an array of anthropogenically modified land types: selectively logged forest, clear-cut forest and cattle pasture. I chose to study dung beetles because (1) they have a relatively well-known taxonomy; (2) they are known to be highly habitat specific (Halffter & Favila 1993, Klein 1989, Nealis 1976); and (3) dung beetle communities are known to be particularly species-rich (Hanski & Cambefort 1991a) which allows the comparison of biodiversity within a single taxon.

Dung beetles are predominantly coprophagous insects which play an important role in the ecosystem by aiding in the recycling of nitrogen and other nutrients (Lutz 1931, Rougon & Rougon 1991), removing dung from the soil surface (Gillard 1967, Tyndale-Biscoe 1994), protecting seeds from predation (Andresen 2001, Estrada & Coates-Estrada 1991, Feer 1999), and reducing populations of disease-causing organisms such as flies and hookworms by competing for food (faecal) resources and destroying eggs and larvae (Hanski 1991, Miller 1954). The majority of dung beetle species rely on mid- to large-size mammals for food and are directly affected by changes in mammal populations (Estrada & Coates-Estrada 1999). In addition they are highly sensitive to disturbance and different species specialize in different habitat types such as forest, edge, clearing, and tree and crop plantations (Halffter & Favila 1993, Halffter *et al.* 1992). Thus, the presence of dung beetle species can be linked with both habitat differences and the presence of vertebrate taxa.

In this study I examined dung beetle species diversity, size, and biomass in four habitats: intact forest (defined as forest where logging or other major disturbance had not taken place), selectively logged forest, small forest clear-cuts and pasture.

STUDY SITE

The study was conducted at Fazenda Marajoara in a 8500-ha forest tract and surrounding pasture in the state of Pará, Brazil at 7°50′S 50°16′W (Figure 1). The area is seasonally deciduous forest characterized by an average of 1855 mm of rainfall per year. Over 90% of the rainfall occurs between the months of October and April (Grogan 2001).

The study area is a mosaic of intact forest, selectively logged forest, second-growth forest, and forest clearcuts in a surrounding matrix of cattle pasture. Although the clear-cuts and pasture are maintained by burning, the intact and selectively logged forest have not been affected by runaway fire.

Selective logging was conducted in 1992 under the direction of the Brazilian Forest Service (IBAMA). A maximum of six species (mahogany was the most common) were extracted at a density of 1–4 stems per ha. In 1996 two 0.5-ha areas within the intact forest were clear-cut: all trees were removed, the areas were burned and they have been re-cleared annually as part of a study on the ecology of mahogany (Grogan 2001). The pasture is maintained by fire and was burned 6 mo before the commencement of the study; although cattle were absent from the pasture sites at the onset of collection, they were returned to the area between the third and fifth day of collection.

The site is 34 km from the nearest areas of permanent domicile and nearly 70 km by road from the nearest town. Due to its remote nature and protection by the owner, very little hunting has taken place within the forest and it continues to support large carnivores such as jaguar (*Panthera onca*) and bush dog (*Speothos venaticus*). Howler monkeys (*Alouatta* spp.), capuchin monkeys (*Cebus* spp.), saki monkeys (*Chiropotes albinasus*), coati (*Nasua nasua*), peccary (*Tayassu* spp.), paca (*Agouti paca*), agouti (*Dasyprocta* spp.), armadillo (*Dasypus* spp.), tapir (*Tapirus terrestris*), anteater (*Tamandua tetradactyla* and *Cyclopes didactylus*), brocket deer (*Mazama* spp.) and rabbit (*Sylvilagus brasiliensis*), as well as several species of forest rats, mice and squirrels are commonly seen in the area (Scheffler, *pers. obs.*), however, no studies of vertebrates have been conducted in the area.

