TEMPORAL CHANGES IN A COMMUNITY OF DUNG BEETLES (INSECTA: COLEOPTERA: SCARABAEINAE) RESULTING FROM THE MODIFICATION AND FRAGMENTATION OF TROPICAL RAIN FOREST

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ABSTRACT. In order to determine the changes in biological diversity over time in different habitats of a fragmented tropical rain forest in Manaus, Brazil, we compared capture data from two windows in time: 1986 and 2000. We used beetles of the subfamily Scarabaeinae as an indicator group. Both sets of samples were collected from the same sites and following the same methodology. The only difference was that in 2000 most of the pastures that had been created as isolation barriers had been replaced by secondary vegetation in different stages of development. Beetles were collected from the following habitats: pasture, secondary vegetation, 1 ha, and 10 ha fragments of forest, and continuous rainforest. The main results follow. 1) After the dramatic decrease in Scarabaeinae species richness that followed the creation of the pastures and the isolation of the fragments there was a notable recovery of biodiversity. We associate this with the enormous tract of continuous rainforest that surrounds the study area since the sites were recolonized by rainforest species. 2) The high number of tourist species recorded for the pastures is evidence of the ease with which Scarabaeinae can overcome the physical barriers imposed by fragmentation. Over time, many of the tourist species coming from the intact forest can become colonizers. 3) Even when there is no human intervention, there is a high degree of heterogeneity in the spatial and temporal distributions of the Scarabaeinae in the rainforest. 4) For coprophagous beetles, the effects of forest fragmentation are a function of both forest fragment size and the nature of the matrix in which the fragments occur. In our study the development of secondary vegetation favored the connection between fragments and the continuous forest.
Key words: Diversity, matrix effect, forest fragmentation, long-term effects, secondary forest.

RESUMEN. Con el propósito de determinar los cambios en la diversidad biológica a través del tiempo en distintos hábitats de una selva lluviosa tropical fragmentada (Manaus, Brasil), comparamos dos ventanas: la primera correspondiente a las capturas realizadas en 1986, y la segunda en 2000. Como grupo indicador usamos los escarabajos de la subfamilia Scarabaeinae. En las dos ventanas, las colectas se realizaron en los mismos sitios y siguiendo la misma metodología. La única diferencia fue que para el 2000, la mayor parte de los pastizales establecidos como barreras de aislamiento habían sido remplazados por vegetación secundaria con distintos grados de desarrollo. Se colectó en los siguientes hábitats: pastizal, vegetación secundaria, fragmentos de bosque de 1 ha, y 10 ha, bosque original continuo. Los principales resultados fueron: 1) Después de la reducción drástica en la riqueza de especies de Scarabaeinae que siguió a la creación de los pastizales y al aislamiento de los fragmentos, se presentó una importante recuperación de la biodiversidad. Este fenómeno lo asociamos a la enorme extensión de selva continua que rodea al área de estudio, ya que la recolonización ocurrió con especies de selva. 2) El alto número de especies turistas encontradas en los pastizales es evidencia de la facilidad con que los Scarabaeinae "saltan" las barreras físicas impuestas por la fragmentación. Con el tiempo, al repetirse los casos, muchas especies turistas que proceden del bosque continuo pueden convertirse en colonizadoras. 3) Aún sin ninguna intervención humana, existe un alto grado de heterogeneidad en las distribuciones espacial y temporal de los Scarabaeinae en la selva tropical lluviosa. 4) En lo que respecta a los efectos de la fragmentación del bosque sobre los escarabajos coprófagos, además de la extensión de los fragmentos, es importante la naturaleza de la matriz en que éstos quedan incluidos. En nuestro estudio el desarrollo de la vegetación secundaria favoreció la interconexión entre los fragmentos y el bosque continuo.
Palabras clave: diversidad, efecto de la matriz, fragmentación de la selva lluviosa, efectos a largo plazo, bosque secundario.

INTRODUCTION

Fragmentation and habitat loss are likely the main threats to the local and regional biodiversity in the tropics (Noss 1983, Wilcox & Murphy 1985). The effects range from the loss of some species (Powell & Powell 1987, Bierregaard *et al.* 1992, Brühl *et al.* 2003, Lehtinen *et al.* 2003) to changes in community structure and composition (Lovejoy *et al.* 1986, Laurance 1990, Didham *et al.* 1996, Alcala *et al.* 2004, Hill & Currian 2005). Ecosystem function and high order interactions are also affected (Aizen & Feinsinger 1994, Benítez-Malvido *et al.* 1999, Malo *et al.* 2001, Bruna & Kress 2002, Tscharntke & Brandl 2004).

Disturbances do not usually occur simultaneously over large areas, and so the result at the landscape level is frequently a complex mosaic of pastures, croplands, areas with secondary vegetation and remnants of the original forest (Nestap *et al.* 1991, Turner 2005). Under these conditions, the attributes of the matrix that surrounds the fragments are of great importance for maintaining species richness within the fragments. Complex matrices that have abundant arboreal cover can mitigate the loss of the species that are characteristic of the forest (Perfecto & Vandermeer 2002, Pineda *et al.* 2005), facilitate the movement of individuals between fragments (Aberg *et al.* 1995, Renjifo 2001) and reduce the severity of edge effects on forest remnants (Gascon *et al.* 1999, Borges & Stouffer 1999). On

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the other hand, although the modification and fragmentation of the landscape causes changes in the diversity and abundance of animal species (Lovejoy *et al.* 1986, Wolff *et al.* 1994, Robinson *et al.* 1995, Hagan *et al.* 1996, Powell & Powell 1987, Didham *et al.* 1996, Davies & Margules 1998, Debinsky & Holt 2000), there is a tendency to think that these are definitive, rather than taking into account that with the development of secondary vegetation or other changes that occur over time, communities can begin to recover (Dunn 2004, Quintero & Roslin 2005). Furthermore, there have been few studies that examine these effects in the long term (Debinsky & Holt 2000, McGarigal & Cushman 2002) owing to the practical and logistical difficulties of repeat sampling in the same place using the same methodology.

The Biological Dynamics of Forest Fragments Project is a large-scale effort in central Amazonia to evaluate the effects of fragmentation of tropical rainforest on the diversity of different groups of organisms, and is being done in an ideal setting for studying what happens over time. It has forest fragments of different sizes and for each fragment there is a detailed record of its age and isolation processes (Bierregaard *et al.* 1992).

The copronecrophagous beetles of the subfamily Scarabaeinae were chosen as the indicator group for this study because they have been widely used in biodiversity studies in fragmented rainforest, they are sensitive to anthropogenic change and are of functional importance in tropical ecosystems (Halffter & Matthews 1966, Favila & Halffter 1997, Estrada *et al.* 1998, Andresen & Feer 2005). This group also lends itself to regular and controlled sampling.

The main objective of this study was to compare the alpha, beta and gamma diversity (Whittaker 1972, Halffter 1998), the community composition and Scarabaeinae guild structure among continuous forest, fragments of different sizes, pastures and the entire landscape at two points in time, between which important changes had occurred on the landscape.

Given that matrix quality can influence the dynamics of the populations and communities in fragmented landscapes, we expected: 1) a significant increase in the alpha diversity of the fragments and the gamma diversity of the landscape once the pastures bordering the fragments had been replaced by secondary vegetation; and 2) greater similarity in the composition and structure of Scarabaeinae communities in the matrices, fragments and continuous forests as the landscape became more complex and connectivity increased.

