



Comparison of dung beetle communities (Coleoptera: Scarabaeidae: Scarabaeinae) in oil palm plantations and native forest in the eastern Amazon, Brazil

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ABSTRACT

In order to evaluate the impact of oil palm cultivation on dung beetles in the eastern Brazilian Amazon, comparisons were made of communities in oil palm plantations and native forest. Pitfall traps baited with human feces were buried to soil level in plantations and surrounding forests. Fifty traps were used in each type of vegetation, placed at 50 m intervals along five transects. Dung beetle communities in oil palm plantations have lower species richness (18 spp.) than in surrounding tropical rainforest (48 spp.), as well as altered species composition. Total abundance of individuals was not significantly different between the two habitats, but species composition was greatly different. Species evenness was greater in the forest. Forest corridors for the preservation of dung beetle species may need to be much wider than current designs. The erosion of biodiversity in dung beetles due to oil palm monoculture parallels what has been seen in other animal taxa in tropical tree plantations.

Introduction

African oil palm (*Elaeis* sp.) is a major and rapidly expanding crop, responsible for high levels of deforestation and species loss in south east Asia (e.g. Fitzherbert et al., 2008). In recent years it has also spread across the eastern Amazonian state of Pará, where monoculture plantations now occupy more than 200,000 hectares (Butler and Laurance, 2009; Butler, 2011; Englund et al., 2015). Governmental incentives and a steady demand for palm oil for biofuels, industrial lubricants, and food products are causing the planted areas to expand at the expense of tropical lowland forests that are clear-cut for new plantations (Lees et al., 2015).

In order to evaluate the impact of oil palm plantations on one target group, the dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae), comparisons were made of communities in oil palm plantations and in surrounding intact forests. Dung beetles have been recommended for studies of biological conservation, especially as a proxy for hard to detect mammals (Spector, 2006; Barlow et al., 2007; Gardner et al., 2007, 2008a; Nichols and Gardner, 2011; Bicknell et al., 2014). They are a bio-indicator of soils and microclimate (Halffter and Favila, 1993;

Nichols et al., 2007), and influence important ecosystem functions and services such as secondary seed dispersal, nutrient recycling, soil aeration, and biological control of pest insects and helminth parasites (Halffter and Matthews, 1966; Nichols et al., 2008; Ridsdill-Smith and Edwards, 2011). We expected to find a high species turnover between the two types of sampled environments. In general, species with a more restricted niche, specialized in forested areas, are expected to be found only in the remnants of native forest (Halffter and Favila, 1993; Nichols et al., 2007). The different microclimate and food supply conditions found between the Amazon rainforest and palm plantations may restrict the maintenance of stable populations in the latter areas. In this way, we hypothesize that only species with generalist habits or capable of withstanding adverse environmental conditions will be found in the palm monoculture. As it is a more simplified ecosystem, the palm plantation monoculture should provide a vacant niche for generalist species or those typical of open areas such as the *cerrado*. As the remnants of the Amazon rainforest are “disturbed” or replaced by palm monoculture, we expect that these new environments will favor

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colonization by generalist species from open areas that are pre-adapted to these new habitats.

Body size in dung beetles has been associated with sensitivity to tropical forest modification and fragmentation. In general, it is expected to find larger species within undisturbed tropical forests (Chown and Klok, 2011). In a severely degraded habitat lower survival of larger specimens tends to occur due to thermal intolerance (Larsen and Forsyth, 2005; Larsen et al., 2008). In addition, large beetles can more effectively allocate feces deposits from large mammals, which are rarer in degraded rainforests. As such, key functional groups, such as the rollers, tunnelers, and dwellers, coprophages, scavengers or generalists, and body size are useful proxies of functional integrity of the community.

In this study, we examine the value of palm oil plantations for Amazonian dung beetle communities in a large plantation in the state of Pará. We compare between native forest and palm oil, assessing the difference in (1) species richness, (2) abundance, (3) species composition, (4) patterns of dominance (rank abundance), and (5) the abundance of key functional groups. Finally, we (6) assess whether there is any evidence that spillover from forest to nearby plantation is occurring such that forest, rather than oil palm plantation, is the main source of dung beetle species (Lucey et al., 2014).

Materials and Methods

Study area

- The study was conducted in Tailândia municipality in northeastern Pará state, Brazil, in plantations belonging to Agropalma S.A. that has about 39,000 hectares of oil palm plantations (*Elaeis* sp.) and 64,000 hectares of forests (Fig. 1). The matrix vegetation is dense Amazonian broadleaf lowland rainforest (Hueck, 1972). According to the Köppen-Geiger classification (Köppen and Geiger, 1928), climate is type Afi, or humid tropical, with a rainy season from December to May and a dry season from June to November. Average yearly rainfall recorded is 2,038 mm, and average daily temperature is 26.5° C, with air relative humidity near 87%. Mendes-Oliveira et al. (2017) presented an historical background to the ecology of the study area, including a list of mammal species in both plantation and forests as detected by camera trapping and line transect surveys.

