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# RESPONSES OF DUNG BEETLE ASSEMBLAGES TO CHARACTERISTICS OF RAIN FOREST EDGES

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*Abstract*. The widespread creation of habitat edges resulting from habitat fragmentation has recently stimulated studies on edge effects and their consequences for biodiversity. Edge effects are quite variable, depending on the type of edges, the patterns of abiotic environmental gradients, and the biotic community. In this study, abundance, species richness, and the distribution of scarabaeine dung beetles were examined at a sharply demarcated rain forest – savanna edge (SEF) and at an anthropogenic edge along a road (RSF) in Paracou, French Guiana. Species richness and abundance in SEF were significantly positively correlated with distance from the edge. In RSF, a similar pattern was observed for abundance only. Patterns of faunal changes were similar to the patterns of the microclimatic and vegetation structure variables. Community analyses showed a clear segregation between both open habitat and forest assemblages. The majority of the most common species in SEF were negatively affected at the edge. Two species that were positively affected were also abundant in savanna. The majority of the common species in RSF were not affected, whereas none of the common species in roadside habitat penetrated into the forest. Higher abundances in deep edge-forest than in interior forest for 10 common species suggest that an edge effect may also be present at a larger scale. *Accepted 16 October 2007.*

*Key words*: *Dung beetles*, *edge effect*, *French Guiana*, *habitat disturbance*, *microclimate*, *rain forest*, *savanna*, *Scarabaeidae*, *vegetation structure*.

## INTRODUCTION

Change in the structure of species assemblages across ecotones, or zones of transition between adjacent ecological systems, provides examples of how organisms may perceive and respond to environmental gradients. Ecotones can be sharp or gradual and be characterized by varying biotic or direct and indirect abiotic conditions called edge effects (Murcia 1995). Edge effects at natural or anthropogenic ecotones have been the focus of wildlife management and ecological research for some time (Odum 1971), but their influences on animal communities are still poorly understood. The widespread creation of habitat edges related to fragmentation have recently stimulated interest in assessing the effects of ecotones on biodiversity (Gascon *et al*. 2000, Laurance 2000, Harper *et al*. 2005). Edges are a consequence of fragmentation, and also significantly contribute to its biological impact because they may dramatically alter the environment of the fragments (Murcia 1995). Area and edge effects are the principal processes shaping abiotic conditions and biotic communities within fragments (Turner 1996, Didham *et al*. 1998, Davies 2002) but it may be difficult to discriminate between these effects because they interact, especially in small fragments that contain the highest proportion of edge habitat. For this reason there is a need for studies of edge effect without the confounding influences of fragment size. The patterns and processes within biotas are related to these physical modifications and their direct and indirect biological effects at habitat edges (Malcolm 1997). The edge effect associated with fragmentation is becoming evident in all types of forests (Laurance & Bierregaard 1997). Invertebrates often have critical functional roles in ecosystems and hence are considered a useful model to study edge-related patterns or mechanisms because of their sensitivity to abiotic habitat disturbance (Didham *et al*. 1996).

Invertebrate communities commonly increase in abundance and diversity at forest edges (e.g., Didham 1997, Laurance & Bierregaard 1997, Bierregaard *et al*. 2001, and references therein), mostly due to an increase in disturbed-habitat species and an influx of species from human-modified habitats. In other cases, if edge-adapted species are absent, interior forest invertebrates are negatively affected by edges (Kohlman 1991, Halffter *et al*. 1992, Hill 1996, Ingham & Sam-

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ways 1996, Ozanne *et al.* 1997, Davis *et al.* 2000, Golden & Crist 2000). Edge effects may be modulated by distance from the interior in non-linear or unpredictable patterns (Murcia 1995). Bimodal patterns in species richness and abundance have been observed which correspond to an "ecotone-type" interface between the edge zone and the interior zone; however a wide range of responses can be observed at the level of species or guilds (Didham 1997).

Temperate and tropical dung beetle species are highly sensitive to disturbance (see Nichols *et al.* 2007 for a review) and different species specialize in different habitat types (Doube 1983, Cambefort & Walter 1991, Lumaret & Kirk 1991, Halffter & Favila 1993, Estrada *et al.* 1998, Shepherd & Chapman 1998, Davies *et al.* 2001, Roslin & Koivunen 2001, Feer & Hingrat 2005, Scheffler 2005, Vulinec *et al.* 2006). For that reason dung beetles have been considered valuable indicators of disturbance level, especially in the tropics (Favila & Halffter 1997, Halffter & Arellano 2002, Andresen 2005, Nichols *et al.* 2007). Abiotic conditions, especially humidity and temperature, influence population abundance through reproduction (Hanski & Cambefort 1991, Martinez & Montes de Oca 1994, Sowig 1995, Vernes *et al.* 2005, Feer & Cerdan 2006, and references therein). In addition, the majority of dung beetle species rely on mid- to large-size mammals for food and reproduction and so are directly affected by changes in mammal populations (Cambefort & Walter 1991, Estrada *et al.* 1998). Lack of mammals, which provide a substantial portion of the Neotropical dung beetle diet, affects the dung beetle community (Howden & Nealis 1975, Estrada *et al.* 1993, Andresen 2003, Feer & Hingrat 2005).

In this study I investigate the changes in species richness and abundance in dung beetle assemblages across two different ecotones between forest and open habitat. One edge is at a natural forest-savanna boundary while the other is a recent anthropogenic edge created by road construction. The sampling scheme was designed to detect a possible pattern at different spatial scales: landscape versus microhabitat scale. Measurements with respect to microclimate and vegetation structure were made to describe and compare the edge habitats.