MATERIAL AND METHODS

Study Area. The study was done in the reserves of the Biological Dynamics of Forest Fragments Project (BDFFP) SI/INPA, located 80 km north of Manaus, Brazil (2?24'26"-2?25'31" S, 59?43'40"-59?45'50" W). The original vegetation of this

landscape is classified as *Terra Firme* forest (Pires & Prance 1985). For the BDFF project forest fragments with areas of 1, 10, 100 and 1000 ha were separated by cattle pastures. The strips of pasture are 70 to 600 m wide and isolate the fragments from the continuous forest that extends for kilometers in all directions. The creation and isolation of the fragments started in 1980 and continued until 1991 (Bierregaard *et al.* 1992).

The first sample (T1) was obtained during the dry season (May-June) of 1986 by Bert Klein (Klein 1989). The second sample (T2) was also collected during the dry season (June-July) in 2000 by Ingrid Quintero, in order to obtain comparable data. Andresen (2002) observed no significant differences in the richness and abundance of Scarabaeinae on comparing collections from the dry and rainy seasons. The two sets of samples were collected from three reserves: Dimona (located in Fazenda Dimona), Colosso and Cidade Powell (located in Fazenda Esteio) (see Antongiovanny & Metzger 2005 for a general map of the area and the location of the reserves). The same four habitats were sampled on both occasions: continuous forest, 1 ha and 10 ha fragments, and the matrix between the fragments (pastures and secondary vegetation).

There were important changes to the landscape over the time. At T1, six years after selective fragmentation had occurred; the fragments were isolated by pastures. In one of these pastures (Cidade Powell) there were small patches of vegetation (scattered small trees) that were starting a fast process of secondary regeneration. Approximately 4 or 5 years later the majority of the pastures were abandoned owing to the lack of incentives for the cattle farmers and low production (see Bierregaard *et al.* 1992, Bierregaard & Stouffer 1997). The pastures were then cut or burned to a greater or lesser degree, resulting in the formation of mosaics of secondary vegetation in different stages and states of succession, and these now surround the fragments. The younger secondary vegetation that regenerated in the pastures of Colosso was cut and burned regularly and is dominated by species of *Vismia*. In Cidade Powell, the secondary vegetation originating from cutting the forest and later abandoning the pasture is dominated by species of *Cecropia* (see Borges & Stouffer 1999, Mesquita *et al.* 2001, Nascimento *et al.* 2006) (Fig. 1).

The sizes of the fragments have remained constant over time with the exception of the continuous rainforest located in Dimona which was transformed into a 100 ha fragment (see Antongiovanny & Metzger 2005). This fragment was sampled at T2, as was a new area of continuous forest located 2.5 km to the west of the fragment in order to have a reference site for the continuous forest. Given the replacement of pastures by secondary vegetation, new pasture sites (Dimona and Colosso) were sampled for their inclusion in the comparison and in order to have, for T2, data for all the habitats that had been sampled in 1986.

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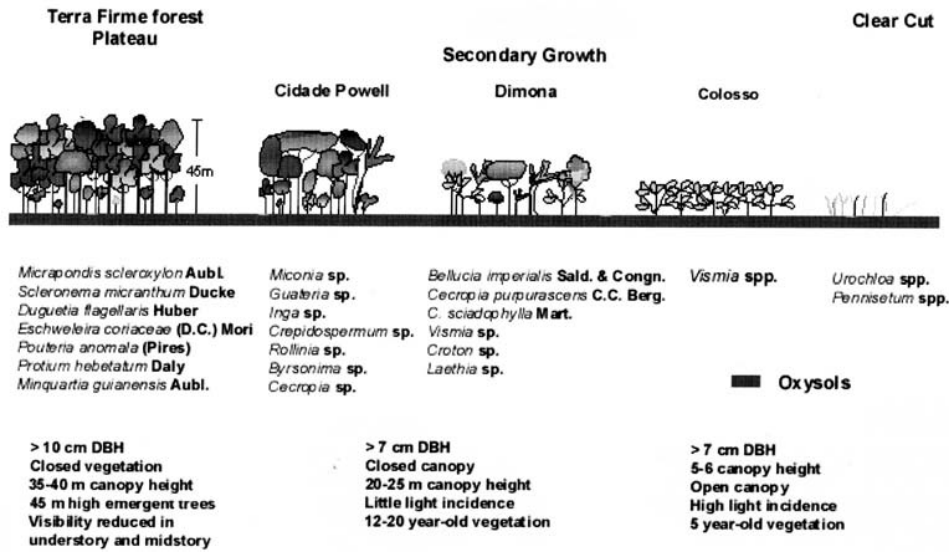
Figure 1. Characteristics of the vegetation, its composition and floristic structure at the study sites. Mature forests located on solid ground (both intact and fragmented forests) and the matrices at each site (secondary vegetation in different stages of succession and pastures) (Source: PDBFF staff) in Manaus, Brazil.

Beetle sampling and comparison of the species collected in 1986 and 2000. Collection methodology and site selection in 2000 were based on Klein's proposal (1989) for his 1986 collection. To capture the beetles we used pitfall traps made from a collecting jar 14 cm in diameter and 5 cm deep. This was half filled with a solution of chloral hydrate 25% (T1) and 5% (T2), inside which we placed a smaller jar (4 cm diameter x 5 cm deep) containing the bait. The trap was protected with a plastic plate to prevent water from getting in. We set up a line of six traps, 17 m apart at each sampling point. These were alternately baited with human excrement and decomposing meat. The traps were left in place for four days and were checked every 12 h at dawn (approx. 0600 h) and dusk (approx. 1800 h). The bait was changed every 24 h. A total of 266 traps/day were used at T1 and at T2, plus the traps placed in the new pastures for T2. The traps in the rainforest were placed 350 m away from the edge. For the other sampling points we applied the same criteria used by Klein (1989).

The specimens captured during T2 were identified using taxonomic keys, checked against collections and by consulting specialists. It was not possible to identify some specimens to the species level given the current knowledge of their genera. All of the material that had been collected at T1 and deposited in the Bureau of Entomology

(USDA) in Gainesville, Florida was examined, with the exception of a few examples that had been sent to Antonio Martínez (Argentina) for identification; i.e. species that appeared to be unique to Klein's collection (1989) (R. E. Woodruff *personal communication*). Another exception in the reconstruction of the material from Klein's (1989) collection concerns the data from the continuous forest in Cidade Powell, which did not exist in 2000. However, we verified that the material collected in the continuous forest located in Dimona represented twice the sampling effort of the other habitats. Therefore, although there was only data for the two continuous forests that had been sampled (Dimona and Colosso) the sampling effort was the same in all habitats. Hence, the data that we include in T1 are not identical to those of Klein (1989) as they represent a reconstruction of collection data and the verification of identifications based on collection material.

Data Analysis. To evaluate the representativeness of the samples from T1 and T2, and determine the expected richness for each site, we used species accumulation curves compared with abundance dependent non-parametric richness estimators (ACE, Chao1, Jackknife 1) (Colwell & Coddington 1994, Boulinier *et al.* 1998, available in EstimateS v. 7.0 software Colwell 2004). Randomizing the sample addition sequence 100 times smoothed the curves out and revealed the asymptote. Total abundance per species in 1986 was added to the program as independent samples given that we did not have the abundance data per trap.

