ECOLOGY, BEHAVIOR AND BIONOMICS

Dung Beetle (Coleoptera: Scarabaeidae) Assemblages across a Natural Forest-Cerrado Ecotone in Minas Gerais, Brazil

RENATA DURÃES[1], WALDNEY P. MARTINS[2] AND FERNANDO Z. VAZ-DE-MELLO[3]

[1]*Depto. Biologia Geral, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais*
Current address: Dept. Biology, Univ. Missouri-St. Louis and International Center for Tropical Ecology, One University Blvd., 63121, Saint Louis MO, USA rrd32@umsl.edu
[2]*Depto. Zoologia, Instituto de Ciências Biológicas, UFMG, C. postal 486, 31270-901, Belo Horizonte, MG, Brazil wpmonkey@yahoo.com.br*
[3]*Lab. Ecologia de Comunidades, Depto. Biologia Geral, Universidade Federal de Viçosa.Current address Instituto de Ecología, A. C., Depto. Biodiversidad y Ecología Animal, km 2.5, Carretera Antigua a Coatepec 351 Congregación El Haya, 91070, Xalapa, Veracruz, Mexico, scarab@insecta.ufv.br, vazdemello@gmail.com*

Neotropical Entomology 34(5):721-731 (2005)

Comunidade de Besouros Rola-Bosta (Coleoptera: Scarabaeidae) ao Longo de um Ecótono Natural Entre Floresta e Cerrado em Minas Gerais

RESUMO - Variações em comunidades ao longo de ecótonos fornecem exemplos claros de como os organismos percebem e respondem a mudanças ambientais, mesmo em escalas reduzidas. Besouros rola-bosta (Scarabaeidae) têm sido usados como bioindicadores de qualidade de hábitat devido à sua sensibilidade a mudanças ambientais. Neste estudo, foram feitas amostragens de escarabeídeos ao longo de um ecótono natural entre hábitats de floresta e cerrado no Brasil e examinaram-se as mudanças associadas na estrutura da comunidade. Também foram examinados os efeitos de borda, aqui definidos como mudanças consistentes em atributos da comunidade em relação à distância da borda entre os dois hábitats. Densidades de indivíduos e espécies foram maiores na floresta do que no cerrado, porém a riqueza total foi similar entre os dois hábitats depois que as diferenças em tamanho amostral foram controladas. A composição de espécies foi bastante diferente entre a floresta e o cerrado, e as espécies compartilhadas pelos dois hábitats foram consistentemente mais abundantes em um ou outro. Efeitos de borda não foram detectados na riqueza ou composição de espécies, e apenas efeitos sutis foram observados na abundância. Conclui-se que o tipo de hábitat tem um efeito muito mais acentuado na estrutura da comunidade do que a presença da borda: escarabeídeos responderam fortemente à mudança de hábitat, mas muito mais sutilmente à proximidade da borda entre os dois hábitats.

PALAVRAS-CHAVE: Biodiversidade, Mata Atlântica, efeito de borda, distribuição espacial

ABSTRACT - Variations in assemblage attributes across ecotones provides clear examples on how organisms perceive and respond to environmental changes, even at small scales. Dung beetles (Scarabaeidae) have been used as bioindicators of habitat quality due to their sensitivity to environmental changes. Dung beetles were sampled across a natural forest-cerrado ecotone in Brazil, and associated changes in assemblage structure were examined. Edge effects, here defined as consistent changes in assemblage parameters in relation to the distance to the forest-cerrado border, were also examined. Density of individuals and species were higher in the forest than in the cerrado, but overall richness was similar between habitats after controlling for sample sizes. Species composition differed greatly between habitats, and shared species were consistently more abundant in one or another habitat. Edge effects were not detected on richness nor species composition, and only weak effects were observed on abundance. It is concluded that the effect of the habitat (forest *vs*. cerrado) has a much stronger effect on the assemblage structure than the presence of the edge: dung beetles responded strongly to change in habitats, but weakly to the proximity of the edge between these habitats.

KEY WORDS: Biodiversity Atlantic Forest, edge effect, spatial distribution

Organisms have naturally patchy distributions within their species ranges, even in the absence of physical barriers, due to the interplay between their ecological requirements and habitat characteristics imposing environmental limits to expansion (Hoffmann & Blows 1994, Brouat *et al*. 2003). Variation in the attributes of species assemblages across ecotones provides clear examples on how organisms may perceive and respond to environmental changes, even at very small scales (Heliöla *et al*. 2001).

Ecotones are zones of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between the systems (Holland & Risser 1991). The transition between adjacent environments can be sharp or gradual and be characterized by abiotic and biotic conditions dissimilar from the adjacent habitats, collectively called edge effects (Murcia 1995). The intensity and direction of edge effects on the population levels of organisms can be extremely variable across species (Heliöla *et al*. 2001, Kotze & Samways 2001, Baker *et al*. 2002), and even among populations of a single species (Baker *et al*. 2002). Thus, although the term edge effect was first introduced to describe the tendency for increased population abundance at the transition between two habitats (Odum 1971), it is clear that different species can respond positively, negatively or neutrally to edges (Murcia 1995, Baker *et al*. 2002). Edge effects caused by forest fragmentation are known to affect insect abundance and diversity, and can influence directly and indirectly higher-order interactions and ecosystem functioning (Didham *et al.* 1996). However, very little is known about processes and patterns across natural ecotones, especially sharp ones (Kotze & Samways 2001). The responses of organisms to transitional environments can provide information about ecological factors determining their spatial and geographical distributions, as well as on the possible effects of anthropogenic-driven environmental changes upon the distribution of these species.