METHODS

All fieldwork was conducted in October 1998 at the beginning of the rainy season. Habitat specificity of dung beetle species was studied in intact forest, selectively logged forest, clear-cuts, and pasture using faeces-baited pitfall traps; two lines of five traps were used in each of the four habitats.
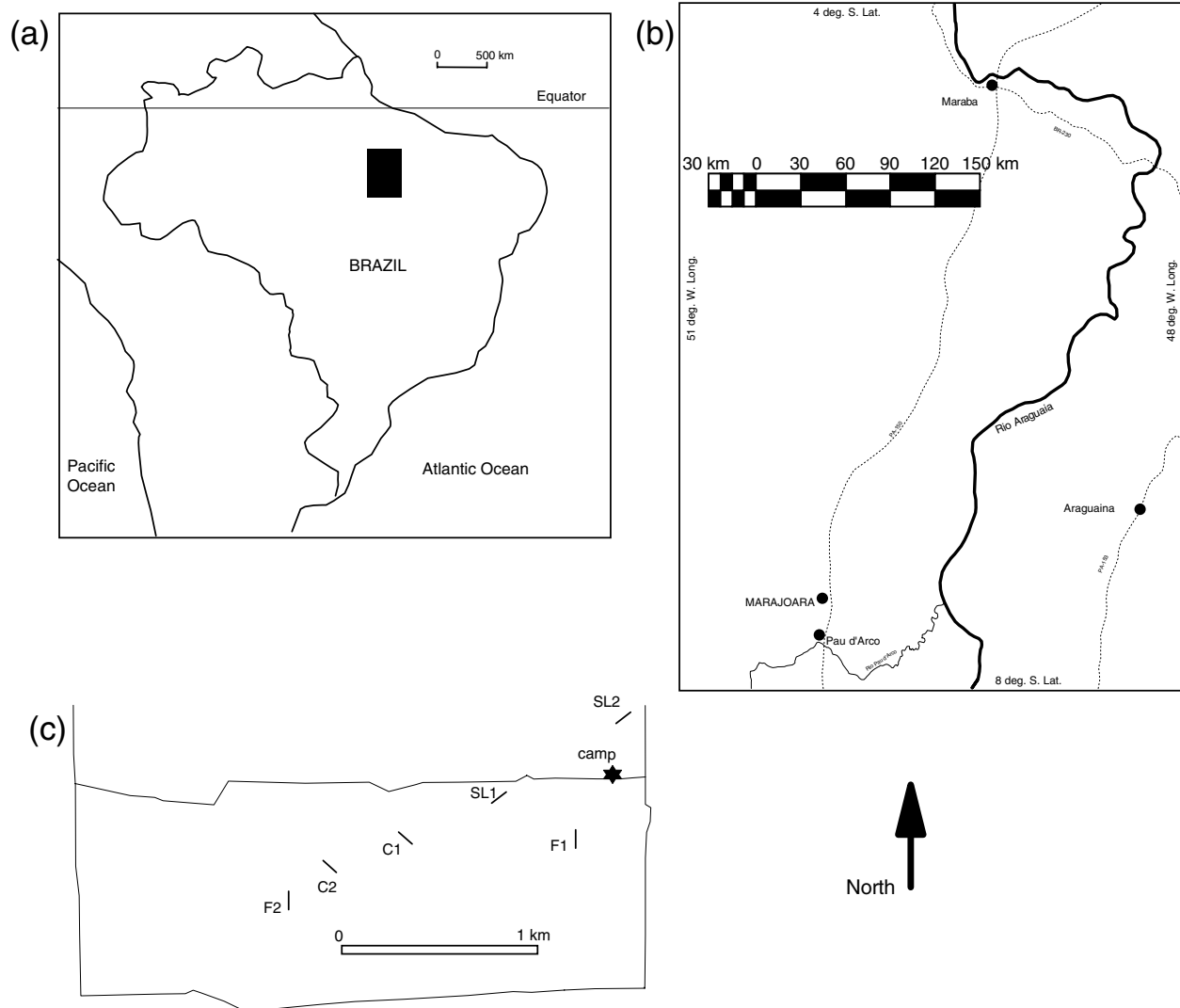
Figure 1. The location of the study site. (a) The country of Brazil with the study region shaded; (b) an enlargement of the study (shaded) region showing the location of Fazenda Marajoara; solid lines are rivers, dashed lines paved roads; (c) the central study area at Fazenda Marajoara. F1 and F2 indicate trapline locations in intact forest, SL1 and SL2 indicate traplines in selectively logged forest and C1 and C2 indicate traplines in clear-cuts. Pasture traplines are located a minimum of 7 km to the east from the nearest of these traplines. Solid lines are dirt roads.

One-litre pitfall traps were designed after Halffter & Favila (1993) and baited using approximately 22 g of human faeces, an amount that corresponds to weights common for howler monkey faecal clumps (Andresen 2001). Pitfall traps were laid-out in 120-m traplines of five traps spaced at 30-m intervals. Rainfall was measured daily at a central location; thermometers were placed at two or three randomly selected traps at the intact forest, selectively logged forest and clear-cut areas.

The location of the traplines in intact forest was selected by randomly choosing a starting location 30 m from one of the forest trails. Traplines in the selectively logged areas were established so as to maximize the number of traps in the area disturbed by logging: the first trap was located at one stump and the trapline was oriented between other stumps in the area. Those in clear-cuts were established at a diagonal to the clearing in such a way that Traps 1 and 5 were closest to standing forest (< 5 m) and Trap 3 was the furthest (25 m). Traps in the pasture were established in straight lines running parallel to and a minimum of 750 m from the edge of the forest.

Trapping was conducted for 4 d at each trapline over an 11-d period. Traps were checked at approximately 48-h intervals and rebaited after 48 h, at this time, maximum and minimum temperature for the 48-h period were recorded. Beetles were removed from the traps each time the trap was checked. Eight faeces-baited traplines (two at each location) were established in intact forest (F1 and F2), selectively logged forest (SL1 and SL2), forest clearings (C1 and C2), and pasture (P1 and P2) (Figure 2).
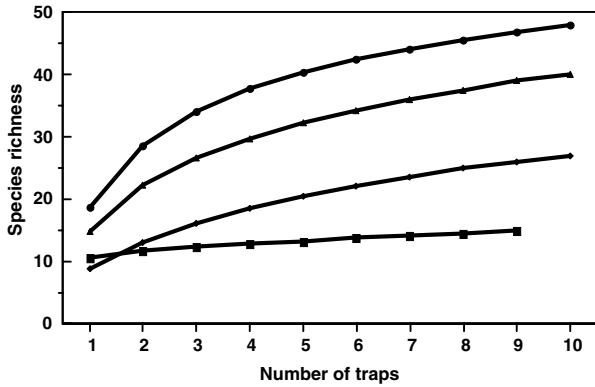
Figure 2. Species accumulation curves (after 100 randomized iterations) for baited pitfall traps at Marajoara, Pará, Brazil. Intact forest is represented by circles, selectively logged forest by triangles, clear-cut areas by diamonds, and pasture by squares.