Changes in species composition over time: Alpha, Beta and Gamma diversity. To quantify the contribution of local richness (alpha diversity) –mainly that of the community that was richest in species– and the heterogeneity of sites (beta diversity) to regional richness (gamma diversity) (Whittaker 1972, Halffter 1998) for each sample (T1 and T2) we did the following analysis: At each sampling site, we calculated the value of local alpha diversity, defined as the total number of species collected, and from these we calculated mean alpha diversity per habitat. To determine species turnover between the sites of a given habitat and along the continuum or disturbance gradient, we used Whittaker's beta index: $Bw = S/\cdot - 1$; where S is the number of species recorded in a set of samples and $\cdot$ is the mean number of species (Whittaker 1960, Koleff *et al.* 2003). To calculate gamma diversity we used the formula proposed by Lande (1996): $Y = \alpha + \beta$; where α is mean alpha diversity for the landscape and β, is the mean diversity between the communities studied.

Changes in the Scarabaeinae community structures over time. To identify the nature of the changes in the beetle community over time caused by fragmentation and the modifications to the vegetation, we did the following analyses. To observe changes in the hierarchy of species at each site over time we plotted Whittaker curves (Feinsinger 2001), and coded the most abundant species. Additionally, some species that were rare but important for the purpose of comparison were also coded. To

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ensure that these abundance distributions were not the product of random variation we used two methods, both related to the availability of abundance data per trap at each site. For T1, we generated a new distribution based on the sum of the frequencies for the species recorded in each site and we tested the fit with a Kolmogorov-Smirnov test. With this new distribution (fit to a Poisson distribution) we generated resamplings of the mean and obtained the probability values for rejecting the null hypothesis. For T2 we calculated mean abundance for each species and generated a new matrix fit to a Poisson distribution and then modeled the quality and quantity of species that added up to 70% of all the individuals on randomizing 10000 times. These simulations were done with R Project software (R Development Core Team 2005). Changes in dominance between sites over time were measured with the reciprocal of Simpson's index (1/D) which we selected for its sensitivity to common species and the wide use it has been given (Magurran 1988). This returned a differential value (θ) that determines the statistical significance with 1000 randomizations (statistical package: Species, Diversity & Richness 3.0, www.irchouse.demon.co.uk).

To determine the spatial and temporal distribution of resource use, we classified the Scarabaeinae along three dimensions: 1) size: small and large (Cambefort 1991); 2) temporal segregation: diurnal and nocturnal (Halffter *et al.* 1992); and 3) food relocation habit: tunnelers and rollers (*Eurysternus* is considered a roller) (Bornemissza 1969). Species were classified according to these criteria and we obtained a matrix of possible combinations in each of the sites sampled for both T1 and T2. To estimate the proportion represented by each of the combinations and observe tendencies in species richness and abundance for both T1 and T2, as well as their relationship with disturbance intensity, we used a multinomial test based on the Monte Carlo series from the R statistical software package (R Development Core Team 2005) with the MNP library (Imai & Dyk 2005). The calculations were done as a function of combinations of the relative species richness and abundance data, and we ran three series of 64000 events from which we estimated the probability based on the last 1000 events. For those sites that had only been sampled during T2, such as secondary vegetation and the 100 ha fragment in Dimona, the simulation was extrapolated from T1 to evaluate tendencies over time.

RESULTS

Sample Representativeness. The species accumulation curves obtained from our samples did not reach asymptotes (Fig. 2). However, total mean representativeness values were close to 80%. As a qualitative observation, the majority of the sites that had low representativeness values was also highly disturbed and were characterized by a high number of species that were locally rare but regionally abundant.
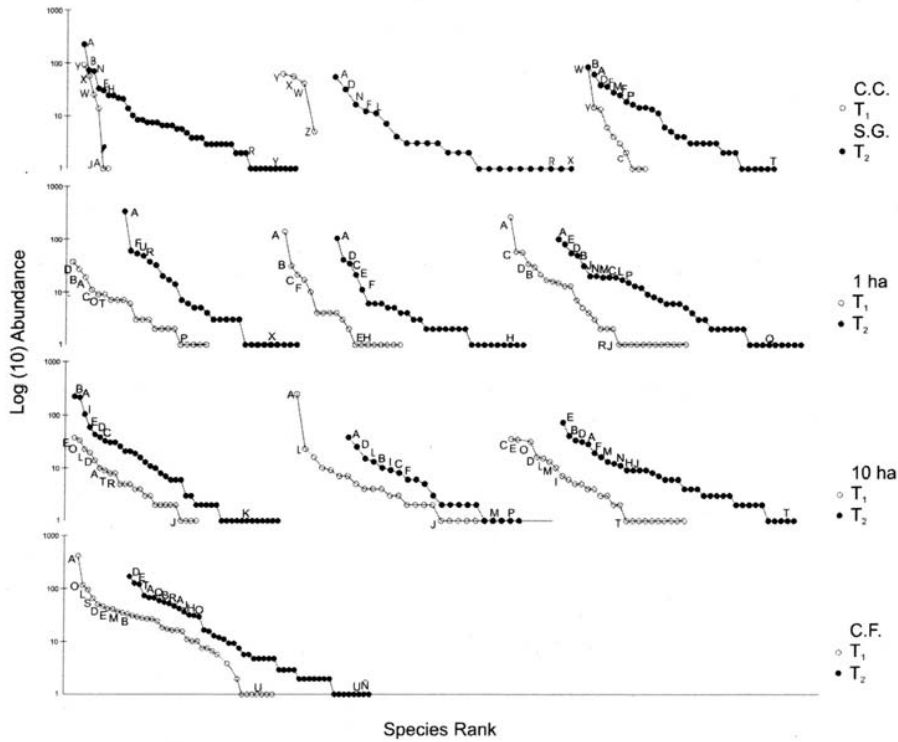
Figure 2. Scarabaeinae species accumulation curves (± 95% C.I.) for each of the three sites in Manaus, Brazil (Dimona, Colosso, C. Powell) in each of the habitats (1986-2000); pastures (C.C.), pastures replaced by secondary growth (S.G.), fragments (1 ha, 10 ha) and continuous forest (C.F.).

Diversity

Alpha, Beta and Gamma. For T1 total richness was 53 species; for three of these there was only one specimen and two were not reported by Klein (1989). For T2 we recorded 61 species (Table 1). Of the abundant species, *Onthophagus haematopus* was abundant in both T1 and T2. The abundance of *Dichotomius* aff. *boreus* and *Dichotomius* sp. (grp. *lucasi*) decreased between T1 and T2 while *Ateuchus murrayi* and *Uroxys* sp. increased in relative abundance. *Canthon* aff. *acutiformis*, another of the most abundant species, was exclusive to pastures with the same relative percentage in T1 and T2. Taking both samples into account 15 genera were recorded, 14 from continuous forest and fragments, and one restricted to pastures. In T2 eight new species were recorded, and a new genus (*Trichillum*). *Dichotomius imitator* was the only species that was present in T1 but not recorded in T2 (*Dichotomius* sp. 5 for Klein 1989) (Appendix 1).

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For T1 the continuous forest contributed the greatest alpha value to the landscape diversity. Diversity values decreased as the degree of disturbance increased. Comparing T1 and T2, there is a significant increase in diversity (36% more new species) even for fragments that are small and surrounded by pastures. The secondary vegetation that replaced the pastures has alpha values similar to those of the fragments. The new pastures that we sampled qualitatively have the same mean alpha richness as the pastures that were sampled in T1 (Table 1).