Dung beetles (Scarabaeidae) compose an extremely abundant and species rich group of organisms, as well as taxonomically and functionally well defined (Finn *et al.* 1999), hence being especially suitable for community studies. Their efficiency in locating and removing debris (Janzen 1983, Gill 1991), controlling parasites (Fincher 1973) and secondarily dispersing seeds (Janzen 1983, Estrada & Coates-Estrada 1991, Shepherd & Chapman 1998) make them important components in the functioning of terrestrial ecosystems. Neotropical dung beetles are characteristically generalist foragers, an attribute that might contribute to their large diversity in this region (~1,250 species; Gill 1991; Hanski & Cambefort 1991a, b). Both adults and larvae are detritivorous, and food resources are composed mainly of feces, along with carrion and fallen fruits (Favila & Halffter 1997). Dung patches provide islands of an energetically rich feeding resource, and are often used for mating and oviposition as well. However, dung constitutes a resource spatially and temporally unpredictable and ephemeral, what influences significantly the spatial distribution and the competitive relationships within and between species that depend on it (Cambefort 1991, Hanski & Cambefort 1991a, Hirschberger 1998). Thus, some degree of niche partitioning (ecological, temporal or spatial) is expected to be important in promoting species coexistence within a guild (Janzen 1983, Gill 1991, Hirschberger 1998). Indeed, most coprophagous beetles do not disperse long distances to find food and have a stenotopic distribution in relation to vegetation types (Cambefort & Hanski 1991). Because of this, they usually are very sensitive to environmental changes and are considered well-suited as bioindicator organisms (Howden & Nealis 1975, Klein 1989, Favila & Halffter 1997).

Ecological studies on Southeastern Brazilian dung beetles are scarce (Louzada *et al*. 1996, Louzada & Lopes 1997, Vaz-de-Mello & Louzada 1997), and virtually non-existent for species occurring in the biome of Cerrado. In this study, we sampled dung beetles across a natural ecotone between an area of Atlantic Forest and an area of Cerrado shrubland in order to examine the associated changes in patterns of assemblage structure. These habitats are structurally very different and the transition between them is very sharp in the study area. Considering that dung beetles, as a group, are sensitive to environmental changes, we expect assemblage parameters (abundance, richness, diversity, species composition) to be more similar between dung patches within a same habitat than between patches located in different habitat, regardless of the distance between patches. Additionally, we expect to find significant edge effects on the populations, demonstrated by consistent changes of assemblage parameters according to the distance from the forest-cerrado border.

Material and Methods

Study Area. The study was carried out in the Barreiro Protection Area (43º50'W 19º50'S, 900 m a.s.l., 1,406 ha), located in the Rola-Moça State Park, Belo Horizonte municipality, Minas Gerais state, Brazil. The region is situated in the transition between the biomes of Atlantic Forest and Cerrado (Ab'Saber 1977). The area presents floristic and faunistic elements characteristics of each one of these provinces, alternating formations of cerrado, rupestrian fields, riparian forests and mesic forests according to the soil type and elevation (CETEC 1993). Climate in the region is characterized by a rainy and hotter season between October and March, and a dry and milder season between April and September. Mean temperature ranges from 18°C and 24°C and total annual rainfall is around 1,300 mm (CETEC 1983).

The study site consists of a natural ecotone between a 50-ha mesic Atlantic Forest fragment at advanced succession stage (~150 yr old) and an area of cerrado *stricto sensu* shrubland. The forest has a relatively open understorey, and a canopy layer of 20 m with emergent trees up to 30 m in height. The cerrado area is composed of a dense shrubby understorey (up to 2-3 m high), and scattered higher trees. The transition between the two formations is very sharp, enabling us to recognize a borderline between both environments.

Assemblage Composition and Spatial Distribution. The insects were sampled between 14 and 26 November 1998, hence during the wet season, with baited pitfall traps (Finn *et al.* 1999). Plastic vials (19 cm diameter and 11 cm depth) were buried with the rim level with the ground, and half filled with a solution of water, dishwashing soap and formaldehyde used to kill and preserve the insects. The bait was placed in a small plastic cup suspended by wires in the center of the plastic vials, at ground level. A plastic roof was mounted over each trap as protection against rain. These roofs were high enough so as not to interfere with the access of insects to the bait. The bait consisted of a homogeneous mixture of maned wolf (*Chrysocyon brachyurus*), capuchin monkey (*Cebus apella*) and coati (*Nasua nasua*) fresh feces. The feces were provided by a zoological garden (Fundação Zoobotânica de Belo Horizonte). These three mammal species are omnivorous in nature and occur in the study area (Câmara *et al.* 1999, Marcos Maldonado-Coelho & Renata Durães, pers. obs.). In the zoo, the monkeys feed on fruits, vegetables, eggs and dog food; coatis receive fruits, sweet potatoes and dog food; maned wolves receive bananas, meat and dog food.

Six trap lines were established, three in each environment, at 15, 45, and 75 m from the forest-cerrado border and running parallel to it. Three traps (a, b, and c) were established in each transect, separated from each other by 20 m. Thus, an area of 150 x 40 m was sampled (0.6 ha), with a total of 18 pitfall traps (9 in each environment). After being baited, the traps were checked after 48h (or, at one occasion, after 120h). The entire content of the plastic vial was removed, and the preserving solution and bait were renewed. Captured insects were preserved in a 70% solution of ethanol. In the laboratory, dung beetles were sorted, counted and identified to the species or genus taxonomic level. Each trap was baited four times, totaling 5,185 trap-hours along 11 sampling days. All individuals are deposited as voucher specimens at the Laboratório de Ecologia, Departamento de Biologia of the Universidade Federal de Lavras and in the private collection of one of the authors (FZVM).

Data Analyses. The four samples taken for each pitfall trap were pooled for the analyses. In all cases when parametric tests were used, data was previously checked for normal distribution with Kolmogorov-Sminof test and for variance homogeneity with Bartlett chi-square test.

Density of individuals or species (individuals or species/trap) was compared between habitats by Student's *t*-tests (Sokal & Rohlf 1981). Because it is not biologically informative to compare absolute values of richness or diversity (Shannon diversity index *H*', Magurran 1988) between samples of different sizes, rarefaction analyses were conducted to make these comparisons between cerrado and forest. Rarefaction analysis uses randomization techniques to build new assemblages with comparable sample sizes. A total of 1,000 randomizations were performed, and mean values of richness or diversity, along with 95% confidence intervals, are presented. If the observed richness (or diversity) in the assemblage with the smaller sample size fell within this confidence interval, the parameter was considered not significantly different between assemblages at comparable sample sizes. These analyses were performed in Ecosim version 7.58 (Gotelli & Entsminger 2001).

Species accumulation curves for each habitat were built with randomized sample order; mean richness values and standard deviations after 100 randomizations are presented. Total richness in each habitat was estimated by extrapolation of the species accumulation curve, using Chao1 estimator, $S^*_1 = S_{obs} + (a^2 / 2b)$, where S_{obs} is the observed number of species in a sample, *a* is the number of observed species that are represented by only a single individual in that sample (singletons), and *b* is the number of observed species represented by two individuals in that sample (doubletons) (Colwell & Coddington 1994). Colwell & Coddington (1994) recommended the Chao1 estimator because it was found to perform well in several test data sets, and especially when most of the species are represented by few individuals, as in this study. Community similarity between forest and cerrado was estimated by the Morisita-Horn quantitative index (modified by Wolda; Magurran 1988). This index considers both species richness and abundance and varies from 0 to 1. The program EstimateS version 6.0b1 was used to estimate similarity, total richness and to build randomized richness curves (Colwell 1997).