Collection methods

- We selected five oil palm plantation sites of comparable ages in relation to overall habitat structure (7–15 years-old), which were paired with five neighboring primary forest sites. Pitfall traps baited with human feces and containing salt solution were buried to soil

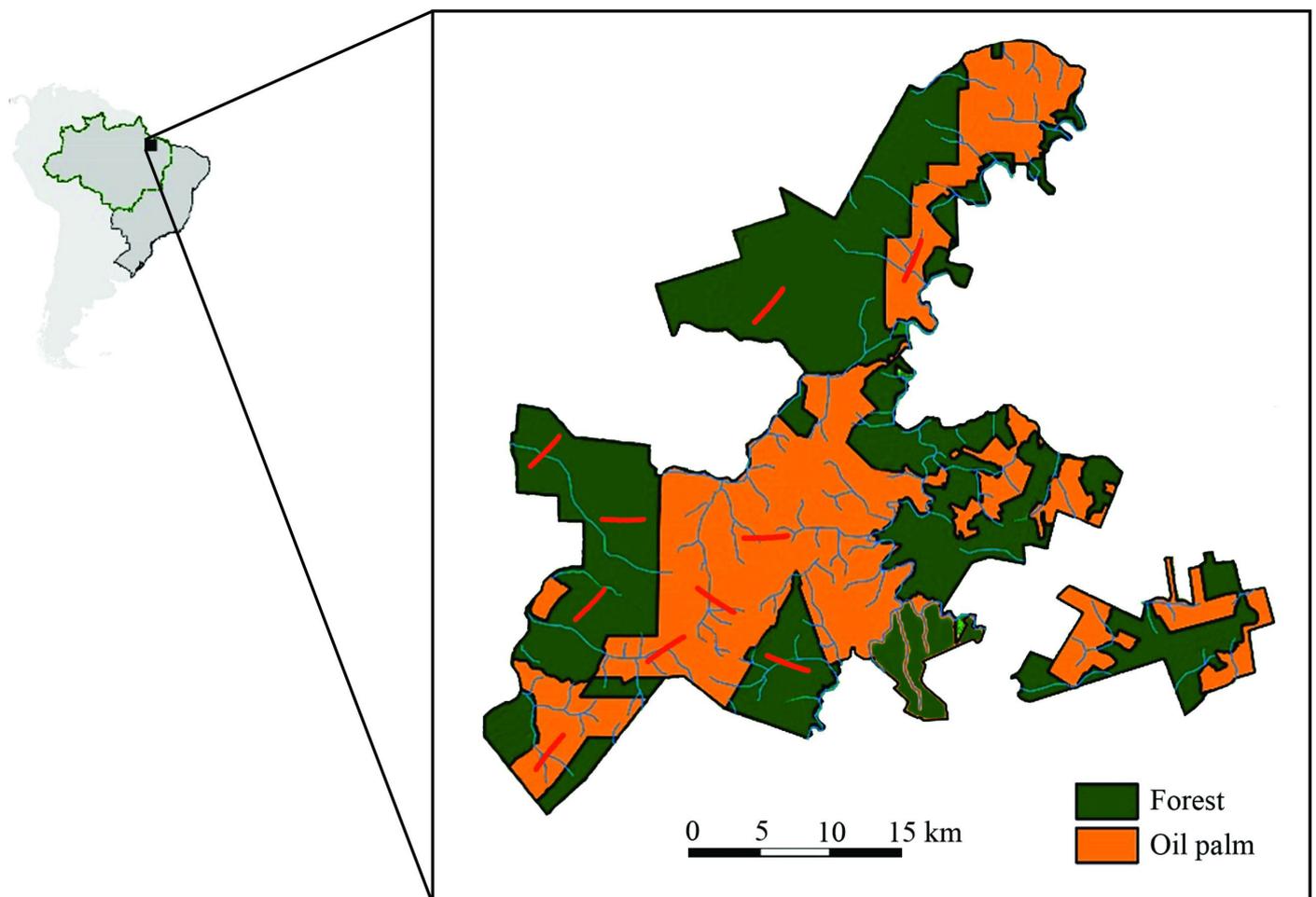


Figure 1 Location of the study area in the Brazilian Amazon, in the state of Pará. The right map represents the study area and the spatial distribution of 10 transects (red lines) in forest and oil palm habitats. Green and orange areas indicate primary forest and oil palm plantations, respectively (modified from Mendes-Oliveira et al., 2017). This figure is in color in the electronic version.