Table 1. Local richness, and abundance for Scarabaeinae in the three replicates (Dimona, Colosso, Cidade Powell) for each habitat on two sampling occasions: pastures (clear cut: C.C.), secondary vegetation replacing pastures in 2000 (S.G.) and continuous forest (C.F.) in Manaus, Brazil. The fields left blank (-) for continuous forest (1986) and clear cut (2000) in Cidade Powell were not sampled (refer to Methods).

	Habitat/Year	Dimona	Colosso	C. Powell		Dimona	Colosso	C. Powell
			1986				**1986**	
	C.C.	6	4	10		218	159	125
	1ha	21	20	30		159	245	584
	10ha	26	26	28		208	359	238
	C.F.	38	24	-		1139	395	-
Richness	Total		53		**Abundance**		3829	
			2000				**2000**	
	C.C.	9	7	-		608	86	-
	S.G.	42	25	30		763	163	395
	1ha	33	39	30		668	546	273
	10ha	41	21	37		995	153	385
	C.F.	44	29	35		1125	459	371
	Total		61				6990	

For beta diversity, our results suggest that for the two periods sampled there is a high degree of dissimilarity in species composition between the sites of the same habitat. For the fragments compared, over time there is a decrease in species turnover, but this does not happen when pastures are compared with small fragments or with secondary vegetation (data for the latter comparison not presented). Species turnover values decrease when the larger fragments are compared with continuous forest (Fig. 3).

The three diversity values are: 53 species (γ) = 21.33 (α) + 31.66 (β) for T1, and 61 species (γ) = 28.66 (α) + 32.34 (β) for T2.
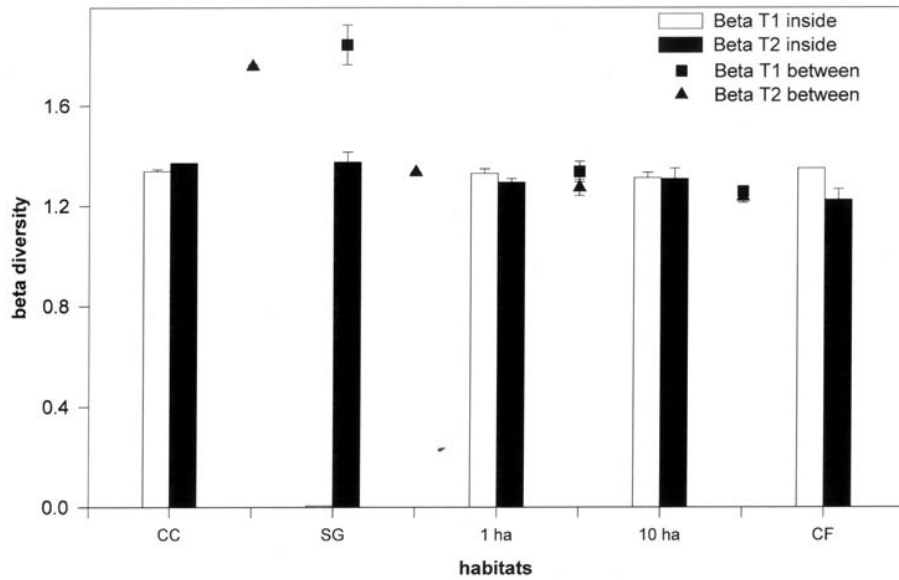
Figure 3. Mean species turnover for the two sampling dates (1986 and 2000) measured within habitats and between habitats using Whittaker's Index.

Structure

Species hierarchy and the dimensions of the Scarabaeinae guild. The analyses based on simulations for T1 show that the distributions for the frequency of observed species were not random (Kolmogorov-Smirnov $P>0.80$). The dominance-diversity curves clearly show changes between habitats and times, both in the slope of the curves and in species hierarchy and dominance. For the pastures sampled in T1, the distribution was simple, represented by four species with relatively uniform abundances. When the pastures were replaced by secondary vegetation in T2 there was a change in dominance to forest species with distributions similar to those observed in the forest. The curves for fragments in T2 are smoother and with less dominance compared to those for T1 (Fig. 4), and the differential value (θ) was significant (Table 2). The simulation test done on the T2 sites shows that in the majority of sites, the species that reach 70% of the abundance within the 95% confidence intervals are responsible for the dominance (Table 2). In general there were changes in species hierarchy, especially for the 10 ha fragments and continuous forest (Fig. 4).

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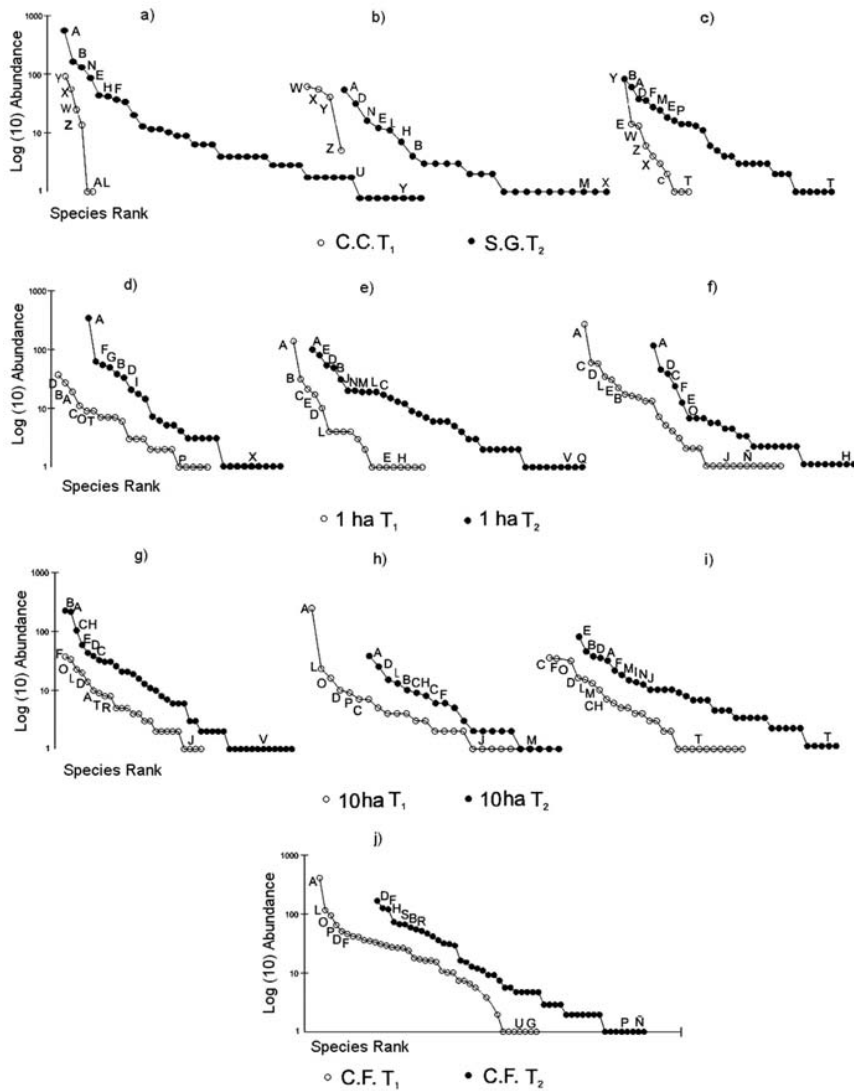
Figure 4. Dominance-diversity graphs for Scarabaeinae assemblages collected in anthropic areas, fragments of 1 ha 10 ha, and continuous forest in Manaus, Brazil on the two sampling dates (1986 and 2000). Graphs a), d), and g) represent Scarabaeinae abundance for the habitats sampled in Dimona. Graphs b), e), and h) represent the habitats sampled in Colosso. Graphs c) f) and I) represent the habitats sampled in Cidade Powell. Graph h) represents a mix of total abundance by species for the three continuous forests. White dots are the hierarchical abundance of species at T1, and the black dots at T2. Codes for some species (capital letters) are given in Appendix 1.