## METHODS

*Study area*. The study site Paracou (managed by "CIRAD-forêts") is located in French Guiana (5°02'N, 53°0'W, 40 m a.s.l.), approximately 37 km northwest of Kourou. The site is a lowland tropical rain forest on ferralitic soil. The mean annual rainfall in this area is 3160 mm, with peaks in April–June and December. There are two dry seasons: a long one from August to November and a shorter one in March. The mean temperature is 26° C, with minor seasonal variations. The woody plant community of the forest is dominated (in decreasing order of importance) by Lecythidaceae, Chrysobalanaceae, and Caesalpiniaceae (Favrichon 1994, Goulet-Fleury *et al.* 2004). Most of the forest is well drained with high canopy (*ca.* 30–40 m) and open understory (interior forest, hereafter IF1 and IF2). To the north and east, forest sharply abut on savanna in a flat littoral zone (Fig. 1). Savannas on poor sandy soil are dominated by Gramineae and Cyperaceae dotted with small trees. They are partially inundated during the rainy season and locally burnt in the dry season. Savanna edge forest (hereafter SEF) is a *Symphonia-Virola* swamp forest (de Granville 1993) with a lower canopy (*ca.* 15–25 m) than in well-drained forest. Soils are seasonally waterlogged near creek bottoms and locally along savanna rivers. Palms are abundant, especially *Euterpe oleracea* near wet sites. Canopy height decreases from 120 m from the edge to the forest boundary but large emergent trees occur as close as 30 m from the edge. Low understory near the edge becomes rich in Rubiaceae, Maranthaceae, entangled lianas, and Strelitziaceae. The forest-savanna edge is oriented parallel to dominant winds coming from the east. The SEF contains cleared areas with small experimental plantations of oil-palm, hevea, or coffee between the SEF site and the N1 road. The road N1, oriented north-south, cuts through the forest in a strip about 100 m wide. Open roadside is covered with grass, Piperaceae, and sparse *Cecropia* trees on sandy soil. Roadside forest (hereafter RSF) comprises a strip about 30 m wide of secondary regrowth of 13-year-old *Cecropia* trees *ca.* 15 m high along the boundary of cut primary forest. The understory under *Cecropia* trees is dense with *Vismia*, *Solanum*, *Goupia*, and regenerating trees from the nearby primary forest. Canopy height is 20–30 m, abruptly decreasing from 60 m to the edge. Primary forest has been disturbed up to about 60–80 m wide (e.g., 90–110 m from RSF edge) as shown by the presence of gaps and sparse *Cecropia* trees. The RSF edge is oriented perpendicular to dominant winds.

The Paracou mammalian community comprises 142 species (Voss *et al.* 2001). Subsistence and recrea-

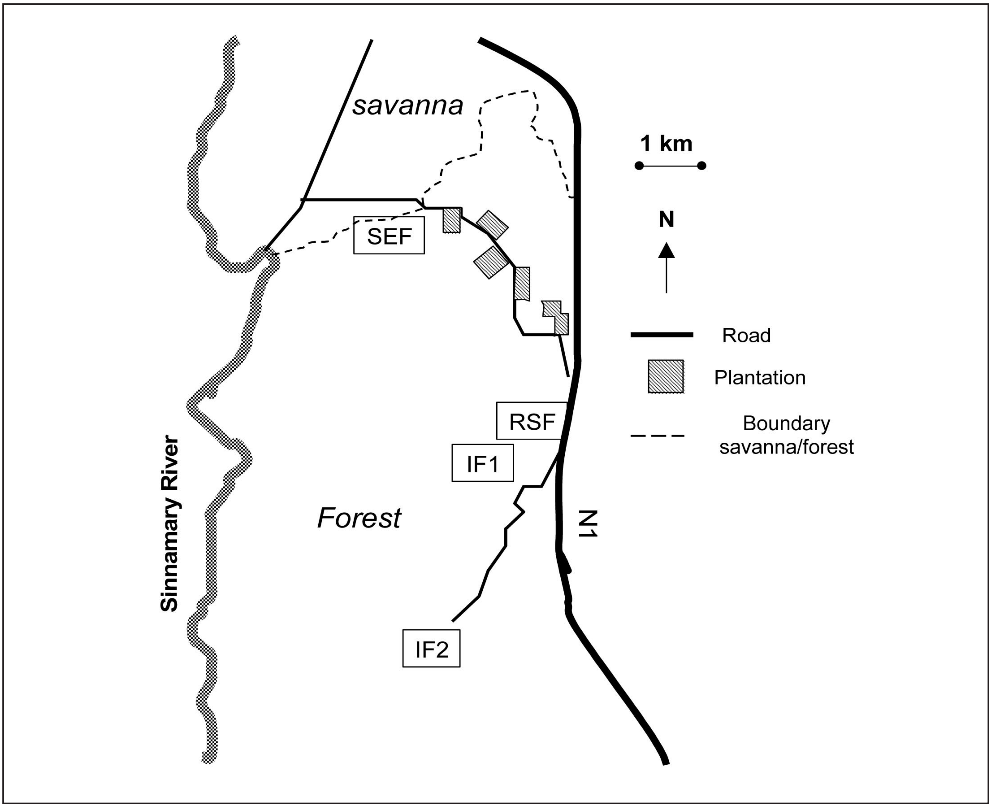

FIG. 1. Study sites in Paracou with savanna edge forest (SEF), roadside forest (RSF) along road N1, and the two interior forest stations IF1 and IF2. The dashed line is the boundary between savanna in the north from forest in the south.

tional hunting have clearly affected local populations of some large, non-volant mammals, especially after 1992 when the road was opened. Only one species of primate is common in all forest habitats (*Saguinus midas*); others are very rare or restricted to a few areas of interior forest. For example, howler monkey (*Alouatta seniculus*) is confined to the most remote interior forest site (IF2). Some ungulate species (e.g., peccaries and tapir) are uncommon or wary. Large marsupials and dasyproctid rodents are regularly seen but neither seem really common (Voss *et al.* 2001; Feer, pers. obs.). There is sparse cattle husbandry in the savanna but not in the study area.