Table 1. Days of trapping (shaded) for each of the eight traplines and daily rainfall (in mm) at Fazenda Marajoara, Pará, Brazil. F1, F2 = intact forest; SL1, SL2 = selectively logged forest; C1, C2 = clear-cut areas; P1, P2 = pasture.

Trapline	Day									
	1	2	3	4	5	6	7	8	9	10
F1	■	■	■	■						
F2			■	■	■	■				
SL1							■	■	■	■
SL2							■	■	■	■
C1	■	■	■	■						
C2			■	■	■	■				
P1				■	■	■	■			
P2				■	■	■	■			
Rain	7.0	0	0	0	15.5	0	0	0	0	0

The onset of trapping at each line was staggered such that trapping at each trapline overlapped with at least three other lines (Table 1).

After collection, all beetles were preserved in 70% alcohol overnight, then dried in a gas-powered dry box. After drying for 3 d, beetles were removed, identified to species or morphospecies, weighed using an Ohaus scale accurate to 0.01 g, and length and width were measured with calipers accurate to 0.1 mm. Species that were too small to register on the scale were weighed in groups of two or more individuals and an average weight was used for each individual in the group. Final species identifications were made by comparisons to collections at the Universidade Federal de Viçosa (UFV) in Minas Gerais, Brazil. The collection is vouchered at UFV. When identification to species level was not possible, beetles were identified to the level of genus and given unique number codes to represent the species.

Species accumulation curves were plotted for each habitat. The curves were obtained from 100 randomized

iterations using the EstimateS software package (Estimate S: Statistical estimation of species richness and shared species from samples. Volume 6.0v1. http://viceroy.eeb.uconn.edu/estimates).

Temperature (maximum and minimum) and rainfall were compared between habitat and traplines using a multivariate General Linear Model (GLM) where trapline was nested within habitat. Differences within the habitats were compared using a Bonferroni-adjusted pairwise comparison at $\alpha = 0.05$.

Species diversity was calculated using three species diversity indices: species richness (S = number of species present), the Shannon index (Shannon & Weaver 1949) and the reciprocal of Simpson's (1949) index. Although there are many possible indices which can be used to portray diversity, each with strengths and weaknesses, these three were chosen because they are familiar to and readily interpretable for most ecologists; the triad is used to minimize the inherent bias of individual measures. The Shannon (H') and reciprocal Simpson (1/D) indices are both based on proportional species abundance, however the Simpson's index, a dominance measure, is more influenced by common species (Magurran 1988). Mean diversity and abundance for the traplines were compared between habitats.

Differences in dung beetle size between the habitats were determined using multivariate general linear models in which trapline was nested within habitat and individual traps nested within trapline and habitat. Significant differences between the habitats were compared using Tukey's HSD; differences within the traplines (within habitat) and traps (within trapline and habitat) were explored using pairwise comparisons with a Bonferroni adjustment at $\alpha = 0.05$. Because of the very strong correlation ($P \leq 0.001$, $R^2 = 0.98$) between length and width of beetles collected in this study, differences in width are not reported. Length and weight were also correlated ($P \leq 0.001$, $R^2 = 0.47$), but due to the weak correlation, both length and weight are used in the multivariate analyses. A trap in one of the pasture lines was destroyed during the study, leaving only nine pasture traps. To compensate for this, cumulative data (biomass and abundance) are presented as corrected values (i.e. value/no. of traps × 10).

Principal components analysis (PCA) was used to analyse the relative abundance of dung beetle species. PCA is a valid method of differentiating species abundance between habitats when the number of taxonomic groups exceeds the number of replicates (Jüttner et al. 1996, Kitching et al. 2000). Preceding the PCA analysis, data were rotated orthogonally using the Varimax method to maximize the differences between the principal components extracted. All statistical analyses were performed using SPSS (SPSS v.10.0, SPSS, Inc., Chicago, Illinois, USA).

Table 2. Mean daily rainfall (mm) and temperature (maximum and minimum over a 48-h period, °C) for intact forest, selectively logged forest, forest clear-cuts, and pasture at Fazenda Marajoara, Pará, Brazil. Superscript letters indicate values significantly different according to Tukey's HSD ($P \leq 0.05$), bold values indicate significant difference between traplines within the same habitat using pairwise comparisons with a Bonferroni correction at $\alpha = 0.05$.

Habitat	Mean daily rainfall (SE)	Minimum temperature (SE)	Maximum temperature (SE)
Intact forest (F1)	3.5 (1.2)	19.6 (1.1)	31.6 (0.2)
Intact forest (F2)	7.8 (2.6)	21.5 (0.0)	33.8 (1.4)
Intact Forest (total)	5.6 (1.5)[a]	20.3 (0.8)	32.1 (0.6)[a]
Selectively logged forest (SL1)	0.0 (0.0)	21.8 (0.4)	**33.8 (1.0)**
Selectively logged forest (SL2)	0.0 (0.0)	21.6 (0.7)	**37.0 (0.4)**
Selectively logged forest (total)	0.0 (0.0)[b]	21.7 (0.4)	35.4 (0.4)[b]
Clearcuts (C1)	3.5 (1.2)	21.0 (0.0)	**44.0 (2.1)**
Clearcuts (C2)	7.8 (2.6)	20.2 (1.2)	**39.3 (1.3)**
Clearcuts (total)	5.6 (1.5)[a]	20.6 (0.6)	41.7 (1.5)[c]
Pasture (P1)	7.8 (2.6)	*	*
Pasture (P2)	7.8 (2.6)	*	*
Pasture (total)	7.8 (2.6)[a]	*	*

* no data available.