level in plantations and surrounding forests (Marsh et al., 2013). Trap diameter was 14 cm and depth was 9 cm. Fifty traps were used in each type of vegetation, placed at 50 m intervals along 5 transects with their origin at the forest-plantation border (Larsen and Forsyth, 2005; Andrade et al., 2014; Silva and Hernández, 2015) Although Silva and Hernández (2015) suggested using a minimum distance of 200 m between traps within Amazonian forest environments to avoid pseudo-replication, in this study we used a distance of 50 meters to make our results comparable with other multitaxon studies that were being carried out in the sampled area. To avoid border effects, forest traps were located at least 100 m from the plantations (Feer, 2008). The experiment took place from 9 to 16 July 2016 and was carried out only in the dry season due to the need for integrated field logistics with other teams that worked on the same site. The use of dung beetles for the rapid diagnosis of areas along a gradient of land use has been frequently performed at least since the 1990s in tropical forest areas (Halffter and Favila, 1993; Spector and Forsyth, 1998; Nichols et al., 2007; Hayes et al., 2009). Thus, since our objective was to carry out a quick assessment of the conservation value of the analyzed areas and not an exhaustive inventory of the regional species, nor a seasonal analysis, the sampling protocol employed here has achieved the objective proposed for the study. Each trap was open for 48 hours, and all captured dung beetles were identified to species or morphospecies. Specimens were collected under IBAMA/SISBio permit nr. 35898-1. Voucher material was deposited in the Universidade Federal do Pará, Universidade Federal de Mato Grosso, and Museu Paraense Emílio Goeldi. Locations of the forest and plantation transects are shown in Table 1. Each transect had 10 traps, totaling 50 forest traps and 50 plantation traps.

Data analysis

- Comparisons of species richness and rank abundance were made with the non-parametric Mann-Whitney U test. Dominance was verified through abundance curves of each species in each vegetation type. Statistica version 6.0 (StatSoft Inc., 1996) was used for calculations, and probability for significance was $p < 0.05$ (Zar, 2010). Estimates of species richness were made with the program EstimateS version 9.2 using 100 randomizations without replacement (Colwell, 2013). Non-parametric estimates of species richness were chosen: Chao 1 and 2, and Jackknife 1 and 2. Cluster analysis using Bray-Curtis index of similarity was employed to construct a dendrogram of similarity among transects with the program Primer version 5 (Clarke and Gorley, 2006). Extrapolation of species richness was made using the R package iNext (Hsieh et al., 2016).

Functional groups

- Dung beetle species can be diurnal or nocturnal, tunnellers, dwellers or rollers, and coprophages, necrophages or generalists (Hanski and Cambefort, 1991). In addition, their body sizes can vary over at least

one order of magnitude. Data used for most species are from the studies of Beiroz et al. (2017), Griffiths et al. (2015, 2016), Silva et al. (2014), and observations of author FABS. Body length and pronotal width were measured from representative individuals of each species. Coloration was observed in dried specimens. Biomass estimates of dung beetle assemblages could not be obtained, although these could have been useful measures (Cultid-Medina and Escobar, 2016).

Results

Richness and abundance

- In total, 1863 dung beetles were collected, representing 54 species in 16 genera. Forest yielded more species (48) than oil palm plantation (18), with 12 species present in both habitats (Table 2). Species richness in plantation was significantly lower than in forest (Mann-Whitney U, $Z = 2.62$; $p = 0.009$). Estimates of total species richness (S) are around 70 species in forest and 27 in oil palm plantation (Table 3, Jackknife 2). With the iNext package for R (Hsieh et al., 2016), extrapolated species richness estimates for the two environments show that the forest dung beetle community is more speciose at all levels of collection effort (Fig. 2).

Dung beetle abundance was not significantly different between forest and plantation (Mann-Whitney U, $Z = 0.731$; $p = 0.464$). The most abundant species in palm plantations was *Canthon conformis* (Harold, 1868) (431 individuals) but with much lower presence in the forest (4 ind.). This widespread species is a generalist and found in disturbed areas throughout Amazonia. Other abundant species in plantation were: *Onthophagus* sp. (148 ind.), *Canthidium* sp. 3 (90 ind.), and *Canthidium* aff. *barbacenicum* Preudhomme de Borre, 1886 (28 ind.) (Table 2). In forest, the most abundant species was *Canthidium* aff. *deyrollei* Harold, 1867 (252 ind., but absent from plantation), followed by *Dichotomius* aff. *lucasi* (Harold, 1869) (133 ind.), and *Canthon proseni* (Harold, 1869) (123 ind.) (Table 2). These species are known to predominate in primary and secondary Amazonian forests (Braga et al., 2013). Other forest species, such as *Eurystemus caribaeus* (Herbst, 1789) and *Ontherus sulcator* (Fabricius, 1775), have widespread geographical distributions in Brazil (Génier 1996, 2009). Rare species with 3 or fewer individuals (21 spp.) were found mostly in forest (18 vs 5 spp.). However, we are aware that the number of rare species recorded in this study may be biased by the type of experimental design adopted in this study. Rapid assessments of a site's biodiversity status do not allow exhaustive specimen collections, being a momentary portrait of the local community (Beiroz et al., 2017).