*Beetle sampling.* Dung beetles were sampled mid-March to mid-April 2005 (rainy season). During that time it rained almost daily. The same sampling stations as vegetation and microclimate measurements were used in forest habitats with one trap per station: SEF (5 x 6 stations), RSF (5 x 6 stations), and IF sites (total 2 x 10 stations). Samples in savanna were taken from two parallel transects at 6 and 100 m from the SEF edge (total 2 x 5 stations 20 m apart).

At the roadside, I sampled from one transect parallel to the RSF edge at a distance of 50 m (10 stations 20 m apart). I captured beetles in pitfall traps made of plastic pots buried flush with the ground. The pots, 10 cm in diameter by 15 cm deep, contained a killing and preservative solution. A small plastic container filled with approximately 40 g of fresh human dung was hung on a wire over the middle of the trap. Traps were placed at each station for four days and baits were renewed once after 48 h. A second trapping session was performed in interior forest and savanna sites a minimum of 10 days after the first session. I identified species in the laboratory by comparing specimens with collections in the Laboratoire d'écologie (Brunoy) and the Laboratoire d'entomologie (Paris). Some species without corroborative specimens for comparison were classified to genus level. Voucher specimens from Paracou were deposited in Brunoy. Groups other than Scarabaeidae like Aphodidae, Hybosoridae, Geotrupidae, and Hydrophylidae were rare in the collected material and were not used in the analysis.

*Vegetation structure and microclimatic data*. The forest structure and microclimatic variables were measured with respect to habitat and distance from edge. The two interior forest sites, IF1 and IF2, were situated at 900 m and 1700 m from the road respectively (Fig. 1). At each site, measurements were taken at 10 stations 40 m apart along a 400 m transect. In RSF and SEF the sampling design was based on five parallel transects 50 m apart oriented perpendicularly to the edge. Measurements were taken at seven distances from the edge along each transect: 0 (under vegetation cover as close as possible to the boundary), 15, 30, 60, 120, 180 and 240 m.

The density of low understory was estimated by measuring the maximum distance at which soil was visible from a height of 1.6 m. Four perpendicular measurements were taken in each station and the resulting mean values used in the subsequent analyses. The palms and trees (stem diameter ≥ 30 cm) were counted in each station inside the quarters of a 10 m diameter circle and the mean value was used in analyses. Air temperature and humidity were measured 1 m above ground level with an electronic probe. A minimum of five measurements per station and per transect were taken randomly during the driest and the warmest period of the day (14:00–16:00 h) which was estimated from measurements taken over 24 h. Mean values were used to calculate the difference in microclimate variables between pooled IF, edge forests, and open habitats during the study period.

*Analyses*. Species accumulation curves were calculated for each year and each site with EstimateS software (Colwell 2000) based on 100 randomizations without replacement. Species richness values were corrected for sample abundance using the rarefaction method of Simberloff (1972).

Trends in dung beetle species richness and abundance in SEF and RSF were analyzed with respect to proximity to the edge. I used the total number of species and individuals per trap to test for correlation

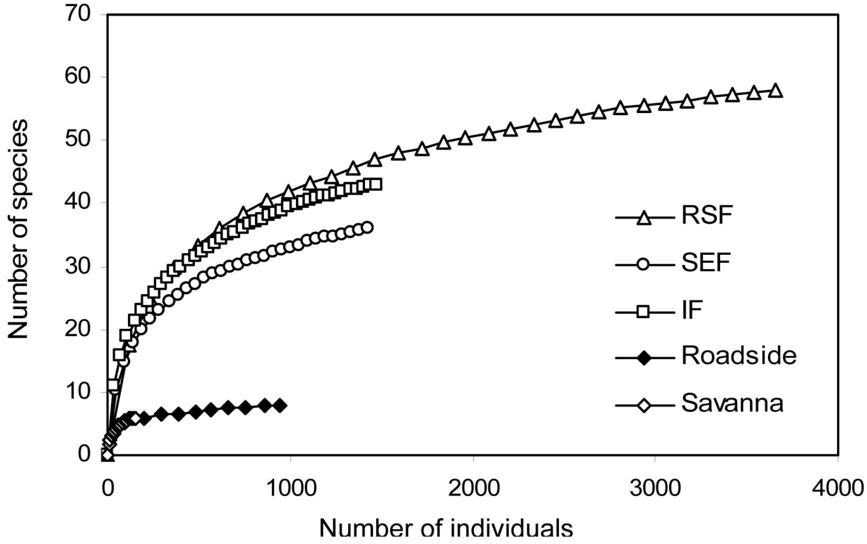

FIG. 2. Species accumulation curves in SEF, RSF, interior forest, and open habitats.