Table 2. Dominance, measured as the reciprocal of the Simpson index for each habitat on two sampling occasions: pastures (C.C.), secondary vegetation replacing pastures in 2000 (S.G.) and continuous forest (C.F.) in Manaus, Brazil.

Site	Habitat	T1	T2	θ_a	P
Dimona					
	C.C.	0.35	0.1	-2.86	
	1ha	0.11	0.27	-0.53	<0.0001
	10 ha	0.09	0.12	2.86	0.013
	C.F.	0.09	0.01	2.71	0.053
Colosso					
	C.C.	0.31	0.16	3.17	<0.0007
	1ha	0.34	0.18	2.47	<0.0001
	10 ha	0.48	0.11	6.59	<0.0001
	C.F.	0.13	0.07	-4.45	<0.0001
C. Powel					
	C.C.	0.43	0.09	8.08	<0.0001
	1ha	0.17	0.08	6.15	<0.0001
	10 ha	0.09	0.07	2.72	0.068
	C.F.		0.07		

[a] Differential theta value between sampling periods (T1 & T2).

Based on the classification of Scarabaeinae by size, temporal segregation and food relocation habit there were seven combinations of these properties. In species richness and especially in abundance the best represented group was small, nocturnal tunnelers; though the pastures are only able to support the group of small, diurnal rollers (with the accidental collection of a few individual species classified as other combinations). For T2, and as the vegetation developed, all the groups of beetles recovered. In T1 a smaller number of large species were recorded in small fragments, especially nocturnal rollers. For T2 there is a recovery of large species on the landscape and an apparent similarity between all the communities with canopy cover (Fig. 5). For both large and small species there is a tendency to a greater number of diurnal rollers in more disturbed habitats.
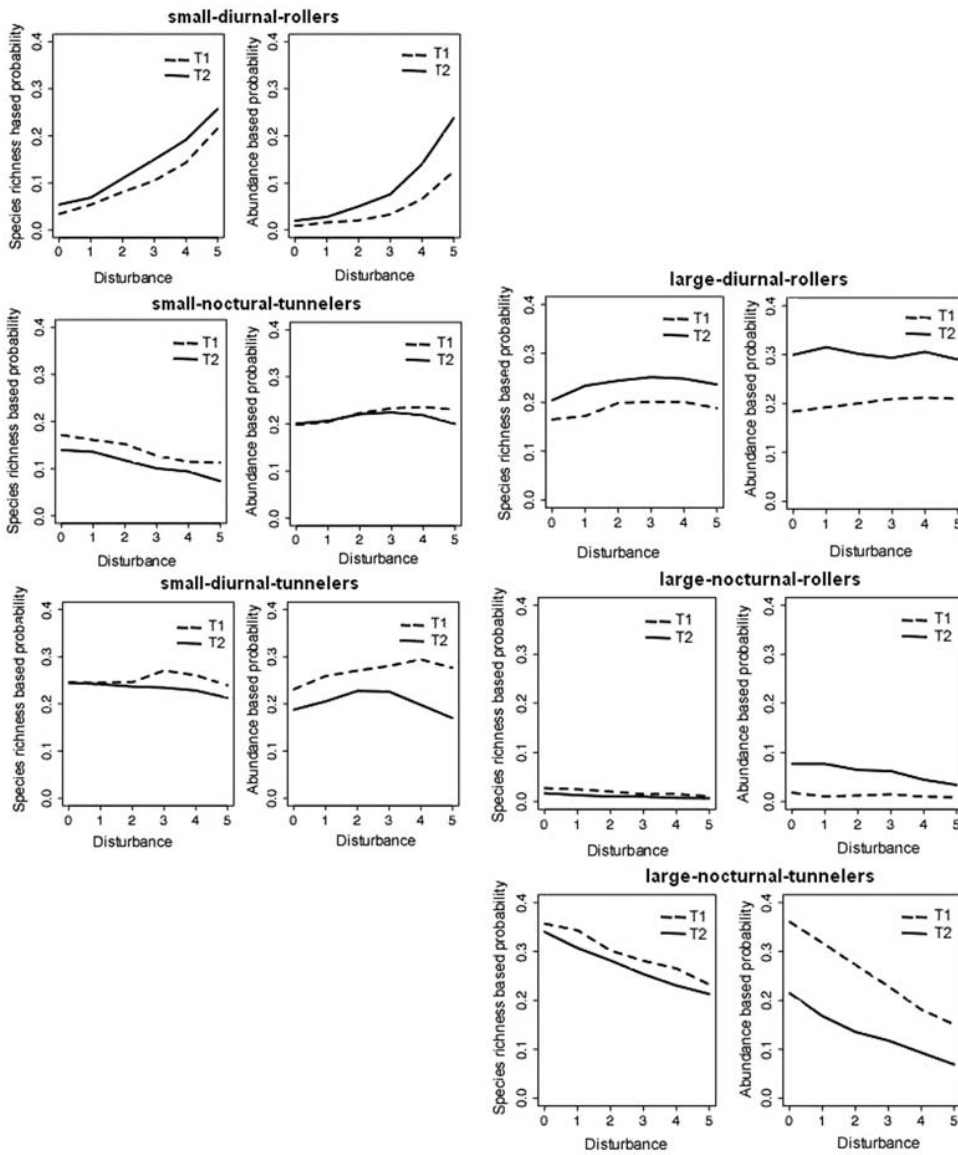
Figures. 5a and 5b. Observed tendencies in the loss and gain of species and individuals classified by three factors: size, diurnal activity and food relocation habitat across the disturbance gradient in Manaus Brazil. 0 = Continuous forest; 1 = 100 ha fragments; 2 = 10 ha fragments; 3 = 1 ha fragments; 4 = Secondary growth, 5 = Clear cut (pastures). Species richness and abundance values lower than 0.005 are not shown in order to avoid cluttering the graph.

DISCUSSION

Although this study and that of Quintero and Roslin (2005) are complementary, the analyses are based on different data. Quintero and Roslin (2005) used T1 data from Klein (1989) where abundance was summarized by treatment (C.C., fragments of 1 ha, 10 ha and C.F.), and not by site. Our T2 data includes the entire June to August 2000 collection effort, representing three times Klein's sample in 1986 (page 3305 and the Ecological Archives E086-181-A1 in Quintero & Roslin 2005). For the present study, T1 data were rebuilt from Bureau of Entomology of USDA Gainesville FL material. T2 Data includes the same sampling effort used by Klein, i.e. 288 traps/day + 24 traps/day in a fragment of 100 ha at Dimona.

Sample representativeness. Species accumulation curves did not reach asymptotes in either T1 or T2, but the reasons are likely different in the different habitats. In the pastures and small fragments there were many species that only appeared once but that were common on the scale of the landscape. Some heliophile forest species can cross small distances of pasture, and species typically found in this environment can invade small remnants of forest that have a pronounced edge effect (Ås 1999). These tourist species do not establish viable populations (Schmida & Wilson 1985), but can inflate expected richness values in each habitat. On the other hand, in large fragments and continuous forest there was a significant number of rare species and therefore the accumulation curves did not reach their asymptote. Novotny & Basset (2000) mention the difficulty in reaching asymptotic values in inventories of insects in tropical forests. However, observed richness values for each site do fall within the expected values according to the estimators used and therefore do support our interpretation of the results.