Table 1
Coordinates of forest and plantation transects used for the collection of dung beetles in Tailândia, Pará, Brazil.

| Transect | Forest | Oil Palm Plantation |
|----------|---------------------------|---------------------------|
| 1 | 02°22'50.1"S;48°48'08.4"W | 02°40'07.0"S;48°54'40.8"W |
| 2 | 02°36'36.9"S;48°46'10.1"W | 02°37'03.0"S;48°52'17.8"W |
| 3 | 02°34'41.1"S;48°52'51.0"W | 02°34'45.1"S;48°49'00.8"W |
| 4 | 02°29'08.9"S;48°56'06.9"W | 02°36'35.9"S;48°51'09.3"W |
| 5 | 02°31'44.9"S;48°52'58.5"W | 02°32'26.0"S;48°47'56.2"W |

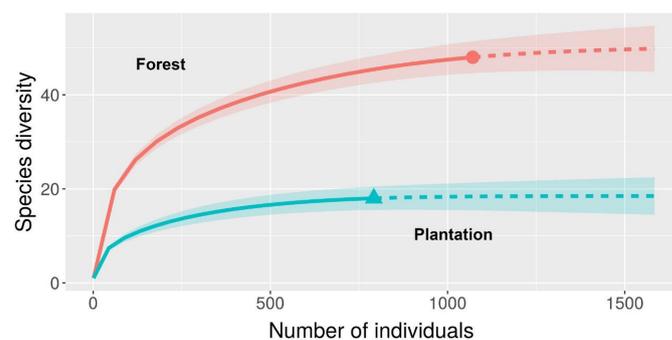


Figure 2 Extrapolation and rarefaction of species richness in forest and oil palm plantation dung beetle communities. Shaded area represents 95% confidence limits. This figure is in color in the electronic version.

Table 2
Dung beetles collected in forest or oil palm plantation, by habitat and transect.