The Sørensen Similarity Index (C_N) was used to compare similarity between habitats. Although there are several indices of similarity, according to Halffter *et al.* (1992), the Sørensen Similarity Index most accurately reflects changes in the dung beetle community. This index ranges from 0 (no shared species) to 1 (no difference in species composition).

A one-way Analysis of Variance (ANOVA) was used to compare the difference in relative abundance and biomass of individual dung beetle species between the four habitats. Pairwise differences were further compared using Tukey's HSD.

RESULTS

Rainfall was sporadic and minimal throughout the trapping period; rainfall was essentially the same during trapping at the intact forest, clear-cuts and pasture but no rain fell during the trapping period in the selectively logged forest (Table 1, Table 2). The minimum temperature did not vary between the three habitats in which temperature was recorded but the maximum temperature was significantly higher in the clear-cuts, followed by the selectively logged areas, and lowest in the intact forest (ANOVA, $F_{2,14} = 22.7$, $P \leq 0.001$; Table 2). There were no differences between lines in the same habitat for rainfall or minimum temperature; however, the maximum temperature varied significantly (at the $\alpha = 0.05$ level) between the traplines in the selectively logged forest and in the clear-cut areas (Table 2).
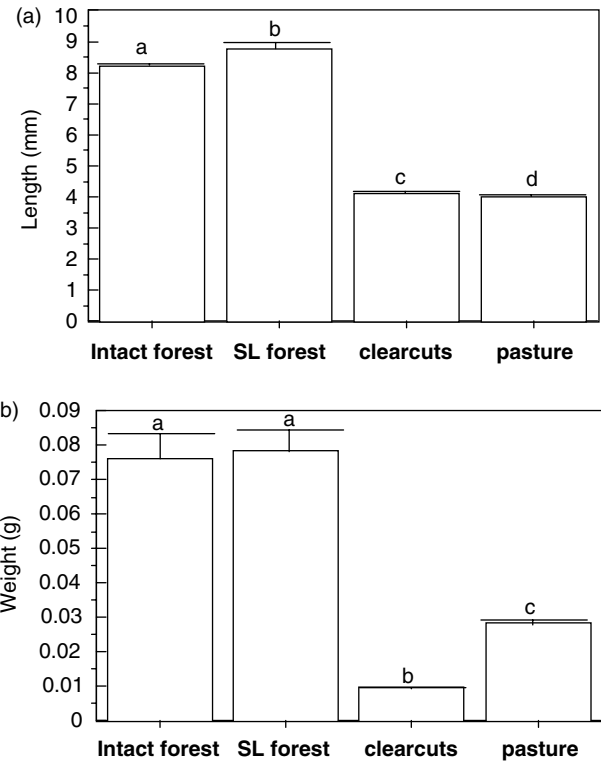

Figure 3. Differences in (a) length (mm) and (b) weight (g) of dung beetles between intact forest, selectively logged (SL) forest, clear-cut areas, and pasture areas at Fazenda Marajoara, Pará, Brazil. Error bars represent the standard error of the mean; letters indicate significant groupings using Tukey's HSD at $\alpha = 0.05$.

It is unlikely that the loss of one of the pasture traps had much effect on the estimation of species diversity in this habitat since approximately 60% of all pasture species were represented in a single trap and 90% of the trapped species in four of the nine traps used (Figure 3).

A total of 6213 individual dung beetles from 60 species was captured during this study. Seventy-eight per cent of the species occurred in the intact forest, 67% in the selectively logged forest, 42% in the clear-cut areas and 23% in the pasture traps. Twenty-two per cent of the species represented by more than a single individual were habitat specialists (species which occurred in a single habitat); the remainder occurred in at least two of the four habitat types. While only 3% of the species were full generalists and occurred in all four habitat types, 46% of the individuals captured belonged to species that were full generalists (Appendix).

Significant differences between the habitats were found in dung beetle length (GLM, $F_{3,5510} = 254$, $P \leq 0.001$) and weight (GLM, $F_{3,5510} = 28.1$, $P \leq 0.001$); there were no differences between traplines in the same habitat. However, beetle size did vary significantly between traps within the intact forest, selectively logged forest and

Table 3. Mean value per trapline and standard error (SE) for species diversity (species richness (S), Shannon index (H'), Simpson's index (D)), beetle abundance (N), and beetle biomass (g) for dung beetle collections in intact forest, selectively logged (SL) forest, clear-cuts, and pasture at Marajoara Ranch, Pará, Brazil.

Habitat	Species richness (SE)	H' (SE)	1/D (SE)	N (SE)	Biomass (g) (SE)
Intact forest	37.0 (11.0)	2.65 (0.27)	8.63 (2.45)	497 (272)	37.3 (19.4)
SL forest	30.0 (5.00)	2.43 (0.33)	12.13 (2.03)	262 (88)	20.2 (9.09)
Clear-cut	20.0 (5.00)	2.10 (0.04)	5.94 (0.37)	482 (273)	3.84 (2.35)
Pasture	13.5 (1.50)	1.15 (0.11)	2.02 (0.30)	2073 (671)	49.7 (15.7)

Table 4. Comparison of similarity of dung beetle species composition using Sørensen's Index for four Eastern Amazonian habitats (intact forest, selectively logged forest (SL), forest clear-cuts, and pasture) at Fazenda Marajoara, Pará, Brazil.