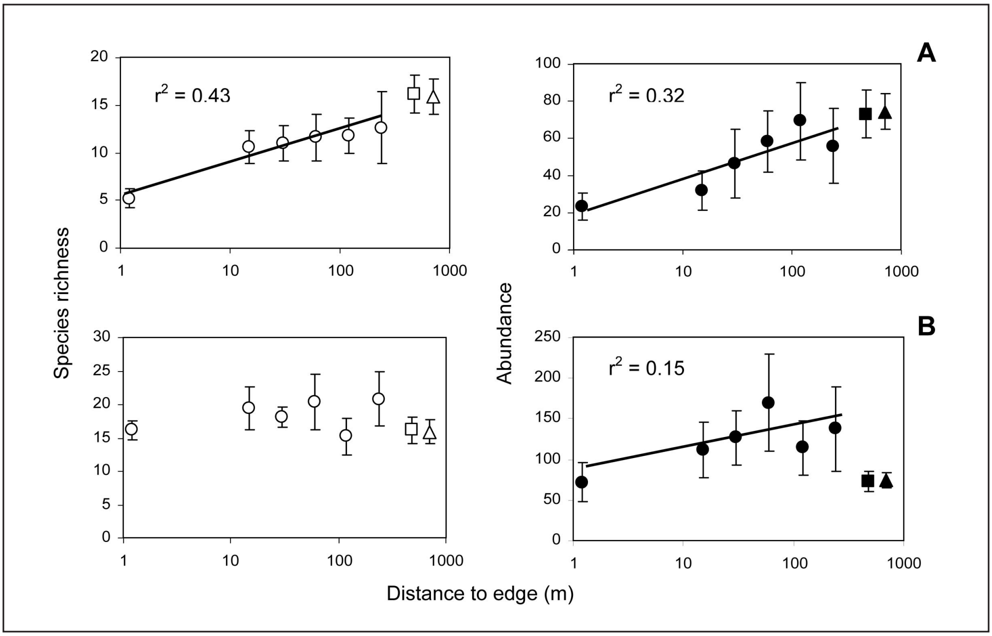

FIG. 3. Varying dung beetle species-richness and abundance responses to the distance to forest edge: (A) SEF: species richness, F1, 28 = 21.34, $P < 0.001$; abundance, $F_{1,28} = 13.39$, $P < 0.001$; (B) RSF: species richness, $F_{1,28} = 1.20$, $P = 0.28$; abundance, $F_{1,28} = 5.09$, $P = 0.032$. The distances for IF1 (square) and IF2 (triangle) are not to scale.

with distance and $\log_{10}$ (distance) to edge. The mean numbers of species and individuals in the two IF sites were calculated from the two pooled trapping sessions.

The similarity of species composition between edge forests and IF or open habitats was measured using a quantitative similarity index, Bray-Curtis. Similarity to IF was calculated as the mean similarity of each station of the SEF and RSF transects to each of the IF or open habitat stations. Trends in similarity were analyzed with respect to distance to edge. I used the arcsin transformed index to test for correlation with distance and log10 (distance) to edge. Variation in species composition between sites was analyzed with the similarity matrix (Bray-Curtis) of the sites by multidimensional scaling (MDS) to give a two-dimensional picture where spatial proximity correspond to similarity in species composition.

Trends in abundance with respect to distance to edge were analyzed for the 15 most abundant species of each edge habitat, using the average number of individuals per trap. I characterized the species according to their changes in abundance relative to the edge, their presence or absence in open habitats and IF and, when possible, to the difference of abundance between IF and deep edge forest (e.g., at 120 and 240 m).

## RESULTS

*Species richness and abundance.* The total number of dung beetles collected was 7657 individuals of 69 species (Appendix 1). Species individual accumulation curves (Fig. 2) and rarefied values showed that species richness was greater in forest habitats than in open habitats. Rarefied species richness calculated within forest habitats showed that RSF was richer (47.7, SD 2.3) than IF (42.3, SD 0.5) and SEF (36). The IF sites were pooled because they showed very similar richness and abundance in both years.

Species richness and abundance in SEF decreased toward the forest edge and were significantly correlated with log10 (distance to edge) ($0.43 \geq r^2 \geq 0.32$) (Fig. 3 A). Correlations of species richness and abundance with distance to edge were significant but ex-

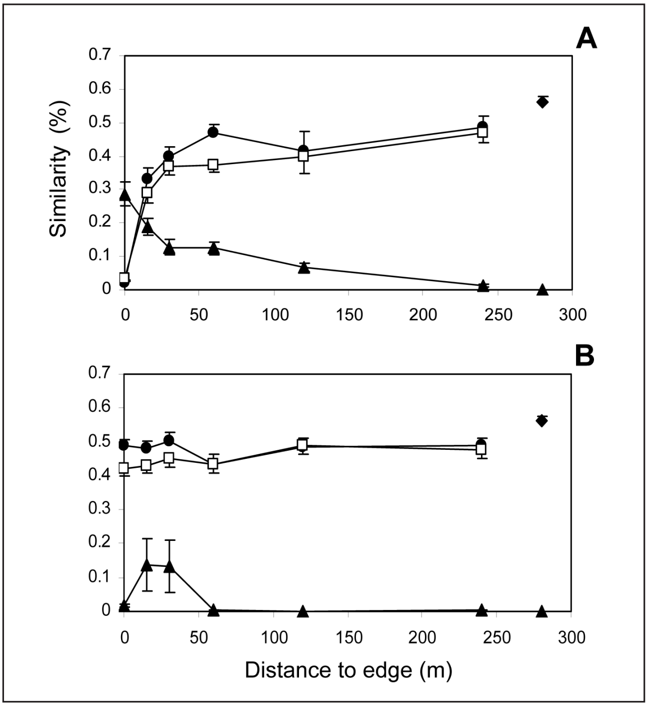

FIG. 4. Changes with the distance to edge in the mean similarity (Bray Curtis, ± 95% confidence interval) between interior forest (IF1, closed circle and IF2, open square) and (A) SEF and (B) RSF. Similarity between interior forest (pooled data) and savanna (A), roadside (B) shown as closed triangle. Similarity within interior forest, top right, was 56.1 % (± 1.6).

plained less variation of the data. Richness and abundance were not correlated ($P = 0.29$) and there was no detectable difference in rarefaction across distances to the edge ($P > 0.05$).

Species richness in RSF showed no significant changes with distance to edges or $\log_{10}$ of the same variable ($r^2 \leq 0.04$) (Fig. 3 B). Abundance decreased toward the forest edge and was significantly correlated with log10 (distance to edge) ($r^2 = 0.15$) but not with distance to edge ($r^2 = 0.04$). Raw species richness and sample raw abundance were not correlated ($P = 0.37$) and there was no detectable difference in rarefaction across distance to edge ($P > 0.05$).