Frequency distribution of species in abundance classes was compared between environments using two-sample Kolmogorov-Sminof test (Sokal & Rohlf 1981). Two-way ANOVAs were used to test the effect of distance from the forest-cerrado borderline in the species density or richness in each environment (Sokal & Rohlf 1981). Habitat and distance from the border were used as fixed factors, and abundance or richness was used as dependent variables. These analyses were conducted using Statistica for Windows 5.1 (StatSoft 1996).

To test the hypothesis that pairs of dung patches located in a similar habitat are more similar in terms of species composition than pairs of patches located in different habitats, regardless of geographical distance, we used partial Mantel tests (Mantel 1967, Smouse *et al*. 1986, Fortin & Gurevitch 2001). Partial Mantel tests examine the relationship between two matrices, while controlling for a third matrix. Statistical significance of the observed *Z* value is then assessed by comparison to a null-model distribution obtained by permuting the arrangement of the elements of one of the matrices. The three matrices used in these analyses were as follow: matrix A depicts pairwise Morisita-Horn similarities; matrix B, the treatment matrix, exhibits a value of 1 when the two patches being compared are located in the same habitat, and a value of 0 when they are in different habitats; matrix C contains the Euclidean distances, in meters, between the two patches being compared. We first tested for the influence of habitat on similarity by correlating matrices A (similarity) and B (habitat) while controlling for matrix C (distance). We then tested the alternative hypothesis that distance between patches is more important than habitat in determining the similarity between them by correlating matrices A and C, while controlling for matrix B. A total of 9,999 iterations were performed for each test.

We also used partial Mantel to test the hypothesis that the distance from the border forest-cerrado influences the species composition in the samples. If this hypothesis holds, we expect the similarity between patches to be smaller the more different are their locations in relation to the border. Therefore, we examined the relationship between species similarity (matrix A) and a distance matrix where pairs of patches received a value of: 1, if both were separated from the border by the same distance (e.g., both are at 15, 35, or 75 m from the border); 2, if they were at different but adjacent distances from the border (at 15 and 35 or at 35 and 75 m, respectively); 3, if they were at different and non-adjacent distances from the border (at 15 and 75 m, respectively). The relationship was controlled for habitat (matrix B as the constant matrix), and a total of 9,999 iterations were performed. All Mantel tests were performed with PASSAGE 1.0 (Rosenberg 2001).

Additionally, Detrended Correspondence Analysis (DCA) was used to ordinate traps according to similarities in species composition and abundance (Hill & Gauch 1980, Ludwig & Reynolds 1988). Our expectation was that traps located in the same habitat (forest vs. cerrado) would be grouped closer to each other than to traps located in a different habitat, regardless of distance between them. DCA is a derivative of correspondence analyses that has the advantage of reducing the compression at the first axis and the distortion at the second and further axes (Hill & Gauch 1980). For this analysis, the abundance of each species at each sample was entered in a matrix (samples in columns and species in rows). This analysis was carried out in PC-ORD for Windows version 4.01 (McCune & Mefford 1999).

Results

Patterns of Richness and Abundance. A total of 754 individuals was captured, 128 in the cerrado and 626 in the forest (Table 1). The pooled total of individuals sampled per trap varied from 5 to 31 in the cerrado, and from 38 to 100 in the forest. Density of dung beetles was significantly higher in the forest than in the cerrado (forest: 69.5 ± 21.6 individuals/trap, cerrado: 14.2 ± 7.5; $t = -7.253$; d.f. = 16; $P < 0.001$).

Ten genera and 22 species in four tribes were represented in the samples (Table 1). Nine species were captured exclusively in the forest, five species exclusively in the cerrado, and eight were present in both habitats. The mean number of species per trap was significantly higher in the forest than in the cerrado (forest: 8.4 ± 1.1 species/trap, cerrado: 4.2 ± 1.8; $t = -5.829$; d.f. = 16; $P < 0.001$). Although the observed richness in the forest was higher than in the cerrado (17 vs. 13 species, Table 1), the result of the rarefaction analysis shows that, at similar sample sizes, the observed richness in the cerrado fell exactly at the lower bound of the 95% confidence region of forest richness (mean richness in the forest for $N = 128$: 15.17 species; 95% confidence interval: 13-17 species). Thus, taking in consideration the difference in sample sizes, richness does not seem to be significantly different between both habitats.

Species accumulation curves showed tendency to stabilization in cerrado and forest, although richness was still increasing in both habitats after the last sample was taken (Fig. 1). Standard deviations around mean values of richness after 100 randomizations were larger for the cerrado than for the forest, indicating that species composition among samples was more heterogeneous in the cerrado, in comparison to more similar samples in the forest (Fig. 1). Estimated richness using Chao1 indicated that the cerrado was more completely sampled in absolute terms (observed richness = 13 species; estimated richness = 16.6 ± 4.9 species) than the forest (observed richness = 17 species; estimated richness = 21.5 ± 0 species). However, in terms of percentage of the estimated richness, cerrado and forest were equally sampled (78.3 and 79% of the estimated richness sampled in cerrado and forest, respectively).

Considering the complete samples, species diversity was lower for the forest assemblage ($H'_{\text{cerrado}} = 1.72$; $H'_{\text{forest}} = 1.52$). However, using rarefaction analysis to compare species diversity at similar sample sizes resulted in a significantly lower diversity in the cerrado (mean H'_{forest} across 1,000 randomizations = 2.10, 95% confidence interval = 1.97 – 2.21; compare with $H'_{\text{cerrado}} = 1.72$). The Morisita-Horn similarity between the two assemblages was moderate, estimated as 56%. The frequency distribution of species abundance classes was statistically similar between habitats ($D_{\text{max}} = -0.439$, $n_1 = 13$, $n_2 = 17$, $P > 0.10$), indicating that species dominance and evenness are similar between habitats (Fig. 2).