	Intact forest	SL forest	Clear-cuts	Pasture
Intact forest	–	0.73	0.50	0.47
SL forest		–	0.44	0.40
Clear-cuts			–	0.39
Pasture				–

The selectively logged and intact forest were the most similar of the habitats with a similarity (as calculated by the Sørensen's Index, C_N) greater than 0.70; pasture areas were least similar to intact habitat ($C_N = 0.39$; Table 4). The majority of individuals in the pasture (87% of total capture) were species in the genus *Trichillum* (which accounted for over 30% of the individuals in the small clear-cuts as well). The most common genus in the clear-cuts comprised only 44% of the total capture, whereas in the intact and selectively logged forest less than a quarter of the individuals captured belonged to a single genus. The majority of species (59) were from the subfamily Scarabaeinae; Aphodiinae were represented by a single species (*Ataenius* sp.) which occurred in the clear-cut and pasture areas (Table 5). Based on biomass and relative abundance, ten species showed significant associations with one or more habitats; these species could be divided into highly disturbance-sensitive species, moderately disturbance-sensitive species, and disturbance-adapted species (Table 6).

Based on the PCA analysis of the species, the first two components together accounted for 74% of the total variance of the data set. The first component accounted for 43% of the variance, the second for an additional 31%; after the second component, there was a decrease in the amount of variance explained by

pasture (length: GLM, $F_{31,5510} = 4.4$, $P \le 0.001$; weight: GLM, $F_{31,5510} = 2.5$, $P \le 0.001$).

Mean diversity (per trapline), by both the Shannon and Simpson's indices as well as simple species richness, was highest in the forest traps and lowest in the pasture. By the Simpson's index, diversity was highest in the selectively logged forest (1/D = 12.1) and lowest in the pasture (1/D = 2.02), and by the Shannon index diversity was marginally higher in the intact forest than the selectively logged (H'=2.65 and 2.43, respectively) and lowest in the pasture (H'=1.15). Like diversity by the Shannon index, species richness declined from intact forest to selectively logged forest to clear-cuts to pasture. Mean abundance and biomass were highest in the pasture and lowest in the clear-cuts (Table 3).

Table 5. Number of species and per cent of total individuals within the habitat for genera caught in pitfall trapping at in intact and selectively logged (SL) forest, clear-cuts, and pasture at Fazenda Marajoara, Pará, Brazil in 1998. † indicates genera which composed less than 0.5 per cent of the total catch. Values are rounded to the nearest per cent.

Genus	Subfamily	No. of species	Intact forest	SL forest	Clear-cuts	Pasture
Ataenius	Aphodiinae	1	†	0	1	4
Ateuchus	Scarabaeinae	5	11	17	†	0
Canthidium	Scarabaeinae	8	10	5	16	1
Canthon	Scarabaeinae	9	15	13	44	4
Deltochilum	Scarabaeinae	6	†	1	†	0
Dichotomius	Scarabaeinae	6	10	18	1	4
Digionthothophagus	Scarabaeinae	1	0	0	0	†
Eurysternus	Scarabaeinae	8	6	14	†	0
Ontherus	Scarabaeinae	1	7	†	†	1
Onthophagus	Scarabaeinae	5	24	20	0	2
Oxysternon	Scarabaeinae	1	†	0	0	0
Phanaeus	Scarabaeinae	1	†	†	0	0
Pseudocanthon	Scarabaeinae	1	0	0	0	†
Scybalocanthon	Scarabaeinae	1	2	†	0	0
Sylvicanthon	Scarabaeinae	1	†	†	0	0
Trichillum	Scarabaeinae	3	3	9	31	83
Uroxys	Scarabaeinae	3	8	1	7	†

Table 6. Mean relative abundance and biomass in grams (bold) per trapline with standard error (SE) of dung beetle species which differed between habitat (intact forest = IF; selectively logged forest = SL; clear-cut = Cl; pasture = Pa) at Fazenda Marajoara, Pará, Brazil. Superscript letters indicate significant groupings using Tukey's HSD at $\alpha = 0.05$.