*Species composition*. Species composition in SEF compared with IF1 and IF2 changed significantly with decreasing distance to the forest edge ($r^2 = 0.566$ and 0.640 respectively, $P < 0.0001$). At 0 m species composition was the least similar to IF. Similarity with savanna increased toward the edge and was significantly correlated with distance to edge ($r^2 = 0.366$, $P < 0.0001$) (Fig. 4A). Species similarity between RSF and interior forest declined toward forest edge but was only significantly correlated with IF2 in distance to edge ($r^2 = 0.045$, $P < 0.0005$) (Fig. 4B). At 0 m similarity of RSF with IF1 and IF2 was more pronounced than at SEF (48.9 and 42.0% respectively).

*Community analyses*. MDS analysis showed that samples from savanna and especially roadside are distinct in species composition from those in forest sites (Fig. 5A and 5B). The SEF stations were intermediate between the IF stations and the savanna station. The RSF stations at 60–240 m from edges were more similar in species composition to the IF sites.

*Species responses to edge*. Species in edge forests were examined for variation of abundance with distance to edges. Most of the 15 abundant species from SEF were negatively affected at edges (positive correlation, Table 1). These 12 species, and one species not affected by distance to edge (*Dichotomius robustus*), were all present in IF but absent from savanna. Differences in mean abundance between deep SEF (120 and 240 m) and IF were not significant for most of the species (Table 1) but four species (*Oxysternon festivum*, *Canthon triangularis*, *Onthophagus rubrescens*, *Deltochilum septemstriatum*) were significantly more abundant in deep edge forest than in IF. Two species positively affected at edges (*Ontherus sulcator*, *Dichotomius nisus*) were absent from IF but they were among the most abundant species in savanna.

A majority of species from RSF were not affected by proximity to edges (e.g., *Trichocanthon sordidus*, Table 1). Five species were negatively affected, as they were in SEF. The only species positively affected in RSF, (*Canthon triangularis*), was negatively affected in SEF. All RSF species were also present in IF but absent from the roadside, except *C. triangularis* with a few individuals. The four most abundant species at the roadside (*Glaphyrocanthon subcyaneus*, *Canthon cinctellus*, *Canthidium* sp4 and *Canthon* sp1) were absent from RSF. Nine species in RSF (60 %) were significantly less abundant in IF than in deep RSF and three of them showed a similar pattern in SEF.

*Forest structure*. Visibility in the undergrowth in SEF was similar to IF and decreased toward the edge from a distance of 120 m. Visibility in RSF was close to SEF and IF up to a distance of 60 m then decreased abruptly toward the edge (Table 2). Palm tree density in SEF was higher than in RSF and IF, decreasing toward the edge from a greater distance from it than in RSF. Tree density in SEF was similar to IF then decreased abruptly at the edge. Lower densities were recorded in RSF which decreased regularly toward the edge.

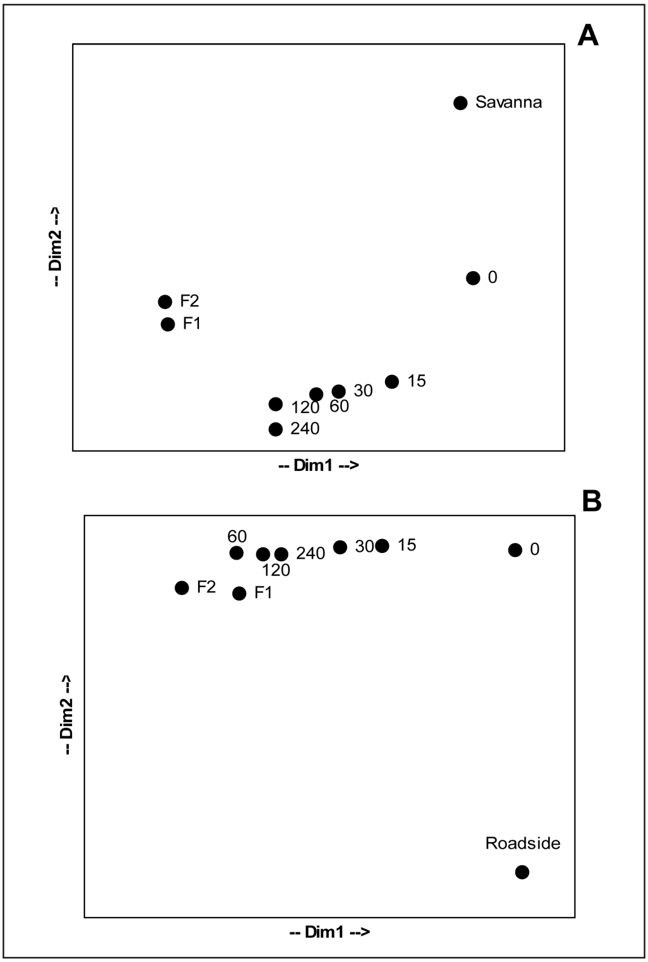

FIG. 5. Two-dimensional ordination of nine sites from metric multi-dimensional scaling (MDS), applied to a similarity matrix (Bray-Curtis). (A) savanna-forest and (B) roadside-forest.