| Species | Forest | | | | | Oil palm plantation | | | | | Total |
|--|------------|------------|------------|------------|------------|---------------------|-----------|-----------|------------|------------|-------------|
| | F1 | F2 | F3 | F4 | F5 | P1 | P2 | P3 | P4 | P5 | |
| <i>Agamopus</i> sp. | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Ateuchus</i> aff. <i>substriatus</i> (Harold, 1868) | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Ateuchus</i> sp. 1 | 6 | 2 | 9 | 8 | 1 | 0 | 0 | 0 | 0 | 0 | 26 |
| <i>Ateuchus</i> sp. 2 | 2 | 2 | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 |
| <i>Canthidium</i> aff. <i>barbacenicum</i> Preudhomme de Borre, 1886 | 0 | 0 | 0 | 1 | 0 | 14 | 0 | 4 | 9 | 1 | 29 |
| <i>Canthidium</i> aff. <i>deyrollei</i> Harold, 1867 | 151 | 13 | 19 | 65 | 4 | 0 | 0 | 0 | 0 | 0 | 252 |
| <i>Canthidium</i> aff. <i>gerstaeckeri</i> Harold, 1867 | 25 | 0 | 6 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 34 |
| <i>Canthidium</i> sp. 1 | 0 | 0 | 2 | 1 | 0 | 5 | 10 | 0 | 11 | 0 | 29 |
| <i>Canthidium</i> sp. 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Canthidium</i> sp. 3 | 21 | 33 | 0 | 0 | 1 | 5 | 9 | 26 | 27 | 23 | 145 |
| <i>Canthidium</i> sp. 4 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 2 |
| <i>Canthon conformis</i> (Harold, 1868) | 2 | 0 | 0 | 2 | 0 | 72 | 36 | 21 | 32 | 270 | 435 |
| <i>Canthon</i> aff. <i>xanthopus</i> Blanchard, 1846 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Canthon</i> aff. <i>simulans</i> (Martínez, 1950) | 0 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 9 | 0 | 29 |
| <i>Canthon histrio</i> (Serville, 1828) | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 8 |
| <i>Canthon lituratus</i> (Germar, 1813) | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 3 |
| <i>Canthon proseni</i> (Martínez, 1949) | 4 | 5 | 45 | 16 | 53 | 0 | 0 | 0 | 0 | 0 | 123 |
| <i>Canthon quadriguttatus</i> (Olivier, 1789) | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Coprophanæus cyanescens</i> d' Olsoufieff, 1924 | 9 | 3 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 1 | 17 |
| <i>Coprophanæus dardanus</i> (MacLeay, 1819) | 9 | 2 | 5 | 1 | 0 | 1 | 0 | 2 | 1 | 0 | 21 |
| <i>Coprophanæus jasius</i> (Olivier, 1789) | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 |
| <i>Coprophanæus lancifer</i> (Linnaeus, 1767) | 4 | 6 | 4 | 0 | 0 | 2 | 0 | 0 | 2 | 3 | 21 |
| <i>Cryptocanthon campbellorum</i> Howden, 1973 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Deltochilum</i> aff. <i>guyanense</i> Paulian, 1933 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Deltochilum</i> sp. | 6 | 2 | 5 | 12 | 10 | 0 | 0 | 0 | 0 | 0 | 35 |
| <i>Deltochilum</i> aff. <i>peruanum</i> Paulian, 1938 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Deltochilum carinatum</i> (Westwood, 1837) | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Deltochilum icarus</i> (Olivier, 1789) | 0 | 1 | 5 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 10 |
| <i>Deltochilum sextuberculatum</i> Bates, 1870 | 0 | 0 | 4 | 18 | 4 | 0 | 0 | 0 | 0 | 0 | 26 |
| <i>Dichotomius</i> aff. <i>globulus</i> (Felsche, 1901) | 3 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 5 |
| <i>Dichotomius</i> aff. <i>lucasi</i> (Harold, 1869) | 35 | 30 | 25 | 38 | 5 | 0 | 0 | 0 | 0 | 0 | 133 |
| <i>Dichotomius robustus</i> (Luederwaldt, 1935) | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Dichotomius</i> aff. <i>worontzowi</i> (Pereira, 1942) | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Dichotomius carinatus</i> (Luederwaldt, 1925) | 22 | 10 | 8 | 3 | 5 | 0 | 0 | 0 | 2 | 0 | 50 |
| <i>Dichotomius bos</i> (Blanchard, 1843) | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| <i>Eurysternus atrosericus</i> Génier, 2009 | 2 | 2 | 3 | 8 | 0 | 0 | 0 | 0 | 0 | 0 | 15 |
| <i>Eurysternus caribaeus</i> (Herbst, 1789) | 14 | 6 | 7 | 2 | 7 | 0 | 0 | 0 | 0 | 0 | 36 |
| <i>Eurysternus cavatus</i> Génier, 2009 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Eurysternus hamaticollis</i> Balthasar, 1939 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Eurysternus wittmerorum</i> Martínez, 1988 | 2 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 5 |
| <i>Hansreia oxygona</i> (Perty, 1830) | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 |
| <i>Ontherus sulcator</i> (Fabricius, 1775) | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 4 |
| <i>Onthophagus</i> aff. <i>bidentatus</i> Drapiez, 1819 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| <i>Onthophagus</i> aff. <i>rubrescens</i> Blanchard, 1843 | 5 | 3 | 26 | 18 | 6 | 3 | 0 | 0 | 1 | 0 | 62 |
| <i>Onthophagus</i> sp. | 34 | 0 | 0 | 0 | 0 | 11 | 4 | 0 | 130 | 3 | 182 |
| <i>Oxysternon conspiciatatum</i> (Weber, 1801) | 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 |
| <i>Oxysternon macleayi</i> (Nevinson, 1892) | 2 | 1 | 9 | 16 | 2 | 0 | 0 | 0 | 0 | 0 | 30 |
| <i>Phanaeus chalcone</i> (Perty, 1830) | 2 | 2 | 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 15 |
| <i>Phanaeus sororibispinus</i> Edmonds & Zidek, 2010 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| <i>Trichillum pauliani</i> (Balthasar, 1939) | 4 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 6 |
| <i>Uroxys</i> sp. 1 | 3 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 7 |
| <i>Uroxys</i> sp. 2 | 7 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 8 |
| <i>Uroxys</i> sp. 3 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Uroxys</i> sp. 4 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| Individuals per transect | 393 | 129 | 212 | 226 | 111 | 130 | 81 | 55 | 225 | 301 | 1863 |
| Species per transect | 28 | 21 | 26 | 27 | 19 | 14 | 7 | 6 | 11 | 6 | 54 |

Species composition and dominance

- Bray-Curtis cluster analysis of transects shows two large groups, one formed by plantation transects and the other by forest transects (Fig. 3). Similarity between the two groups is less than 0.15. For example, of the 54 species recorded, 40 had more than 80% of individuals collected in forest (forest species), while 10 had more than 80% of individuals from the plantation (plantation species). The rank abundance assessment showed that both communities have hyper-abundant species, but these are more predominant in the oil palm plantation. The forest community, in addition to including more species, shows greater evenness (Fig. 4).

Functional groups

- Activity periods of forest species showed two species without information, 19 nocturnal species, and 19 diurnal species. Dietary preferences of forest species showed one species without information, 25 coprophage species, eight generalist species, and six necrophage species. Nesting behavior of forest species showed one species without information, 22 tunneler species, 11 roller species, and six dweller species. 14 forest species had bright colors against a dark background of black, gray or brown (Table 4).