Abundance of dung beetles per trap was significantly affected by both habitat and distance from the border, as well by the interaction between these factors (Table 2). This was the result of, first, reduced abundances in the cerrado in comparison with the forest, at all distances, and, second, reduced abundances in the forest at intermediate distances from the border (45 m, Fig. 3A). Abundance in the cerrado did not differ according to distance to the border (Fig. 3A).

Number of species per trap, on the other hand, varied significantly between habitats, but was not affected by distance from the border neither by the interaction between habitat and distance (Table 2). Richness was higher in forest than in cerrado, at all distances (Fig. 3B).

Species Composition. Species in the Dichotomiini tribe were predominant, followed by Canthonini. Eurysternini and Onthophagini were rare, each tribe presenting only one infrequent species. No species from the tribe Phanaeini were captured. *Canthidium* sp4 and *Uroxys* sp1 were the most abundant species in the cerrado (38% and 27% of total number of individuals captured in this habitat, respectively). In the forest, *Uroxys* sp1 was by far the dominant species (57% of individuals captured in this habitat) (Table 1). Sampled species reflected partially the tribe structure characteristic in the Neotropics, where Dichotomiini accounts for ~50% of the described species, Canthonini for ~27%, Phanaenini for ~13%, Onthophagini for ~8% and Eurysternini for ~2% (Louzada & Lopes 1997). Dichotomiini has broad distribution and is composed basically by dweller species. In this study, both small (*Ateuchus* spp., *Canthidium* spp., *Uroxys* spp.) and large bodied species (*Dichotomius* spp.) were captured. Canthonini includes species inhabiting different environment types, and most are small dung rollers, such as *Canthon* spp. and *Sylvicanthon* spp. Eurysternini is

Table 1. Dung beetles collected in pitfall traps in adjacent areas of cerrado and forest in Belo Horizonte, MG, Brazil.

Habitat	Cerrado										Forest										
Distance from border (m)	15			45			75			Total cerrado	15			45			75			Total forest	Total
Sample replicate	a	b	c	a	b	c	a	b	c		a	b	c	a	b	c	a	b	c		
Tribe/species																					
Dichotomiini																					
Ateuchus sp1	0	0	0	0	0	0	0	0	0	0	3	2	2	4	0	2	0	1	1	15	15
Ateuchus sp2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	0	1	0	0	5	5
Canthidium sp1	0	4	0	0	1	0	0	0	5	10	15	17	3	7	3	6	33	7	3	94	104
Canthidium sp2	0	0	0	0	0	0	0	0	2	2	6	0	5	3	3	7	10	11	4	49	51
Canthidium sp3	1	3	1	6	0	2	0	0	3	16	0	2	1	0	0	0	0	0	0	3	19
Canthidium sp4	10	2	9	6	3	12	4	2	1	49	0	0	0	0	0	0	0	0	0	0	49
Canthidium sp5	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	3	3
Dichotomius affinis	0	0	0	0	0	0	0	1	0	1	13	6	29	4	0	1	1	1	1	56	57
D. bicuspis	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	6	1	2	10	11
D. depressicollis	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1
D. luctuosus	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	3	3
D. aff. *mundus*	0	0	0	0	0	0	0	0	1	1	6	0	0	0	1	2	4	0	1	14	15
Uroxys sp1	0	20	2	1	0	0	0	9	3	35	20	40	34	36	30	19	21	74	82	356	391
Uroxys sp2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	4	4
Canthonini																					
Canthon chalybaeus	0	1	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	2
C. luctuosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
C. septemmaculatus histrio	0	0	0	1	2	1	1	2	0	7	0	0	0	0	0	0	0	0	0	0	7
Sylvicanthon foveiventris	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	3	1	6	6
Euhyboma brasiliense	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Rubrohyboma rubripenne	0	1	0	0	0	0	0	0	0	1	0	1	0	1	0	0	2	0	1	5	6
Eurysternini																					
Eurysternus hirtellus	0	0	0	1	0	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	2
Onthophagini																					
Onthophagus sp1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Total of individuals	12	31	13	15	6	16	5	14	16	128	67	69	78	57	42	38	78	100	97	626	754
Total of species	3	6	3	5	3	4	2	4	8	13	10	7	9	8	8	7	8	9	10	17	22

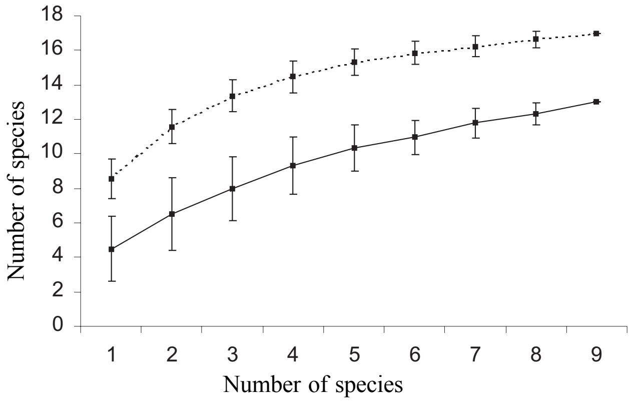

Figure 1. Cumulative curves of dung beetle species discovery for the forest (dashed line) and the cerrado (solid line). Samples were taken at random, without replacement, and the curves represent mean richness values after 100 randomizations. Bars represent standard deviations.

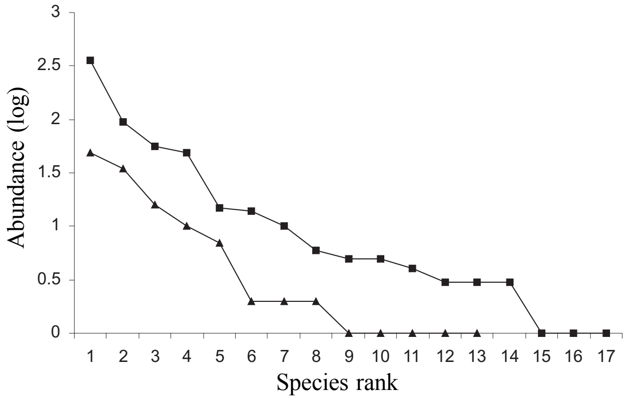

Figure 2. Abundance distributions of dung beetle species in adjacent areas of cerrado (triangles) and forest (squares).

restricted to the Neotropics and includes mostly forest resident species. The small-bodied species *Eurysternus hirtellus* Dalman, captured in the cerrado, was the only representative of this tribe. Ontophagini is distributed predominatly in Amazon and Central America. This tribe was represented by a single individual of *Onthophagus* sp., a small-bodied burying species, captured in the cerrado.