|	IF	SL	Cl	Pa	F	P
Disturbance-sensitive species:						
Erysternus foedus	3.0 (1.0)[a]	0.5 (0.5)[a]	0[b]	0[b]	25.6	0.005
	0.45 (0.12)[a]	**0.09 (0.09)[a,b]**	**0[b]**	**0[b]**	**8.4**	**0.043**
Onthophagus	2.5 (0.5)[a]	0[b]	0[b]	0[b]	25.0	0.005
rubrescens	**0.02 (0.00)[a]**	**0[b]**	**0[b]**	**0[b]**	**28.3**	**0.004**
Moderately disturbance-sensitive species:						
Canthon sp. 4	1.5 (0.5)	5.0 (1.0)	3.0 (2.0)	0	3.5	0.130
	0.02 (0.01)[a]	**0.07 (0.00)[b]**	**0.03 (0.02)[a,b]**	**0[a]**	**12.7**	**0.016**
Deltochilum	0[a]	2.5 (.5)[b]	0[a]	0[a]	25.0	0.005
amazonicum	**0 [a]**	**1.82 (0.52)[b]**	**0 [a]**	**0 [a]**	**12.6**	**0.017**
Eurysternus	9.5 (0.5)[a,b]	18.0 (5.0)[a]	0[b]	0[b]	11.9	0.018
caribaeus	**0.6 (0.2)[a]**	**1.42 (0.08)[b]**	**0[a]**	**0[a]**	**40.7**	**0.002**
Eursternus	7.0 (1.0)[a]	9.5 (1.5)[a]	0.5 (0.5)[b]	0[b]	25.6	0.005
hamaticollis	**0.78 (0.3)**	**0.94 (0.21)**	**0.07 (0.07)**	**0**	**6.9**	**0.047**
Disturbance-adapted species:						
Ataenius sp.	0.5 (0.5)[a]	0[a]	5.5 (2.5)[a]	90.6 (5.0)[b]	249.7	< 0.001
	0.00 (0.00)[a]	**0[a]**	**0.01 (0.01)[a]**	**0.28 (0.03)[b]**	**66.6**	**0.001**
Canthon mutabile	0[a]	0[a]	3.0 (3.0)[a]	20.0 (2.2)[b]	26.5	0.004
	0[a]	**0[a]**	**0.04 (0.04)[a]**	**0.26 (0.04)[b]**	**23.1**	**0.005**
Dichotomius nisus	0[a]	0.5 (0.5)[a]	0.5 (0.5)[a]	91.1 (23.3)[b]	15.1	0.012
	0[a]	**0.21 (0.21)[a]**	**0.00 (0.00)[a]**	**45.3 (11.4)[b]**	**15.7**	**0.011**
Trichillium	0[a]	2.0 (2.0)	121.5 (78.5)	256.1 (15.0)	9.3	0.028
externepunctatum	**n/a**	**n/a**	**n/a**	**n/a**		
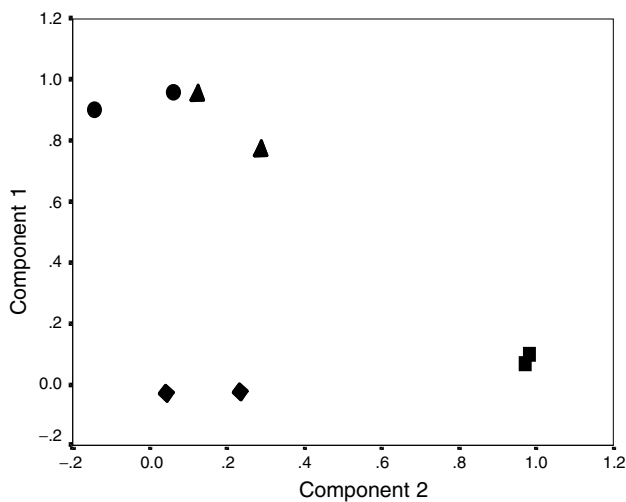
Figure 4. The association of the eight traplines with the first two principal components of the PCA carried out on species abundance. Intact forest is represented by circles, selectively logged forest by triangles, clear-cut areas by diamonds, and pasture by squares.

subsequent factors and only the first two components are considered in the remainder of the analysis. Trap areas are clearly separated from one another, with the intact and selectively logged forest ranking high on Component 1 and low on Component 2, the clear-cut areas ranking low on both components, and the pasture areas ranking high on Component 2 and low on Component 1 (Figure 4).

DISCUSSION

Rainfall is known to have a strong effect on insect abundance (Hill *et al.* 2003, Wolda 1978). However, because rainfall was relatively light during the entire trapping period (a total of just over 2 cm) it is unlikely that the lack of rainfall during the period of trapping in the selectively logged forest would have affected the relative capture rates between that and the other habitats.

By all indices, the dung beetle communities of the intact and selectively logged forest are very similar, whereas those of clear-cuts and pastures differ significantly from the forested areas. Intact and selectively logged forest exhibit higher species richness, higher diversity, and larger beetles than the highly disturbed clear-cuts and pasture.

Of the 60 species caught, 47 (78%) were represented in the intact forest traps and all but 5 (8%) were encountered in either the intact or selectively logged forest. With the exception of a single species native to Africa, *Digionthophagus gazella* (which occurred exclusively in the pasture), all of the species captured were native to Amazonia. This indicates that most species which survive in open areas are not exclusive to them but are simply better habitat generalists and have, perhaps, adapted to natural disturbances such as large multi-treefall gaps that occur in the area.

Many of the species encountered in this study were restricted to one or few habitats (Appendix). Individual

species are differentially affected by disturbance (Hanski & Cambefort 1991a) as was shown by the PCA analysis. The traplines were clearly clustered by habitat (Figure 4): the intact and selectively logged traplines were nearly indistinguishable whereas the pasture traplines and the clear-cut traplines were grouped together but not associated with other habitats. Sørensen's Index, too, showed a strong species similarity between the intact and selectively logged areas and very little similarity between any of the other habitat combinations (Table 4).

Most of the 60 species captured did not exhibit significant variation in abundance or biomass between habitats; relatively large variation between the two traplines was common, and increased replication might have identified more species which differed significantly between habitats. However, for the ten species which varied in abundance and/or biomass between the habitats (Table 6), over half (six) were primarily associated with areas of low disturbance (intact or selectively logged forest); none of these species was found in the pasture, and few were found in the clear-cuts. Disturbance-adapted species tended to be predominantly pasture species which occurred in lower density in the clear-cuts and were rare in the intact and selectively logged forest.