TABLE 1. Correlation of selected species abundances with log distance to edge and difference in abundance between interior forest and deep edge forest (120 and 240 m).

| | S E F 2005 | | R S F 2005 | |
|---|---|---|---|---|
| Species | Correlation Sign ($r^2$) | Interior/ deep edge (*P* t test) | Correlation Sign ($r^2$) | Interior/ deep edge (*P* t test) |
| *Canthon bicolor* | + (0.279) | NS | + (0.108) | < (< 0.023) |
| *Oxysternon festivum* | + (0.362) | < (< 0.048) | + (0.182) | < (< 0.001) |
| *Ontherus sulcator* | – (0.247) | 0 | | |
| *Canthon triangularis* | + (0.172) | < (< 0.001) | – (0.349) | NS |
| *Onthophagus rubrescens* | + (0.372) | < (< 0.046) | + (0.160) | < (< 0.01) |
| *Onthophagus haematopus* | + (0.150) | NS | NS | NS |
| *Eurysternus caribaeus* | + (0.131) | NS | NS | < (< 0.02) |
| *Trichocanthon sordidus* | + (0.283) | NS | NS | NS |
| *Dichotomius lucasi* | + (0.159) | NS | NS | < (< 0.002) |
| *Dichotomius boreus* | + (0.169) | NS | NS | < (< 0.04) |
| *Dichotomius nisus* | – (0.164) | 0 | | |
| *Hansreia affinis* | + (0.135) | NS | + (0.132) | < (< 0.049) |
| *Dichotomius robustus* | NS | NS | | |
| *Deltochilum septemstriatum* | + (0.239) | < (< 0.028) | NS | < (< 0.02) |
| *Ateuchus murrayi* | + (0.137) | NS | + (0.136) | NS |
| *Canthidium deyrollei* | | | + (0.266) | < (< 0.003) |
| *Ateuchus simplex* | | | NS | 0 |
| *Scybalocanthon pygidialis* | | | NS | NS |

*Microclimate*. Air humidity decreased near forest edges in both edge habitats. The afternoon (driest period) humidity in IF increased toward the edge in all sites (Table 3). The driest conditions were recorded in open habitats (with differences from IF of –8.6 to –10 %) where air humidity was lower than at the forest edge. Air temperature during the afternoon (warmest period) was higher near edges and in open habitats than in IF. In SEF, the difference from IF increased regularly toward edges from 120 m (Table 3). The highest temperature differences from IF appeared close to edges. In RSF, differences with IF were negative and showed less variation than in SEF, partly because of the shady conditions in the afternoon. The highest differences were recorded in open habitats (+ 0.6 to + 1.1°C).

## DISCUSSION

Dung beetle species richness and abundance declined from intact forest toward edges at both sites. These findings are in contrast to what is often reported in other groups of forest invertebrates, such as wood and leaf-litter termites in French Guiana (Davies 2002), leaf-litter beetles in Brazil (Didham 1997), or temperate carabids (Molnár *et al.* 2001). My results are consistent with several studies on forest dung beetles in Australia (Hill 1996), Bolivia (Spector & Ayzama 2003), and Mexico (Kohlman 1991, Favila & Halffter 1997, Estrada *et al.* 1998), but other studies show different trends. Escobar (1997) found that species richness at edges is similar or higher than that in two forest habitats in Colombia. In Brazil, dung beetles respond strongly to change in habitats, forest and cerrado, but weakly to the proximity of the edge between these habitats (Durães *et al.* 2005).

The penetration distance of the edge effect observed in this study is the same or less than in other studies in the same type of habitat (see Bierregaard *et al.* 2001 for a review). Hill (1996) showed that changes in dung beetle assemblage structure occur over tens of meters. I recorded changes in species richness and abundance at similar scales in the low forest along the rock savanna surrounding an inselberg in Noura-

TABLE 2. Changes with distance to edge in understory visibility, palm density, and large tree density in SEF, RSF and IF (confidence interval at 5% in parentheses).

| | Distance to edge (m) | | | | | | Interior forest | |
|---|---|---|---|---|---|---|---|---|
| | 0 | 15 | 30 | 60 | 120 | 240 | IF1 | IF2 |
| Visibility (m) | | | | | | | | |
| SEF | 2.9 | 4.1 | 5.5 | 5.6 | 7.6 | 8.1 | 7.1 | 8.0 |
| | (0.5) | (0.8) | (1.7) | (1.4) | (1.5) | (2.1) | (1.1) | (1.3) |
| RSF | 4.4 | 4.6 | 6.0 | 8.5 | 8.4 | 7.9 | | |
| | (0.8) | (1.5) | (0.8) | (3.1) | (1.8) | (1.5) | | |
| Palm density | | | | | | | | |
| SEF | 0.4 | 2.3 | 2.5 | 3.6 | 5.9 | 6.0 | 3.2 | 2.4 |
| | (0.3) | (0.7) | (0.6) | (1.4) | (1.6) | (1.1) | (0.9) | (0.3) |
| RSF | 0.2 | 0.7 | 1.7 | 2.5 | 3.3 | 2.5 | | |
| | (0.2) | (0.4) | (0.5) | (0.8) | (0.8) | (0.5) | | |
| Tree density | | | | | | | | |
| SEF | 0.2 | 1.2 | 1.4 | 1.7 | 1.5 | 2.1 | 2.0 | 2.7 |
| | (0.2) | (0.2) | (0.4) | (0.4) | (0.2) | (0.6) | (0.4) | (0.5) |
| RSF | 0.3 | 0.3 | 0.7 | 0.7 | 1.0 | 1.7 | | |
| | (0.1) | (0.2) | (0.3) | (0.4) | (0.5) | (0.3) | | |

gues area in French Guiana (Feer, unpubl. data). A penetration distance of 60 m suggests that a one-hectare forest fragment is entirely subjected to edge effects in addition to fragmentation effects. However, the impact of edge effects may be confounded if there are also scale-dependent effects. In Paracou, I observed monotonic patterns of edge effect over a short distance but the differences in species richness and abundance between edge habitats and interior forest suggest that edge effect may also be present at a larger scale. Overall diversity and abundance in RSF tended to be higher than in interior forest, while a reverse trend was observed with SEF. Further sampling at larger temporal and spatial scales is needed to determine if a non-monotonic relationship with distance from the forest edge occurs, as observed in litter invertebrates (Didham 1997).