Changes in Scarabaeinae composition over time. At T1, mean richness was lower in the fragments than in the continuous forests (Klein 1989, see Andresen 2003 who collected over the same area) and there were notable differences in composition and diversity between fragments of the same size. Recently isolated fragments that are surrounded by pastures can host small species. These can become locally extinct, gradually decreasing the diversity of the fragments and, owing to stochastic events, there could be wide variations in composition and richness among recently created fragment populations (see Ewers & Didham 2006). However, as demonstrated for T2, with the growth of secondary vegetation there was an increase in the connectivity between fragments and with the continuous forest, and the fragments recovered their diversity (Tocher *et al.* 1997, Malcolm 1997, Bierregaard & Stouffer 1997, Gascon *et al.* 1999). The quality of the matrix surrounding the fragments is a determining factor in both the local and regional permanence of species (Vandermeer & Perfecto 1997, Fahrig 2001, Ricketts 2001). In the secondary vegetation dominated by *Vismia* the Scarabaeinae fauna was less diverse than it was in the secondary vegetation dominated by *Cecropia,* and diversity in the

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latter was similar to that of the continuous forest (Quintero & Roslin 2005). This has also been observed for other groups of fauna (Borges & Stouffer 1999; Vasconcelos 1999; Antongiovanni & Metzger 2005). The high species richness for Scarabaeinae hosted by secondary vegetation–even in its early successional stages–is similar to the richness of other tropical forests (Shahabunddin *et al.* 2005, Avendaño-Méndoza *et al.* 2005), when we take into account the specific and historical characteristics of each group of animals.

The greater diversity recorded at T2 could be the result of the regeneration of the vegetation which, in turn, resulted in the formation of more niches for the mammals that the beetles depend on. For example, *Uroxys besti* and *Canthon quadrigattatus* were not recorded at T1 but are strongly associated with sloths and howler monkeys (Halffter & Matthews 1966, Ratcliffe 1980), and have specific nesting and feeding patterns (Ratcliffe 1980, Vaz-de- Mello & Louzada 1997). The fact that these two mammals are folivores and depend on *Cecropia* allow *U. besti* and *C. quadrigattatus* to survive in disturbed landscapes (Chiarello 2000, Gilbert & Setz 2001, Lopes & Ferrari 2001).

Beta diversity made the strongest contribution to landscape diversity at 59.74% (T1) and 53% (T2). This is not just a result of the anthropogenic changes to the landscape. Our study provides evidence of the high within-site and between-site heterogeneity of tropical rain forest (as recently observed in dung beetle communities by Gardner *et al.* 2008 and Navarrete & Halffter 2008). Regarding the temporal dynamics, spatial heterogeneity–quite obvious in tropical forests–is characteristic of natural communities (Wolda 1983, Condit *et al.* 2002), and should be included as a variable when evaluating the effects of fragmentation (McGarigal & Cushman 2002).

Klein (1989) said that in small forest fragments diversity would decrease and there would be colonization by pasture species. In light of our results, the development of secondary vegetation favored recolonization of the fragments by shade-loving forest species to the point where only 11% of all the species on the landscape were restricted to the continuous forest. So, although Klein's hypothesis is valid for a recently fragmented landscape, it is less representative of the situation fourteen years later. The tendency to extrapolate results observed at a specific time and space to larger scales can overstate the consequences of anthropogenic changes to biological diversity in tropical forests (see Haila 2002, Fahrig 2003) if the fact that the matrix in many landscapes is also changing over time is not also taken into account (Jules & Shahani 2003).

From our results we can deduce that the permanence of species richness in partially fragmented tropical forests not only depends on the fragment size, but also on the nature of the matrix and the time that has elapsed since human intervention; that is, the scales of space and time over which the transformation has occurred. It

is evident that the matrix can change in only a few years and that these changes can have a decisive effect on species diversity. On the other hand, the new conditions created by human activities favor some species, and affect total landscape diversity. For this landscape in Manaus, Brazil the introduction of pastures favored edge or heliophilic species such as *Canthon* aff. *acutiformis*, *Canthon* aff. *acuticularis*, *Canthon lituratus* and *Pseudocanthon* aff. *xantorum* all of which are strongly associated with natural gaps in mature forest (F. Z. Vaz-de-Mello, *personal communication*) and were commonly collected in the pastures (see also Scheffler 2005).

Observed changes in Scarabaeinae guilds. What makes large species–especially nocturnal tunnelers–more likely to disappear when the forest is disturbed? This phenomenon is particularly evident in 1986 before the mitigating effects of the secondary forest took hold (2000). In a savannah-forest system on the Ivory Coast, Krell *et al.* (2003) observed that roller species were "better competitors" than the tunnelers in the savannah (where higher levels of competition were observed), and the tunnelers, in turn, were better than the resident species. However the rollers which exploit the resource more quickly require specific environmental conditions, such as higher dung and soil temperature. In the gallery forests which are shadier and cooler than the savannah, the resident species were more abundant, although there was more competition; lower energetic expenditure made them ecologically more tolerant. This hypothesis might be partially applicable to our study system. In the forest, large, nocturnal tunnelers dominate the resource but once the landscape changes (i.e. when fragments of forest are created), the contrast between the environmental differences in the forest relative to the matrix becomes drastic (Bierregaard *et al.* 1992), with the result that these species become confined to the forest. In contrast, heliophile species common to the edges and forest gaps such as *C.* aff. *acuticularis*, *C. lituratus* and *P.* aff. *xantorum* would be better adapted to the new environmental conditions of the pastures. As occurs in savannahs, these species (small, diurnal rollers) dominate in the pastures (Halffter & Matthews 1966). With the changes in the vegetation of the edges that had occurred by T2, birds and mammals had recolonized the rain forest fragments (Bierregaard & Stouffer 1997, Malcolm 1997, Gilbert 2003, M. Santamaría-Goméz *personal communication*), thus restoring the food supply. There is not much difference in temperature inside the fragments and at their edges (E. Bruna, *personal communication*). Under these conditions large, nocturnal species were more homogeneously distributed in T2.

Our results on the proportion of functional guilds in the forests and pasture cannot be generalized to the entire Brazilian Amazon. In the eastern Amazon, Scheffler (2005) found that in pastures small diurnal rollers represented only 5% of total abundance while tunnelers dominated at 88% of the population. In the Ducke

Reserve, approximately 100 km away from our study sites, Vulinec (2002) found that diurnal rollers were more limited to forests and the nocturnal tunnelers were more widespread in disturbed areas. There is no clear reason for this contradiction, but this is partly a result of the lack of information on the biogeography of the Scarabaeinae in the Amazon and the Neotropics. Studies on this topic are a priority if we are to understand the relationship between the historical and evolutionary processes acting on these species and the scales on which fragmentation and anthropogenic disturbances occur.

New contributions of this study that complement to Quintero & Roslin (2005). The proposed methodological analysis of this work, which included data reconstruction per site for T1 and from our own data collection, allowed us to make a comparison over time (1986 and 2000) using the same sampling effort. This approach allowed us to apply a new approach not included in Quintero and Roslin (2005). We were able to observe high heterogeneity, both spatial (by comparing fragments of the same area and continuous forest that are relatively close to each other) and temporal (by comparing each site at two different times). We also observed that in continuous forest, which has not been altered, there are important changes to species hierarchy over time, and this reflects its dynamism under apparently stable conditions.