Species similarity between patches presented a large variance, ranging from 0 to 0.99 among all pairs, from 0.04 to 0.98 between patches in the cerrado, from 0.48 to 0.99 between patches in the forest, and between 0 and 0.97 between patches located in different habitats. There was a significant positive correlation between pairwise species similarity and habitat treatment, after controlling for distance between dung patches (observed $Z = 14.61$, $r = 0.38$, right-tailed $P = 0.001$; 9,999 iterations). In other words, patches located in the same habitat were more similar in species composition than patches located in different habitats (Fig. 4A). There was no correlation between species similarity and distance between patches, when controlling for habitat (observed $Z = -50.88$, $r = -0.02$, left-tailed $P = 0.40$; 9,999 iterations). This result means that similarity between patches is not significantly higher for those closer to each other, after the effect of the habitat occupied for them is accounted for (Fig. 5). Finally, patches located at more similar distances from the border were not more similar in terms of species composition, after the effect of habitat have been controlled for (observed $Z = 2.46$, $r = -0.04$, right-tailed $P = 0.36$; 9,999 iterations; Fig. 4B).

The DCA ordination produced four axes, which together, accounted for 51% of the total variance observed in the dataset (Table 3). Most of the explained variance (36%), however, was due to the first axis alone. Sampling patches were clearly separated by habitat along this first axis, while there was no clear separation due to distance from the border (Fig. 6).

Discussion

Dung beetles are considered extremely sensitive to habitat changes and have been proposed as bioindicator organisms of habitat quality (Howden & Nealis 1975, Didham *et al.* 1996, Favila & Halffter 1997). For example, dung beetles in forest fragments in Central Amazonia had reduced richness and abundance when compared to the continuous forest (Klein 1989). Although limited to one season, this study can be representative of the dynamics occurring in the contact zone between two very distinct habitats. We investigated two types of habitat effects on the dung beetle assemblages: edge effects related to the presence of the forest-cerrado border, and differences between the forest and the cerrado *per se*.

Edge effects, here defined as consistent responses in relation to the distance to the forest-cerrado border, could be observed in some of the assemblage parameters investigated (abundance), but not in others (richness and species composition), showing how distinct processes of community structure can respond differently to edge effects, as demonstrated by other studies (e.g., Klein 1989, Feener

Table 2. Two-way ANOVAs testing the effect of habitat and distance from the cerrado-forest border on abundance or richness of dung beetles in pitfall traps.

Factor	Abundance			Richness		
	D.F.	*F*	P	D.F.	*F*	P
Habitat	1	181.29	0.001	1	28.31	0.001
Distance	2	10.71	0.002	2	0.53	0.602
Habitat x distance	2	10.85	0.002	2	0.14	0.873

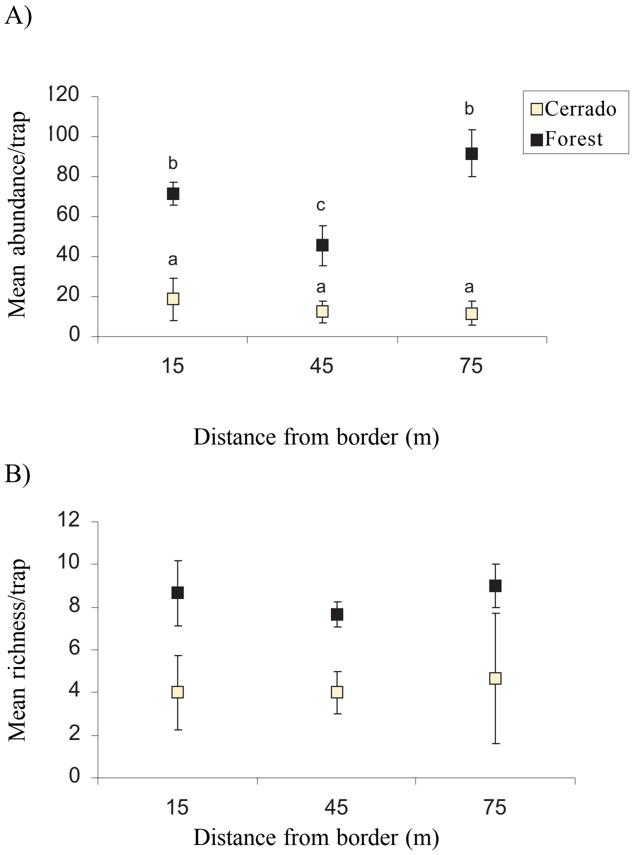

Figure 3. Mean abundance (A) and richness (B) of dung beetles in pitfall traps located in adjacent areas of cerrado and forest, at different distances from the border between both habitats. Bars indicate 1 S. D., N = 3 for each treatment. In (A), equal letters indicate treatments with significantly similar abundances, while different letters indicate treatments with significantly different abundances (tested with Tukey Honest Significant Differences test for post-hoc multiple comparisons, Zar 1999).

& Schupp 1998). Moreover, the effect of the edge can vary among species occupying each one of the adjacent environments. In this study, we observed a decrease in abundance at intermediate distances from the border in the forest, while no effect on abundance was observed in the cerrado. Non-monotonic responses to edge effects have been found in several studies, and Murcia (1995) suggests these may be caused by the interaction among two or more abiotic or biotic variables acting at different spatial scales. Other studies have found that beetles that utilize dung patches may as well respond monotonically to edge effects. Kotze & Samways (2001), for example, observed a steady decrease in carabid beetles abundance and richness along natural forest-grassland ecotones in South Africa, although differences in richness were not significant [carabid beetles are predators rather than coprophages, but they prey on dung beetles and other insects utilizing the dung patches (Hanski 1991)]. Along an open forest-rainforest ecotone in Australia, Hill (1996) observed a sharp increase in dung beetle richness in the direction of the rainforest, but no significant changes in abundance.