At 240 m from the edge, SEF and RSF were similar to IF with respect to vegetation structure and microclimatic conditions. Habitat near edges contained denser understories and declining tree and palm density. Microclimate conditions became progressively warmer and drier, likely due to the decreasing canopy height or density. These changes in

TABLE 3. Changes with distance to edge in air humidity and temperature differences to IF in SEF and RSF during the warmest and driest period of the day.

| | | Distance to edge (m) | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Open habitat | 0 | 15 | 30 | 60 | 120 | 180 | 240 |
| Air humidity difference (%) | | | | | | | | |
| SEF | – 10 | – 7.7 | – 7.0 | – 7.0 | – 4.7 | – 2.0 | – 0.1 | – 0.8 |
| RSF | – 8.6 | – 6.8 | – 5.5 | – 7.0 | – 4.3 | – 3.0 | – 1.2 | + 1.3 |
| Temperature difference (°C) | | | | | | | | |
| SEF | + 1.1 | + 0.6 | + 0.7 | + 0.7 | + 0.1 | – 0.4 | – 0.4 | – 0.3 |
| RSF | + 0.6 | – 0.4 | – 0.4 | – 0.4 | – 0.2 | – 0.9 | – 0.9 | – 0.8 |

abiotic parameters at edges are consistent with the reported patterns in tropical forests (Laurance *et al.* 1997, Harper *et al.* 2005). SEF differed from RSF in a steeper decline of understory and palm densities over distance. The edge effects in RSF did not appear to extend as deeply into the habitat as in SEF. The relatively low tree density in RSF may result from high disturbance and possibly more frequent wind throw related to the road opening. Comparatively fewer changes in microclimate, especially temperature, were recorded near the edge in RSF, despite a greater exposure to wind. The buffering effect of the secondary regrowth, and a less extensive and warm roadside matrix may explain these differences.

The differences in abiotic conditions of the natural and anthropogenic edge habitats are reflected at the dung beetle assemblage level with a much more pronounced edge effect in SEF than in RSF. Dung beetles, like many other invertebrates, are affected by temperature and humidity and correlated factors such as soil moisture (Hanski 1989, Hanski & Cambefort 1991, Sowig 1995). Seasonal variations in dung beetle abundance in Saint Eugène, situated near Paracou, suggested that greater forest disturbance resulted in a higher amplitude of variations in activity over one year (Feer & Cerdan 2006). In SEF a similar pattern was observed in another year in the dry season with an higher overall species richness (Feer, unpubl. data). The partial inundation occurring during the rainy season may have had a negative effect on dung beetles, possibly due to soil saturation. This hypothesis has also been proposed by Escobar (1997) to explain the lower species richness in creek forest compared with hill forest in Columbia. Forest inundation is absent from IF and RSF. In addition, the effect of forest type may also explain the differences between RSF and SEF. The proximity of RSF to IF sites (see Fig. 1), and the degree of disturbance from nearby plantations on SEF, are additional factors that might explain the patterns of species richness and abundance. The lack of replicates in this study do not allow me to assess their influence.

The community analyses showed a strong segregation between forest and open habitats, indicating a high degree of habitat specialization. Similarly, Spector and Ayzama (2003) found a nearly complete dung beetle community turnover in just a few meters between forest and savanna in Bolivia. In Paracou, both edge habitats had a similar overall species composition to the interior forest. A majority of species found in edge habitat can be considered forest specialists because they are completely absent from open habitats. In SEF most of the forest species followed the general pattern by reflecting a similar sensitivity to edge effect. In RSF fewer species were negatively affected by edges, an indication of the difference between the sites. Two common savanna species (*Ontherus sulcator*, *Dichotomius nisus*) were collected well inside SEF but were not collected in IF. These two species may be adapted to edge habitat, which is more similar to savanna than forest, and unlike forest species may be able to tolerate inundation of the soil. In fact, a nearly complete habitat segregation between the RSF and roadside assemblages emerged from the community analyses. None of the dominant species of the roadside habitat entered the nearby forest. This difference with SEF may be explained by the difference between the habitats but also by the difference between the respective matrices, which have distinct assemblages themselves. The similarity between roadside and savanna assemblages was low (4.5 %); the roadside fauna was more similar to that collected from an anthropogenic forest clearing (Feer, pers. obs.). Several species, mostly in RSF, showed a higher abundance in deep edge forest than in IF, confirming that a larger-scale edge effect beyond a few tens of meters might exist.

Most of the forest dung beetles in this study are habitat specialists that are adversely affected by edge proximity. Changes in the physical edge structure and microclimate along an edge-to-interior gradient appear to be important in determining the composition and distribution of dung beetle assemblages. Similarly, the dung beetle assemblages reflect structural differences between natural forest microhabitats and derived forest biotopes (see Davis *et al.* 2000). Dung beetle assemblages have been considered by several authors as a valuable indicator group in tropical forests in Africa (Shepherd & Chapman 1998, Chapman *et al.* 2003), Asia (Davis & Sutton 1998), and Central America (Halffter & Favila 1993).

In this study, those species preferring edge habitat were also found in savanna, indicating that they may be taking advantage of favorable conditions in edges rather than being edge specialists. No such ubiquitous species were present in the newly created edge along the road, which exhibited a very different assemblage. A less extreme habitat segregation exists in Central America, where the proportion of ubiquitous dung beetle species that are found in forest is higher (e.g., Kohlman 1991, Estrada *et al.* 1998, Horgan 2007), perhaps because forests are more fragmented and disturbed while anthropogenic open habitats are dominant and older (Janzen 1983). From a conservation point of view, natural or artificial edge forests are not refuges of dung beetle diversity. The loss of diversity is not balanced by penetration of species from adjacent open habitats or by the creation of new opportunities for tolerant species. Thus, the study of the faunal composition and diversity of various other types of disturbed forests is of key importance in predicting the growing impact of landscape changes.