Table 3
Estimates of total dung beetle species richness (S) in forest and oil palm plantation (calculated in EstimateS).

| Estimate | Forest | | Oil palm plantation | | Total | |
|------------------|--------|------|---------------------|-------|-------|------|
| | S | sd | S | Sd | S | sd |
| Chao 1 | 50.45 | 2.54 | 18.5 | 1.03 | 54.96 | 1.33 |
| Chao 2 | 62.4 | 9.14 | 27.8 | 10.62 | 68.58 | 9.11 |
| Jackknife 1 | 62.4 | 2.04 | 23.6 | 2.71 | 70.2 | 5.16 |
| Jackknife 2 | 69.15 | 0 | 26.9 | 0 | 77.49 | 0 |
| Species recorded | 48 | 3.33 | 18 | 2.52 | 54 | 3.39 |

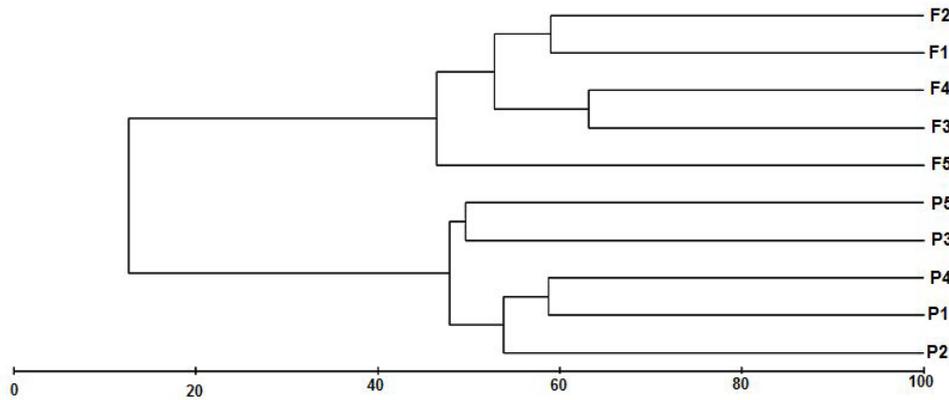


Figure 3 Dendrogram of Bray-Curtis similarity among transects from oil palm plantation (P) and forest (F).

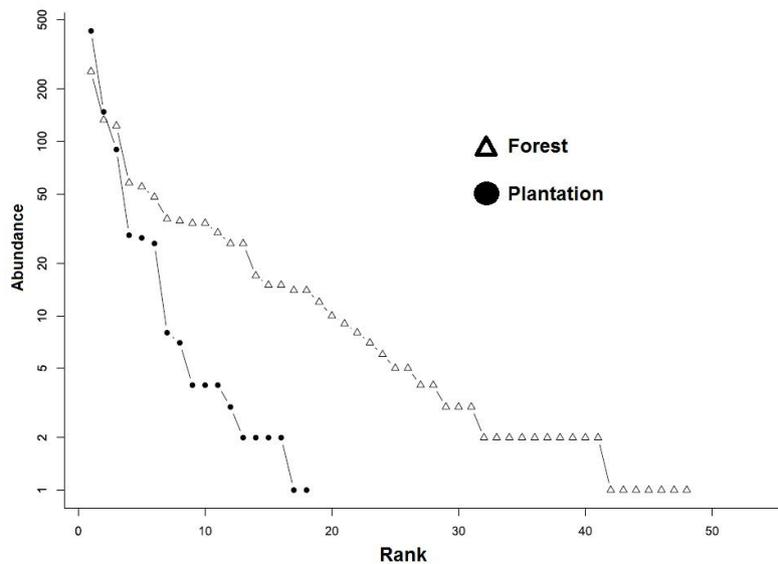


Figure 4 Rank-abundance for dung beetle communities from forest (Δ) and oil palm plantation (•).

Table 4
Dung beetle species and their functional group characteristics. (Noc = nocturnal, Diu = diurnal, Cop = coprophagous, Nec = necrophagous, Gen = generalist, Tun = tunnelers, Rol = rollers; Dwe = dwellers. Body length is the average species body length.)