The known richness and abundance for each site allowed us to include a behavioral analysis of the guild of Scarabaeinae in relation to the disturbance gradient over a significant time span. This analysis clearly shows that for small fragments there is no significant change in parameters such as abundance or diversity when compared to continuous forest (under the circumstances in the PDFBB areas). But, before fragmentation occurs, when environment conditions are stable, there is apparently a prolonged effect or trend in the structure of these communities. Some authors point out that changes in the structure of functional groups in Scarabaeinae can result in changes in the functionality of its ecosystems. Further study will reveal whether this effect over a much longer period of time is reflected in functional changes in the ecosystem that we have studied.

General conclusions

1. The effects of fragmentation and particularly of disturbed areas change depending on the matrix. In this study, the landscape is immersed in a vast expanse of continuous forest and this played a role in the recovery of the vegetation and mammalian fauna over a relatively short period of time, with the consequent beneficial effect for the Scarabaeinae. The high number of tourist species detected in this study is evidence of the ease with which the Scarabaeinae can overcome the physical barriers imposed by fragmentation. Over time, many tourist species that

mainly come from the continuous forest can become colonizers (Avendaño-Mendoza *et al.* 2005 and bibliography therein).

2. The meta-analysis performed by Nichols *et al.* (2007) for some tropical landscapes (Vulinec 2002, Avendaño-Mendoza *et al.* 2005, Quintero & Roslin 2005, Shahabuddin *et al.* 2006 and unpublished data, included on the review from Nichols *et al.* 2007) along with the results of our research, suggest that complex matrices composed of secondary vegetation could be important for conserving some dung beetle species from the original pool that are present in the forest remnants. However, as mentioned by Gardner *et al.* (2008) in some landscapes, the importance of secondary forest to maintaining a typical and significant forest dung beetle fauna is less certain. The caution given by Gardner *et al.* (2008) about the importance of this landscape element should be evaluated according to the specific conditions for each landscape and real possibilities of conservation for the dung beetle fauna.

3. Our study highlights the fact that in the absence of human intervention heterogeneity is high (beta diversity) in the spatial distribution of the Scarabaeinae in tropical forests, and this has been confirmed to be true over time. This heterogeneity is not often taken into account when the effects of human activities on diversity are analyzed.

4. Under the conditions of our study the areas of secondary vegetation were recolonized by Scarabaeinae in a relatively short period of time and by almost all the rainforest species. This process was also influenced by the time elapsed after the disturbance and land use history. Secondary forests should be taken into consideration in effective management plans for the conservation of Amazonian forests exposed to human intervention (see Dunn 2004).

5. The conversion of rainforest into pastures causes changes in the structure of the Scarabaeinae guilds, resulting in a greater proportion of small, diurnal species particularly of the roller habit. These changes appear to be associated with the higher light levels in the pastures.

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Appendix 1. Complete list of beetles collected during two time windows (1986 and 2000) at the three sites (Dimona, Colosso and Cidade Powell) in five communities in Manaus, Brazil: Size (S): p-small, g-large; Dial activity (DA): d-diurnal, n-nocturnal; Food relocation method (FRM): c-tunnelers, r-rollers; pastures (C.C.), secondary vegetation (S.G.), and continuous forest (C.F.).

Code	Species	S	DA	FRM	1986 Dimona C.C.	1986 Dimona 1ha	1986 Dimona 10ha	1986 Dimona C.F.	1986 Colosso C.C	1986 Colosso 1ha	1986 Colosso 10ha	1986 Colosso C.F.	1986 Cidade C.C.	1986 Cidade 1ha	1986 Cidade 10ha	1986 Cidade C.F.	2000 Dimona C.C.	2000 Dimona S.G.	2000 Dimona 1ha	2000 Dimona 10ha	2000 Dimona C.F.	2000 Colosso C.C.	2000 Colosso S.G.	2000 Colosso 1ha	2000 Colosso 10ha	2000 Colosso C.F.	2000 Cidade 1ha	2000 Cidade 10ha	2000 Cidade C.F.
V	*Ateuchus connexus* (Harold 1868)	p	n	c	0	0	2	1	0	0	0	0	0	1	0	5	1	0	0	0	0	0	0	3	0	0	2	0	1	1	0
Q	*Ateuchus peuki* Balthasar 1939	p	n	c	0	0	0	8	0	0	0	0	0	2	5	0	0	0	2	8	0	0	0	4	3	13	0	4	1	3	0
B	*Ateuchus murrayi* (Harold 1868)	p	n	c	0	27	24	0	31	0	17	22	5	4	0	96	48	232	48	4	49	13	13	0	81	5	40	44
	Ateuchus pygidialis (Harold 1868)	p	n	c	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0
	Ateuchus simplex (LeConte 1857)	p	n	c	0	0	1	2	0	1	0	0	1	0	0	4	0	6	17	0	1	0	1	0	1	3	3
	Ateuchus sp. 4	p	n	c	0	0	2	48	0	1	0	1	0	0	0	0	1	0	16	0	2	2	0	1	0	2	1
U	*Ateuchus* aff. *setulosus*	p	n	c	0	0	0	0	0	0	1	0	0	1	0	1	4	26	0	0	1	0	1	0	1	0	0
	Ateuchus sp. 3.1	p	n	c	0	0	0	0	0	1	2	2	0	0	1	0	4	3	1	0	1	1	10	4	2	0
	Ateuchus sp. 7	p	n?	c	0	0	0	5	0	0	3	0	0	1	0	3	0	3	2	1	1	3	0	3	0	6
	Ateuchus sp. 5	p	n?	c	0	1	0	1	0	0	0	0	0	0	0	9	0	2	6	0	0	0	0	0	0	0
	Ateuchus sp. 6.1	p	n?	c	0	0	0	0	0	0	1	0	0	0	0	3	0	0	4	0	0	0	0	2	3	0
	Canthidium auricolle Borre 1868	p	d	c	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
	Canthidium aurichalceum Borre 1868	p	d	c	0	0	0	0	0	0	0	0	0	0	0	4	0	1	1	0	0	0	0	0	0	0
	Canthidium auricolle Harold 1867	p	d	c	0	0	5	11	0	0	0	4	0	0	0	0	1	1	0	0	7	0	0	4	0	9	7
	Canthidium bicolor Boucomont 1928	p	d	c	0	2	3	1	0	0	0	16	1	0	1	1	1	12	0	6	3	1	6	1	4	1
S	*Canthidium* aff. *deyrollei*	p	d	c	0	0	2	0	0	0	0	1	0	0	8	6	126	1	1	0	0	0	0	0
T	*Canthidium* sp. 2	p	d	c	0	9	10	28	1	1	10	13	1	0	0	3	10	0	1	0	1	0	1	0
C	*Canthidium* sp. (grp. *bituberifrons*)	p	d	c	0	11	5	15	21	7	3	59	35	0	10	5	39	5	1	3	19	9	3	14	34	4	2
P	*Canthidium* sp. (grp. *globulum*)	p	d	c	0	1	58	1	9	19	1	0	0	2	1	0	0	0	0	0	0	0
N	*Canthidium* sp. (grp. *lentum*)	p	d	c	0	6	5	10	4	2	2	17	0	0	80	3	11	17	0	16	6	7	14	2	13	4
Z	*Canthon lituratus* (Germar 1824)	p	d	r	15	0	0	0	5	0	0	6	0	0	58	0	0	0	3	0	3	0	0	0	0	0
	Canthon quadriguttatus (Olivier 1789)	p	d	r	0	0	0	0	0	0	0	0	0	0	4	1	1	3	0	0	0	0	0	0	3
CH	*Canthon sordidus* Harold 1868	p	d	r	0	3	8	30	0	0	1	15	13	0	30	14	106	132	0	7	6	10	24	3	1	6	23
	Canthon sp. (grp. *sericatus*)	p	d	r	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	2	0	1
Y	*Canthon* aff. *acutiformis*	p	d	r	108	0	0	0	0	0	0	80	0	0	268	1	1	0	0	0	0	0	0	0	0	0
W	*Canthon* aff. *acuticularis*	p	d	r	28	0	0	40	0	0	0	13	0	0	29	0	0	0	23	0	0	0	5	0	0	0
E	*Canthon triangularis* (Drury 1770)	g	d	r	0	7	0	39	17	0	1	14	30	4	0	27	60	13	33	1	12	13	8	15	24	11	28	18
Ñ	*Canthonella* sp. nov (grp. *silphoides*)	p	d	r	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0
	Coprophanaeus jasius (Olivier 1789)	g	n	c	0	3	8	29	4	3	1	0	0	0	1	1	1	4	0	2	1	2	3	0	2	2	1