Habitat type had a much more pronounced effect on assemblage parameters than edge effects. Abundance, species richness and species composition differed markedly between habitats. Both abundance and richness were greater in the forest than in the cerrado, although, after controlling for differences in sample size by rarefaction, richness was very similar in both habitats. Similarly, Janzen (1983) compared forest sites and adjacent pastures in Costa Rica and found that five species of large nocturnal dung beetles occurring in both habitats were much more abundant in the forest. It is likely that the higher abundance of dung beetles in the forest is related to higher resource availability. Mammal feces are the main resource used by dung beetles, and forest habitats usually present a richer mammal fauna than open areas (Alho 1981, Medellin & Redford 1992). A faunal assessment carried out in the study area indeed suggests that mammal abundance is higher in the area of forest than in the cerrado (Câmara *et al.* 1999). Additionally, dung patches in the cerrado are exposed to higher temperatures and light levels than in the forest. This may reduce the time interval during which they are available to beetles and increase adult and

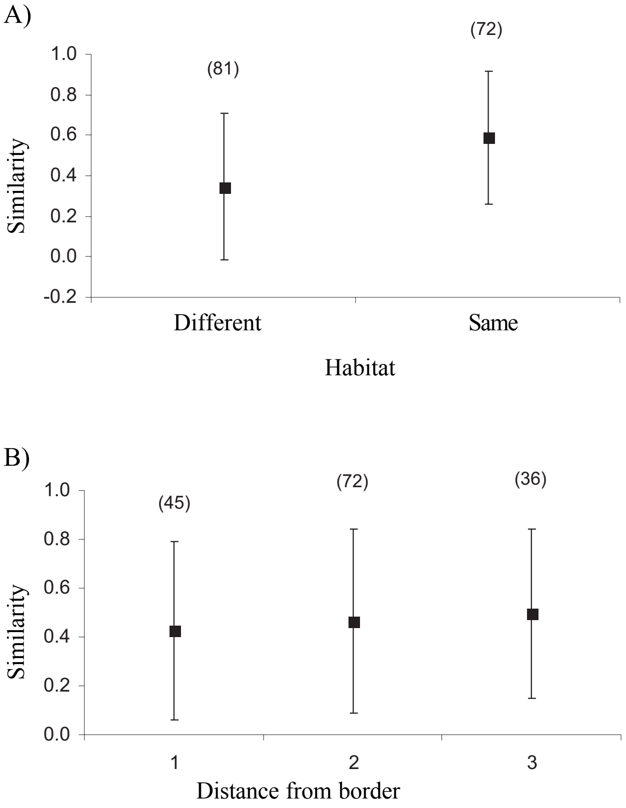

Figure 4. Morisita-Horn similarity values (mean ± 1 S.D.) for pairs of dung patches (A) located in the same habitat or in different habitats, or (B) for pairs of patches separated from the border by a same distance (1), by different but adjacent distances (2), or by different and non-adjacent distances (3). Number of comparisons between parentheses above bars.

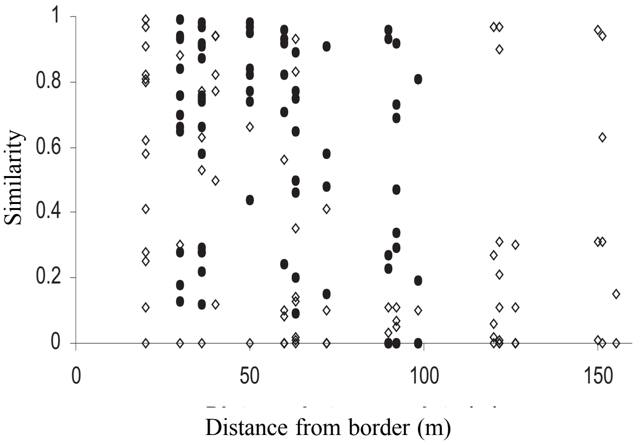

Figure 5. Morisita-Horn similarity for pairs of dung patches separated by distances varying from 20 to 155 meters and located at the same (filled symbols) or different (open symbols) habitats.

Table 3. DCA eigenvalues and coefficients of determination (r^2) for the correlation between ordination distances and distances in the original n-dimensional space described by dung beetle assemblages in a forest-cerrado ecotone.

Axis	1	2	3
Eigenvalue	0.768	0.195	0.056
Explained variance (%)			
Increment	0.361	0.049	0.098
Cumulative	0.361	0.410	0.508

larva mortality (Klein 1989, Galante *et al.* 1995).

Although the frequency distribution of species abundance classes did not differ significantly between both habitats, samples in the forest were more similar to each other in comparison to samples in the cerrado, showing that the spatial distribution of the species in the cerrado is more heterogeneous. It is possible that the insects are responding to fine-scale structural differences within a given habitat, although we do not have enough information to test this hypothesis.

In terms of species composition, the two habitats could be clearly separated in an ordination analysis; however, there was no clear separation between transects, showing once more that the exact location of the dung patches in relation to the border had a lessened effect in comparison to the habitat where the patches were located. Similarly, Heliöla *et al.* (2001) also found marked differences in richness and species composition of carabid beetles between forest and clear cut areas separated by a "hard edge", but did not detect changes in richness or abundance associated with the edge *per se*. Additionally, Kotze & Samways (2001) observed marked differences between forest and grassland carabid assemblages in natural ecotones in South Africa, but no species were especially associated with the edges.

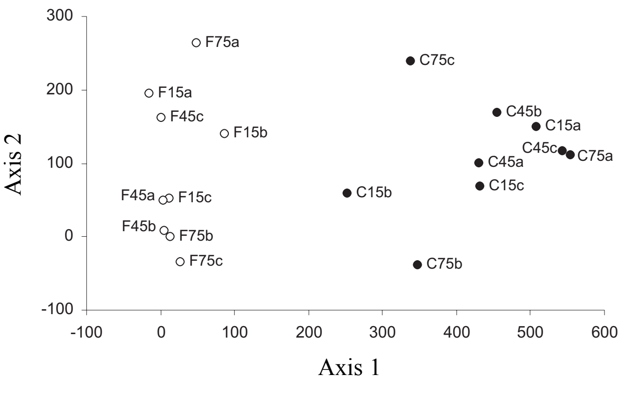

Figure 6. DCA ordination of trapping points used to sample dung beetles in adjacent areas of cerrado and forest, according to species composition and abundance, axes 1 vs. 2 depicted. Sampling point codes: F = forest, C = cerrado; 15, 45, or 75 = distance of pitfall from forest-cerrado border, in meters; a, b, or c = sample replicates.