| Species | Activity period | Diet preference | Nesting behavior | Body length (mm) | Pronotum width (mm) | Color |
|--|-----------------|-----------------|------------------|------------------|---------------------|---------|
| <i>Agamopus</i> sp. | ? | ? | ? | 4.76 | 1.67 | Colored |
| <i>Ateuchus</i> aff. <i>substriatus</i> (Harold, 1868) | Noc | Cop | Tun | 7.50 | 3.00 | Black |
| <i>Ateuchus</i> sp. 1 | Diu | Gen | Tun | 6.14 | 3.45 | Black |
| <i>Ateuchus</i> sp. 2 | Diu | Gen | Tun | 7.20 | 3.21 | Colored |
| <i>Canthidium</i> aff. <i>barbacenicum</i> Preudhomme de Borre, 1886 | Diu | Cop | Tun | 6.10 | 3.04 | Colored |
| <i>Canthidium</i> aff. <i>deyrollei</i> Harold, 1867 | Noc | Cop | Tun | 6.21 | 3.22 | Colored |
| <i>Canthidium</i> aff. <i>gerstaeckeri</i> Harold, 1867 | Diu | Cop | Tun | 6.85 | 3.38 | Colored |
| <i>Canthidium</i> sp. 1 | Noc | Cop | Tun | 4.22 | 1.71 | Colored |
| <i>Canthidium</i> sp. 2 | Noc | Cop | Tun | 7.95 | 3.62 | Black |
| <i>Canthidium</i> sp. 3 | Noc | Cop | Tun | 4.39 | 1.64 | Colored |
| <i>Canthidium</i> sp. 4 | Noc | Cop | Tun | 6.76 | 3.02 | Colored |
| <i>Canthon conformis</i> (Harold, 1868) | Diu | Gen | Rol | 8.19 | 4.84 | Colored |
| <i>Canthon</i> aff. <i>xanthopus</i> Blanchard, 1846 | Diu | Cop | Rol | 6.45 | 3.47 | Black |
| <i>Canthon</i> aff. <i>simulans</i> (Martínez, 1950) | Diu | Cop | Rol | 4.36 | 2.84 | Black |
| <i>Canthon histrio</i> (Serville, 1828) | Diu | Cop | Rol | 9.88 | 5.98 | Colored |
| <i>Canthon lituratus</i> (Germar, 1813) | Diu | Cop | Rol | 5.03 | 2.90 | Colored |
| <i>Canthon proseni</i> (Martínez, 1949) | Diu | Cop | Rol | 11.60 | 6.80 | Colored |
| <i>Canthon quadriguttatus</i> (Olivier, 1789) | Diu | Nec | Rol | 6.89 | 4.25 | Colored |
| <i>Coprophanaeus cyanesceus</i> d'Olsouffeff, 1924 | Diu | Nec | Tun | 23.03 | 16.29 | Black |
| <i>Coprophanaeus dardanus</i> (MacLeay, 1819) | Diu | Nec | Tun | 21.87 | 13.94 | Black |
| <i>Coprophanaeus jasius</i> (Olivier, 1789) | Diu | Nec | Tun | 22.61 | 15.11 | Black |
| <i>Coprophanaeus lancifer</i> (Linnaeus, 1767) | Noc | Gen | Tun | 4.86 | 3.35 | Colored |
| <i>Cryptocanthon campbellorum</i> Howden, 1973 | ? | Gen | Rol | 3.24 | 1.79 | Brown |
| <i>Deltochilum</i> sp. | Noc | Gen | Rol | 12.74 | 6.97 | Colored |
| <i>Deltochilum</i> aff. <i>guyanense</i> Paulian, 1933 | Noc | Gen | Rol | 14.16 | 7.72 | Brown |
| <i>Deltochilum</i> aff. <i>peruanum</i> Paulian, 1938 | Noc | Gen | Rol | 11.61 | 6.05 | Brown |
| <i>Deltochilum carinatum</i> (Westwood, 1837) | Noc | Nec | Rol | 18.06 | 10.32 | Gray |
| <i>Deltochilum icarus</i> (Olivier, 1789) | Noc | Cop | Rol | 13.62 | 8.34 | Colored |
| <i>Deltochilum sextuberculatum</i> Bates, 1870 | Diu | Nec | Rol | 11.75 | 6.35 | Black |
| <i>Dichotomius</i> aff. <i>globulus</i> (Felsche, 1901) | Noc | Gen | Tun | 11.88 | 7.69 | Gray |
| <i>Dichotomius</i> aff. <i>lucasi</i> (Harold, 1869) | Noc | Gen | Tun | 12.26 | 7.38 | Black |
| <i>Dichotomius robustus</i> (Luederwaldt, 1935) | Noc | Cop | Tun | 13.83 | 9.67 | Black |
| <i>Dichotomius</i> aff. <i>worontzowi</i> (Pereira, 1942) | Noc | Cop | Tun | 16.57 | 11.01 | Black |
| <i>Dichotomius carinatus</i> (Luederwaldt, 1925) | Noc | Cop | Tun | 24.17 | 15.87 | Black |
| <i>Dichotomius bos</i> (Blanchard, 1843) | Noc | Cop | Tun | 22.13 | 14.58 | Black |
| <i>Eurysternus atrosericus</i> Génier, 2009 | Diu | Cop | Dwe | 6.46 | 2.50 | Brown |
| <i>Eurysternus caribaeus</i> (Herbst, 1789) | Diu | Cop | Dwe | 14.98 | 6.86 | Brown |
| <i>Eurysternus cavatus</i> Génier, 2009 | Diu | Cop | Dwe | 5.78 | 2.44 | Colored |
| <i>Eurysternus hamaticollis</i> Balthasar, 1939 | Noc | Cop | Dwe | 8.53 | 3.98 | Brown |
| <i>Eurysternus wittmerorum</i> Martínez, 1988 | Diu | Cop | Dwe | 9.60 | 4.42 | Brown |
| <i>Hansreia oxygona</i> (Perty, 1830) | Diu | Cop | Rol | 9.03 | 5.01 | Colored |
| <i>Ontherus sulcator</i> (Fabricius, 1775) | Noc | Cop | Tun | 6.59 | 3.39 | Black |
| <i>Onthophagus</i> aff. <i>bidentatus</i> Drapiez, 1819 | Diu | Cop | Tun | 6.36 | 3.19 | Colored |
| <i>Onthophagus</i> aff. <i>rubrescens</i> Blanchard, 1843 | Diu | Cop | Tun | 5.41 | 3.24 | Colored |
| <i>Onthophagus</i> sp. | Diu | Cop | Tun | 7.16 | 3.21 | Colored |
| <i>Oxysternon conspicalattum</i> (Weber, 1801) | Diu | Cop | Tun | 23.75 | 14.95 | Black |
| <i>Oxysternon macleayi</i> (Nevinson, 1892) | Diu | Cop | Tun | 17.57 | 11.96 | Black |
| <i>Phanaeus chalcomelas</i> (Perty, 1830) | Diu | Cop | Tun | 36.15 | 22.46 | Colored |
| <i>Phanaeus sororibispinus</i> Edmonds & Zidek, 2010 | Diu | Cop | Tun | 12.71 | 6.87 | Black |
| <i>Trichillum pauliani</i> (Balthasar, 1939) | Noc | Cop | Dwe | 4.21 | 2.37 | Black |
| <i>Uroxys</i> sp. 1 | Noc | Cop | Tun | 2.38 | 1.30 | Colored |
| <i>Uroxys</i> sp. 2 | Noc | Cop | Tun | 3.18 | 1.89 | Colored |
| <i>Uroxys</i> sp. 3 | Noc | Cop | Tun | 3.09 | 1.88 | Brown |
| <i>Uroxys</i> sp. 4 | Noc | Cop | Tun | | | Brown |