Although most of the diversity indices show high similarity between the intact and selectively logged forest (Table 3), Simpson's Index indicates that the selectively logged areas have higher diversity than the intact forest, as would be predicted by the intermediate disturbance hypothesis (Connell 1978). The use of the different indices indicates that the diversity of dung beetles in the intact forest is influenced by the presence of rare species whereas in selectively logged areas, rare species contribute less to overall dung beetle diversity.

Overall biomass was lowest in the clear-cut areas and highest in the pasture (Table 3), however, the mean size of the beetles was low in both the pasture and clear-cut areas (Figure 4). Thus, individual beetles in the pasture were small, but they were present in very large numbers, a pattern also found by Hanski & Cambefort (1991b).

The average body size of dung beetles has been found to be correlated with the average size of resident mammals (Cambefort 1991). In the clear-cuts, the combination of small size and low overall biomass of beetles indicates that mammals may be poorly represented in this habitat and the food resource does not exist to maintain a large biomass of beetles. This has implications for future forest regeneration in these areas since small-bodied beetles are less effective seed dispersers than larger species (Andresen 2001, Vulinec 2002).

Vegetation cover is known to have a profound effect on dung beetle species composition (Doube 1983, Hill 1996, Howden & Nealis 1975, Janzen 1983, Peck & Forsyth 1982) an effect substantiated by this study. Some traps in the clear-cut lines were less than 5 m from the forest

boundary yet many species of forest dung beetles were not trapped in the clear-cut lines (in fact, species richness was more variable within the forest traps than within the clear-cut traps). Klein (1989) also found that in areas of sharp transition between vegetational types, dung beetles may not cross the ecotone, even when food resources are readily available on the other side.

Vegetational differences directly affect dung beetle populations in part through increases in insolation (Nealis 1976); even in areas where the mammal populations are equally large, vegetational differences affect dung beetle species richness (Lumaret & Kirk 1991). There was a mean difference of almost 10 °C between the maximum temperature in intact forest and clear-cuts (Table 2) and, although temperature was not recorded in the pasture areas, it was undoubtedly similar to, if not higher than, the temperatures in the clear-cuts (*pers. obs.*).

A change in vegetation cover can also lead to differences in mammalian fauna which, in turn, affects dung beetle populations (Cambefort & Walter 1991, Estrada & Coates-Estrada 1999). The majority of the mammals present in the pasture are clearly different from those of the intact forest. Mammalian biomass is probably highest in the pasture which presumably permits the increased dung beetle biomass encountered there. However, mammalian diversity in pastures is low (Estrada *et al.* 1994) which limits the range of resources available for specialization by dung beetle species (Halffter 1991); the majority of animals in the pasture are non-native, and, due to stock rotation through paddocks, the mammalian biomass is not constant. These factors presumably account for the low dung beetle species richness in the pasture. The difference is less obvious between the clear-cuts, surrounded entirely by forest, and the intact forest. Arboreal species are necessarily absent in the clear-cuts and the lack of mammals such as howler monkeys (*Alouatta* spp.), which provide a substantial portion of the neotropical dung beetle diet (Estrada *et al.* 1993, Hanski & Cambefort 1991a, Howden & Nealis 1975), undoubtedly affects the dung beetle community. It is also possible that different terrestrial mammal species utilize the forests and clear-cut areas, further accounting for the differences between these beetle communities.

In conclusion, while as a whole this area supports a large and diverse community of dung beetles, the majority (95%) of species are found in forested areas (either intact or selectively logged forest) and nearly a quarter of these species are specific to these habitats. Selective logging at the intensity occurring in this area does not appear to have adversely affected the dung beetle community, but more-severe disturbances such as clear-cutting and conversion to pasture result in smaller-bodied beetles, a notable decline in beetle species richness and diversity, and a change in species composition. Degradation and disturbance to Amazonian forest, such as that projected to

occur by 2020 (Laurance *et al.* 2001), have implications for the biodiversity of dung beetles and other taxa which depend on intact forest habitat. Dung beetle diversity in the heavily disturbed habitats was approximately half that of the forested areas. Declines in dung beetle diversity and biomass could have implications beyond this single taxa; their role as prey (Robinson & Robinson 1970), as recyclers of animal waste (Tyndale-Biscoe 1994), and as secondary seed dispersers (Andresen 2001, Vulinec 2000) suggest that drastic changes to dung beetle community structure may cause unpredictable cascade effects through the ecosystem.

ACKNOWLEDGEMENTS

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Appendix. Mean size (weight, length, and width) and abundance of dung beetle species captured in intact forest (IF), selectively logged forest (SL), clear-cuts (C), and pasture (P) at Fazenda Marajoara, Pará, Brazil in 1998.