The relatively low species similarity between forest and cerrado (56%) and the large number of species unique to each habitat (9/22 and 5/22 in the forest and cerrado, respectively) further demonstrate the pronounced differences between both assemblages. Moreover, species common to both habitats were in all cases considerably more abundant in forest [*Canthidium* sp1, *Canthidium* sp2, *Dichotomius affinis* (Felsche), *D. bicuspis* (Germar), *D.* aff. *mundus* (Harold), *Uroxys* sp1, *Rubrohyboma rubripenne* (Gory)] or in cerrado (*Canthidium* sp3), suggesting strong habitat preference. These observations agree with Hanski & Cambefort's (1991a) assertion that, in tropical ecosystems, dung beetle communities are very diverse in forest as well as in more open areas, but present very low species overlap due to the stenotopic behavior of these organisms in relation to vegetation types. Hill (1996), for example, observed that each of the 14 most abundant dung beetle species recorded along a open forest-rainforest ecotone in Australia were consistently more abundant in one of the two habitats.

One could argue that maybe we did not observe marked edge effects on the dung beetle assemblages because of an inadequate choice of the sampling spatial scale. For example, it is possible that the spatial scale was too small, such that edge effects were operating at all distances sampled. We consider this unlikely, for several reasons. First, studies on dung beetles and other arthropods have adopted similar sampling scales when investigating changes on community patterns along habitat gradients, and this scale was shown adequate in these studies (Didham *et al.* 1996, Hill 1996, Heliöla *et al.* 2001). Second, most edge effects seem to be dampened after 50 m into the forest (Murcia 1995). Finally, coprophagous beetles usually do not disperse long daily distances (Cambefort & Hanski 1991). Alternatively, it could be that the scale was too large, and failed to detect edge effects that would be acting between the 15-m transect on the forest and the 15-m transect on the cerrado. Because we did not have a transect right along the border between both habitats, we cannot conclusively exclude this hypothesis. However, the fact that in the study area the transition between the two habitats is natural (or at least is present for a very prolonged period of time) rather than caused by anthropogenic action leads us to believe that the absence of pronounced edge effects on dung beetles is biologically real. Other studies failed to find edge effects on richness and abundance of beetles at natural ecotones, although species composition differed markedly between habitats (Kotze & Samways 2001).

In conclusion, dung beetle assemblages in each habitat were sharply distinct, and this distinctiveness could be detected at a very fine scale, confirming the stenotopic character of dung beetles in relation to habitat use and their suitability as bioindicators of habitat quality. On the other hand, these organisms seemed to be little affected by the presence of the edge, presenting only minor changes in abundance. Although it is unclear whether these observations can be generalized to systems where edges result from anthropogenic action, they demonstrate how different species parameters can respond differently to habitat changes, and suggest that species composition is a better predictor of habitat quality than abundance when using dung beetles as bioindicators.

Acknowledgments

By the time the study was conducted, RD and FZVM were supported by undergraduate research scholarships from FAPEMIG, and WPM by undergraduate research scholarship from CNPq. Presently, the authors are supported by Doctoral (RD and FZVM) or Master (WPM) Scholarships from CAPES. Miguel Ângelo Marini contributed with ideas and comments during several stages of the development of this study. Júlio Louzada, Terry Erwin, Marcos Maldonado-Coelho and Meghan Radtke improved the manuscript with valuable comments. Lucio Malizia and Ivan Jimenez assisted with some of the statistical analyses. Companhia de Saneamento de Minas Gerais (COPASA/MG) allowed access to the study area. Fundação Zoobotânica de Belo Horizonte supplied the mammal feces used as bait.

Literature Cited

Ab'Saber, A.N. 1977. Os domínios morfoclimáticos na América do Sul. Bol. Inst. Geogr. USP 52: 1-21.

Alho, C.J.R. 1981. Small mammal populations of Brazilian cerrado: The dependence of abundance and density on habitat complexity. Rev. Bras. Biol. 41: 223-230.

Baker, J., K. French & R.J. Whelan. 2002. The edge effect and ecotonal species: Bird communities across a natural edge in southeastern Australia. Ecology 83: 3048-3059.

Brouat, C., F. Sennedot, P. Audiot, R. Leblois & Y. Rasplus. 2003. Fine-scale genetic structure of two carabid species with contrasted levels of habitat specialization. Mol. Ecol. 12: 1731-1745.

Câmara, E.M.V.C., P.E. Guimarães-Filho, & S.A. Talamoni. 1999. Mamíferos das áreas de proteção especial de mananciais da Mutuca, Barreiro e Fechos na região metropolitana de Belo Horizonte, Minas Gerais. Bios 7: 57-64.

Cambefort, Y. 1991. From saprophagy to coprofagy, p.23-35. In I. Hanski & Y. Cambefort (eds.), Dung beetle ecology. New Jersey, Princeton University Press, 481p.

Cambefort, Y. & I. Hanski. 1991. Population biology, p.36-50. In I. Hanski & Y. Cambefort (eds.), Dung beetle ecology. New Jersey, Princeton University Press, 481p.

CETEC. 1983. Diagnóstico ambiental do estado de Minas Gerais – Technical report. Belo Horizonte, Fundação Centro Tecnológico de Minas Gerais.

CETEC. 1993. Desenvolvimento de metodologia para recuperação do revestimento florístico natural em áreas de proteção das captações de água da COPASA na região metropolitana da grande Belo Horizonte – Technical report. Belo Horizonte, Fundação Centro Tecnológico de Minas Gerais, 83p.

Colwell, R.K. 1997. EstimateS: Statistical estimation of species richness and shared species from samples. Version 5. http://viceroy.eeb.uconn.edu/estimates.

Didham, R.K., J. Ghazoul, N.E. Stork & A.J. Davis. 1996. Insects in fragmented forests: A functional approach. TREE 11: 255-260.

Estrada, A. & R. Coates-Estrada. 1991. Howler monkeys (*Aloautta palliata*), dung beetles (Scarabaeidae) and seed dispersal, ecological interactions in the tropical rain-forest of Los Tuxtlas, Mexico. J. Trop. Ecol. 7: 459-474.

Favila, M.E. & G. Halffter. 1997. The use of indicator groups for measuring biodiversity as related to community structure and function. Acta Zool. Mex. 72: 1-25.

Feener Jr., D.H. & E.W. Schupp. 1998. Effect of treefall gaps on the patchiness and species richness of Neotropical ant assemblages. Oecologia 116: 191-201.

Finn, J.A., T. Gittings & P.S. Giller. 1999. Spatial and temporal variation in species composition of dung beetle assemblages in southern Ireland. Ecol. Entomol. 24: 24-36.