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## Appendix

| Species | SEF | RSF | IF | Roadside | Savanna |
|---|---|---|---|---|---|
| *Agamopus castaneus* | 4 | 4 | 2 | | |
| *Agamopus* sp 1 | | | 1 | | |
| *Anomiopus* sp 1 | | 9 | | | |
| *Ateuchus murrayi* | 10 | 43 | 29 | | |
| *Ateuchus* near *aeneomicans* | | | | | |
| *Ateuchus* near *obscurus* | | 12 | 11 | | |
| *Ateuchus simplex* | | 53 | | | |
| *Ateuchus* sp 3 | | 4 | | | |
| *Ateuchus substriatus* | | 8 | | | |
| *Ateuchus sulcicolle* | 7 | 11 | 2 | | |
| *Canthidium aterrimum* | | 5 | 2 | | |
| *Canthidium bicolor* | 1 | 6 | 2 | | |
| *Canthidium centrale* | 1 | 10 | 10 | | |
| *Canthidium deyrollei* | 10 | 143 | 83 | | |
| *Canthidium dohrni* | 2 | 7 | 3 | | |
| *Canthidium gerstaeckeri* | 5 | | | | |
| *Canthidium gracilipes* | | 2 | | | |
| *Canthidium lentum* | | | 2 | 1 | |
| *Canthidium* near *guyanense* | | 1 | | | |
| *Canthidium* near *trinodosum* | 3 | | 2 | | |
| *Canthidium* near *viride* | | 1 | | | |
| *Canthidium onitoides* | | 1 | 1 | | |
| *Canthidium* sp 3 | 2 | 1 | 12 | | |
| *Canthidium* sp 4 | | 2 | | 606 | |
| *Canthidium* sp 5 | | | | | |
| *Canthidium* sp 6 | | | 1 | | |
| *Canthon (Glaphyrocanthon) quadriguttatus* | 1 | 22 | 1 | | |
| *Canthon (Glaphyrocanthon) subcyaneus* | | | | 199 | 2 |
| *Canthon bicolor* | 230 | 479 | 196 | | |
| *Canthon cinctellus* | | | | 31 | 1 |
| *Canthon* sp 1 | | | | 90 | 5 |
| *Canthon triangularis* | 181 | 51 | 4 | 3 | |
| *Canthon virens* | | 3 | | | |

Appendix continued

| Species | SEF | RSF | IF | Roadside | Savanna |
|---|---|---|---|---|---|
| *Canthonella* sp 1 | | | | | |
| *Coprophanaeus (Megaphanaeus) lancifer* | | 2 | | | |
| *Coprophanaeus jasius* | | 1 | | | |
| *Coprophanaeus parvulus* | | 4 | | | |
| *Deltochilum carinatum* | | | 3 | | |
| *Deltochilum guyanense* | 5 | | 14 | | |
| *Deltochilum icarus* | | | | | |
| *Deltochilum septemstriatum* | 13 | 71 | 3 | | |
| *Deltochilum submetallicum* | 3 | 6 | 46 | | |
| *Dichotomius apicalis* | | 8 | 24 | | |
| *Dichotomius boreus* | 35 | 88 | 24 | | |
| *Dichotomius lucasi* | 36 | 406 | 91 | | |
| *Dichotomius near robustus* | 14 | 2 | 19 | | |
| *Dichotomius nisus* | 27 | 4 | | | 5 |
| *Dichotomius subaeneus* | | | 1 | | |
| *Eurysternus balachowskyi* | 1 | 8 | 2 | | |
| *Eurysternus caribaeus* | 57 | 177 | 44 | | |
| *Eurysternus cayennensis* | | 1 | | | |
| *Eurysternus confusus* | | 2 | 1 | | |
| *Eurysternus foedus* | 1 | 9 | 6 | | |
| *Eurysternus hamaticollis* | 1 | 7 | 2 | | |
| *Eurysternus hirtellus* | | 13 | 3 | | |
| *Eurysternus velutinus* | | 5 | 1 | | |
| *Hansreia affinis* | 25 | 222 | 71 | | |
| *Ontherus sulcator* | 207 | 14 | | 17 | 134 |
| *Onthophagus bidentatus* | | 1 | | | |
| *Onthophagus haematopus* | 79 | 75 | 97 | | |
| *Onthophagus rubrescens* | 167 | 471 | 227 | | |
| *Onthophagus xanthomerus* | 2 | 4 | 2 | | |
| *Oxysternon (Mioxysternon) spiniferum* | | | | | |
| *Oxysternon festivum* | 229 | 881 | 243 | | |
| *Oxysternon silenus* | 2 | 1 | | | |
| *Phanaeus chalcomelas* | | 3 | 2 | | |
| *Scybalocanthon pygidialis* | 1 | 54 | 17 | | |
| *Sylvicanthon candezei* | 6 | 35 | | | |
| *Trichillum pauliani* | 1 | 1 | | | 11 |
| *Trichocanthon sordidus* | 52 | 188 | 167 | | |
| *Uroxys gorgon* | 3 | 2 | 1 | | |
| *Uroxys* sp 1 | | 1 | | | |
| *Uroxys* sp 2 | | 4 | | | |
| *Uroxys* sp 3 | | 3 | | 1 | |
| Total number of individuals | 1424 | 3652 | 1475 | 948 | 158 |
| Total number of species | 36 | 58 | 43 | 8 | 6 |