Species	Weight (g)*	Length (mm)	Width (mm)	IF	SL	C	P
Ataenius sp. (Aphodiinae)	0.003	3.70	1.70	1	0	11	163
Ateuchus connexus (Harold, 1868)	0.043	7.18	4.92	12	12	0	0
Ateuchus sp. 1	0.010	4.98	3.17	35	26	1	0
Ateuchus sp. 2	0.036	6.81	4.54	62	45	0	0
Ateuchus sp. 4	0.028	7.21	4.67	6	0	2	0
Ateuchus sp. 5	0.016	4.86	3.35	2	1	3	0
Canthidium lentum Erichson, 1847	0.025	7.15	4.73	61	5	0	0
Canthidium sp. 1	0.043	7.61	4.90	13	2	0	0
Canthidium sp. 2	0.030	8.80	5.50	1	0	0	0
Canthidium sp. 3	0.030	6.70	4.37	1	0	1	0
Canthidium sp. 4	0.025	6.35	4.03	5	0	0	0
Canthidium sp. 5	0.006	4.01	2.71	0	0	7	0
Canthidium sp. 6	0.006	4.02	2.75	22	0	143	26
Canthidium sp. 9	< 0.001	4.20	2.80	8	23	13	0
Canthon chalybaeus Blanchard, 1843	0.024	6.74	4.72	0	12	104	0
Canthon lituratus (Germar, 1824)	0.007	5.05	3.15	0	4	250	65
Canthon mutabilis Lucas, 1857	0.013	5.21	3.46	0	0	6	36
Canthon septemmaculatus histrio (Serville, 1828)	0.062	9.13	6.53	1	17	3	0
Canthon smaragdulus (Fabricius, 1781)	0.280	14.85	9.14	128	20	0	0
Canthon sp. 1	0.021	5.15	3.41	0	0	2	0
Canthon sp. 2	0.004	3.53	2.46	2	0	36	47
Canthon sp. 3	0.012	5.13	3.41	37	4	0	0
Canthon sp. 4	0.014	5.32	3.57	3	10	6	0
Deltochilum amazonicum Bates, 1887	0.730	21.80	11.98	0	5	0	0
Deltochilum carinatum (Westwood, 1837)	0.180	13.80	8.60	1	0	0	0
Deltochilum enceladum Kolbe, 1893	1.65	37.13	22.40	2	2	0	0
Deltochilum orbiculare Lansberge, 1874	0.677	23.07	16.70	2	1	0	0
Deltochilum sp. 1	0.157	10.82	7.55	0	2	1	0
Deltochilum sp. 2	0.080	9.20	6.08	1	0	1	0
Dichotomius globulus (Felsche, 1901)	0.056	12.26	7.65	29	29	9	0
Dichotomius lucasi (Harold, 1869)	0.172	13.77	8.78	74	57	4	0
Dichotomius mamillatus (Felsche, 1901)	0.565	19.47	11.99	3	6	0	0
Dichotomius nisus (Olivier, 1789)	0.501	21.39	13.43	0	1	1	164
Dichotomius nr *cuprinus* (Felsche, 1901)	0.277	17.08	10.43	3	1	0	1
Dichotomius melzeri (Luederwaldt, 1922)	0.513	21.63	13.70	1	2	0	0
Digitonthophagus gazella (Fabricius, 1787)	0.055	10.56	6.48	0	0	0	11
Eurysternus caribaeus (Herbst, 1789)	0.078	13.20	6.41	19	36	0	0
Eurysternus cayennensis Laporte, 1840	0.043	9.71	4.78	5	6	2	0
Eurysternus foedus Guérin-Ménéville, 1844	0.153	15.96	7.57	6	1	0	0
Eurysternus hamaticollis Balthasar, 1939	0.106	15.89	7.91	14	19	1	0
Eurysternus nr *hirtellus* Dalman, 1824	0.010	6.10	2.80	0	3	0	0
Eurysternus jessopi Martínez, 1988	0.026	9.41	3.81	7	3	0	0
Eurysternus velutinus Bates, 1887	0.055	12.90	5.45	0	1	0	0
Eurysternus sp.	0.151	17.48	8.57	11	1	0	0
Ontherus appendiculatus (Mannerheim, 1829)	0.065	10.04	6.01	1	1	3	30
Onthophagus bidentatus Drapiez, 1819	0.009	5.19	2.99	248	106	0	62
Onthophagus clypeatus Blanchard, 1843	0.030	5.80	3.63	2	0	0	0
Onthophagus onthochromus Arrow, 1913	0.038	10.52	5.88	3	0	0	0
Onthophagus ranunculus Arrow, 1913	0.008	4.92	2.95	5	0	0	0
Onthophagus rubrescens Blanchard, 1843	0.009	4.88	2.79	12	0	0	3
Oxysternon macleayi Nevinson, 1892	0.330	17.30	11.50	1	0	0	0
Phanaeus chalcomelas (Perty, 1830)	0.208	14.90	9.68	3	2	0	0
Pseudocanthon xanthurus (Blanchard, 1843)	0.008	4.04	2.72	0	0	0	8
Scybalocanthon sp.	0.047	9.08	5.94	20	2	0	0
Sylvicanthon candezei (Harold, 1869)	0.025	6.92	5.04	4	1	0	0
Trichillum externepunctatum Borre, 1880	< 0.001	2.56	1.83	0	4	243	461
Trichillum sp. 1	< 0.001	2.56	1.59	10	2	0	0
Trichillum sp. 2	0.002	3.03	2.05	25	42	46	2652
Uroxys sp. 2	0.002	2.79	1.93	30	0	57	0
Uroxys sp. 3	0.003	2.99	2.05	50	0	7	0
Uroxys sp. 4	< 0.001	3.30	2.50	3	5	0	3

* Weight is dry weight.