Fortin, M.J. & J. Gurevitch. 2001. Mantel tests – spatial structure in field experiments, p.308-326. In S.M. Scheiner & J. Gurevitch (eds.), Design and analysis of ecological experiments (2nd edition). Oxford, Oxford University Press, 415p.

Galante, E., J. Mena & C. Lumbreiras. 1995. Dung beetles (Coleoptera: Scarabaeidae, Geotrupinae) attracted to fresh cattle dung in wooded and open pasture. Environ. Entomol. 24: 1063-1068.

Gill, B.D. 1991. Dung beetles in tropical American forests, p.211-229. In I. Hanski & Y. Cambefort (eds.), Dung beetle ecology. New Jersey, Princeton University Press, 481p.

Gotelli, N.J. & G.L. Entsminger. 2001. EcoSim: Null models software for ecology. Version 7.58. Acquired Intelligence Inc. & Kesey-Bear. http://homepages.together.net/~gentsmin/ecosim.htm.

Hanski, I. 1991. The dung insect community, p.5-21. In I. Hanski & Y. Cambefort (eds.), Dung beetle ecology. New Jersey, Princeton University Press, 481p.

Hanski, I. & Y. Cambefort. 1991a. Resource partitioning, p.330-349. In I. Hanski & Y. Cambefort (eds.), Dung beetle ecology. New Jersey, Princeton University Press, 481p.

Hanski, I. & Y. Cambefort. 1991b. Species richness, p.351-365. In I. Hanski & Y. Cambefort (eds.), Dung beetle ecology. New Jersey, Princeton University Press, 481p.

Heliöla, J., M. Koivula & J. Niemelä. 2001. Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest-clearcut ecotone. Conserv. Biol. 15: 370-377.

Hill, C.J. 1996. Habitat specificity and food preferences of an assemblage of tropical Australina dung beetles. J. Trop. Ecol. 12: 449-460.

Hill, M.O. & H.G. Gauch. 1980. Detrended correspondence analysis, an improved ordination technique. Vegetatio 42: 47-58.

Hirschberger, P. 1998. Spatial distribution, resource utilisation and intraspecific competition in the dung beetle *Aphodius ater*. Oecologia 116: 136-142.

Hoffman, A.A. & M.W. Blows. 1994. Species borders: Ecological and evolutionary perspectives. TREE 9: 223-227.

Holland, M.M. & P.G. Risser. 1991. The role of landscape boundaries in the management and restoration of changing environments – Introduction, p.1-7. In M.M. Holland, P.G. Risser & R.J. Naiman (eds.), Ecotones: The role of landscape boundaries in the management and restoration of changing environments. New York, Chapman & Hall, 616p.

Howden, H.F. & V.G. Nealis. 1975. Effects of clearing in a tropical rain forest on the composition of the coprophagous scarab beetle fauna (Coleoptera). Biotropica 7: 77-83.

Janzen, D.H. 1983. Seasonal change in abundance of large nocturnal dung beetles (Scarabaeidae) in a Costa Rican decidous forest and adjacent horse pasture. Oikos 41: 274-283.

Klein, B.C. 1989. The effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. Ecology 70:1715-25.

Kotze, D.J. & M.J. Samways. 2001. No general edge effects for invertebrates at Afromontane forest/grassland ecotones. Biodivers. Conserv. 10: 443-466.

Louzada, J.N.C. & F.S. Lopes. 1997. A comunidade de Scarabaeidae copro-necrófagos (Coleoptera) de um fragmento de Mata Atlântica. Rev. Bras. Entomol. 41: 117-121.

Louzada, J.N.C., G. Schiffler & F.Z. Vaz-de-Mello. 1996. Efeitos do fogo sobre a estrutura da comunidade de Scarabaeidae (Insecta, Coleoptera) na restinga da Ilha de Guriri, ES, p.161-169. In H.S. Miranda, C.H. Saito & B.S. Dias (eds.) Anais do Simpósio Impacto das Queimadas sobre os Ecossistemas e Mudanças Globais. Brasília, 3º Congresso de Ecologia do Brasil, 187p.

Ludwig, J.A. & J.F. Reynolds. 1988. Statistical ecology: A primer on methods and computing. New York, John Wiley, 337p.

Magurran, A.E. 1988. Ecological diversity and its measurement. New Jersey, Princeton University Press, 179 p.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res. 27: 209-220.

McCune, B. & M.J. Mefford. 1999. PC-ORD: Multivariate analysis of ecological data. Version 4.01. Gleneden Beach, MjM Software.

Medellin, R.A. & K.H. Redford. 1992. The role of mammals in neotropical forest-savanna boundaries, p.519-548. In P.A. Furley, J. Proctor & J.A. Ratter. (eds.), Nature and dynamics of forest-savanna boundaries, London, Chapman & Hall, 616p.

Murcia, C. 1995. Edge effects in fragmented forests: Implications for conservation. TREE 10: 58-62.

Odum, E.P. 1971. Fundamentals in ecology (3th edition). Philadelphia, Saunders, 574p.

Rosenberg, M.S. 2001. PASSAGE: Pattern analysis, spatial statistics, and geographic exegesis. Version 1.1. Department of Biology, Arizona State University, Tempe, AZ. http://lsweb.la.asu.edu/rosenberg/Passage.

Shepherd, V.E. & C.A. Chapman. 1998. Dung beetle as secondary seed disperses: Impact on seed predation and germination. J. Trop. Ecol. 14: 199-215.

Smouse, P.E., J.C. Long & R.R. Sokal. 1986. Multiple regression and correlation extension of the Mantel test of matrix correspondence. Syst. Zool. 35: 627-632.

Sokal, R.R. & F.J. Rohlf. 1981. Biometry: The principles and practice of statistics in biological research (2nd edition). New York, W.H. Freeman and Company, 219p.

StatSoft Inc. 1996. Statistica for Windows. Tulsa, StatSoft.

Vaz-de-Mello, F.Z. & J.N.C. Louzada. 1997. Considerações sobre forrageio arbóreo por Scarabaeidae (Coleoptera, Scarabaeoidea), e dados sobre sua ocorrência em floresta tropical do Brasil. Acta Zool. Mex. 72: 55-61.

Zar, J.H. 1999. Biostatistical analysis (4th edition). New Jersey, Prentice Hall, 663p.

Received 19/VII/04. Accepted 05/V/05.