Code	Species	S	DA	FRM	1986 Dimona 1ha	10ha	C.F.	C.C.	1986 Colosso 1ha	10ha	C.F.	C.C.	1986 Cidade Powell 1ha	10ha	C.C.	S.G.	2000 Dimona 1ha	10ha	C.F.	C.C.	S.G.	2000 Colosso 1ha	10ha	C.F.	C.C.	S.G.	2000 Cidade Powell 1ha	10ha	C.F.	S.G.
	Coprophanaeus lancifer (Linné 1767)	g	d	c	0	0	7	0	0	0	0	0	1	0	1	0	1	6	0	0	0	2	5	0	0	1	0	3	3	3
	Coprophanaeus parvulus (d'Olsoufieff 1924)	g	n	c	0	1	4	0	0	0	0	0	0	1	0	0	0	1	1	0	0	3	0	1	0	3	1	1	0	0
	Deltochilum carinatum (Westwood 1837)	g	n	r	0	0	0	0	0	1	3	0	0	0	0	0	1	2	0	0	1	2	0	0	0	1	1	2	2	2
M	*Deltochilum guyanensis* Paulian 1938	g	n	r	0	0	47	0	5	7	0	0	0	15	0	0	19	15	2	16	0	20	1	21	27	1	2	19	0	26
	Deltochilum icarus (Olivier 1789)	g	n	r	0	0	0	0	0	0	0	1	0	1	0	0	1	2	2	0	1	2	2	1	3	0	0	0	0	1
F	*Deltochilum septemstriatum* Paulian 1938	g	n	r	6	38	44	0	1	7	9	0	2	34	0	0	60	116	0	56	20	80	6	44	35	21	71	50	0	0
	Dichotomius sp. (grp. *melzeri*)	g	n	c	0	0	0	0	1	0	3	0	1	0	0	0	2	0	0	4	2	0	1	0	0	0	0	0	0	0
	Dichotomius sp. nov (grp. *inachus*)	g	n	c	0	2	27	0	1	4	3	0	1	4	2	0	2	5	0	2	2	2	0	5	0	3	2	2	0	2
L	*Dichotomius boreus* (Olivier 1789)	g	n	c	3	23	132	1	4	23	7	0	34	16	0	0	31	30	0	25	3	19	15	14	5	5	9	9	9	2
O	*Dichotomius* sp. (grp. *luczxi*)	g	n	c	9	34	102	0	0	16	10	0	3	33	0	0	3	29	0	3	0	9	2	20	11	6	11	6	9	15
G	*Dichotomius subaeneus* (Laporte 1840)	g	n	c	0	0	1	0	0	0	0	0	0	1	0	0	8	0	0	4	53	0	0	4	0	4	0	0	0	3
	Dichotomius imitator (Felsche 1901)	g	n	c	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	Dichotomius worontzowi (Pereira 1942)	g	n	c	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
P	*Eurysternus balachowskyi* (Halff & Halff 1977)	g	d	r	1	4	15	0	3	2	5	0	0	3	0	0	21	2	0	8	6	12	1	7	18	6	6	14	0	0
	Eurysternus sp. (grp. *caribaeus*)	g	d	r	2	3	30	0	4	3	3	1	1	1	0	0	16	25	0	6	5	19	2	7	3	5	8	8	0	8
	Eurysternus sp. (grp. *foedus*)	g	d	r	0	0	8	0	0	1	0	0	2	0	0	0	7	3	0	2	1	1	0	0	2	3	6	3	0	3
I	*Eurysternus* sp. (grp. *plebejus*)	p	d	r	7	1	11	0	2	2	6	0	5	2	0	0	21	18	0	10	32	17	2	8	13	0	16	16	16	16
J	*Eurysternus* sp. (grp. *vastorium*)	p	d	r	2	4	34	0	1	1	1	0	1	2	0	0	33	32	0	6	7	31	0	22	16	11	31	11	12	32
H	*Eurysternus* sp. (grp. *velutinus*)	g	n	r	2	0	19	0	4	4	0	0	13	7	0	0	31	54	0	31	17	6	0	10	10	6	6	1	12	9
	Onthenes carnifrons (Luederwaldt 1930)	g	n	c	0	0	1	0	0	0	0	0	0	0	0	0	1	42	0	11	3	8	3	0	0	0	0	1	0	0
A	*Onthophagus haematopus* Harold 1875	p	n	c	19	14	249	1	136	247	265	4	271	10	18	0	221	30	1	272	331	100	38	46	59	53	102	31	21	21
	Onthophagus rubrescens Blanchard 1843	p	d	c	0	0	11	0	0	0	0	0	0	0	0	0	1	6	0	1	0	5	0	2	3	0	7	7	0	2
K	*Oxysternon* sp. (grp. *silenum*)	g	d?	c	2	0	0	0	1	0	1	0	1	0	0	0	0	0	1	3	1	1	0	0	1	0	0	0	0	0
	Oxysternon festivum (Linné 1767)	g	d	c	2	0	6	0	0	4	0	0	7	0	0	0	0	0	0	3	0	1	0	1	0	0	1	2	0	1
	Oxysternon durantoni Arnaud 1984	g	d	c	0	0	3	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	3	1
	Phanaeus chalcomelas (Perry 1830)	g	d	c	0	0	15	0	1	0	3	0	1	3	0	0	6	4	0	4	0	4	1	0	2	0	4	4	4	2
X	*Pseudocanthon* aff. *xantorum*	p	d	r	1	0	0	65	0	0	0	4	0	0	226	0	0	0	54	0	1	0	1	0	0	1	0	0	0	0
R	*Scybalocanthon pygidialis* (Schmidt 1922)	p	d	r	0	9	19	0	2	2	8	0	0	1	0	0	0	92	0	2	1	15	0	4	2	0	9	9	2	2
	Sulcophanaeus faunus (Fabricius 1775)	g	n	c	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0
	Trichillum sp.	p	n	c	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	1	0	2	0	0	1	0	1	1	0	0
	Uroxys besti Ratcliffe 1980	p	n?	c	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
D	*Uroxys* sp.	p	n	c	37	20	44	0	10	10	15	3	57	31	3	1	44	164	1	6	37	54	25	159	37	31	33	40	33	43
	Uroxys sp. (grp. *latus*)	p	n	c	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0