Activity periods of plantation species showed three nocturnal species and seven diurnal species. Dietary preferences of plantation species showed nine coprophage species and one generalist species. Nesting behavior of plantation species showed seven tunneler species and three roller species. Six plantation species had bright colors against a dark background, and four were black. Lack of necrophage dung beetles in the more open plantation probably indicates that the scavenger niche is filled by other taxa, possibly vultures. However, as only fecal baits were used during sampling, the register of scavenger species in the forest and in the plantation may be an underestimate.

Body sizes and proportions of dung beetles can vary considerably (Hernández et al., 2011), but in this study forest and plantation species were not significantly different (forest body length average = 11.62 mm, standard deviation = 7.425, pronotum width average = 6.82 ± 5.082; plantation body length average = 8.77 ± 5.333, pronotum width average = 4.97 ± 3.722). Body proportions between forest and plantation species did not differ significantly (pronotal width / body length = 0.56 for forest species and 0.54 for plantation species).

Spillover

- Although the greatest number of species (30 spp.) was collected at 550 m from the forest border (Fig. 5), there were no significant differences in dung beetle abundances or species richness with traps further within the forest. The results of Silva et al. (2017) also show that the addition of traps, rather than their placement in the forest, probably explains species richness in deep-forest trapping. The width of forest corridors for dung beetle conservation should take into consideration the necessities of vertebrate symbionts (Viegas et al., 2014; Van Schalkwyk et al., 2017 for savannah corridors), but in this case, no forest edge effects can be seen at increasing depths of forest penetration.

DISCUSSION

Oil palm plantations support fewer dung beetle species than forests and show a higher dominance of the most abundant species. In this human-modified habitat, the three most abundant species constitute approximately 95% of all individuals. A greater species richness is expected with an increase in environmental heterogeneity and level of habitat conservation (Gardner et al., 2008b; Gibson et al., 2011). Thus, the forest habitat offers the beetles appropriate conditions to

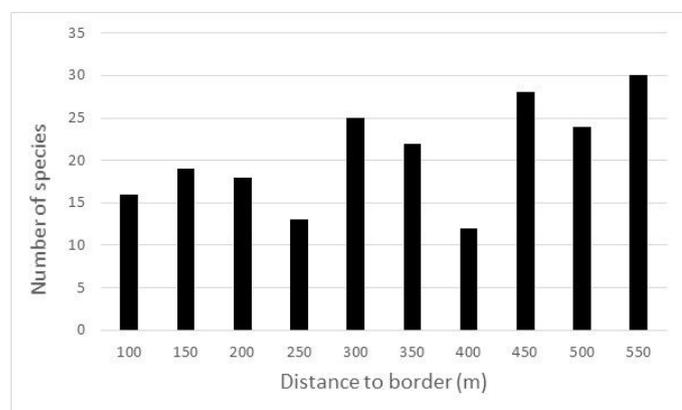


Figure 5 Number of dung beetle species collected in forest at different distances from the forest-oil palm plantation border.

maintain a more diverse community. This is probably due to the altered vegetation cover and associated environmental variables, rendering the oil palm plantation habitat less suitable for forest-dwelling species (Figueiras et al., 2015, 2016).

Similar results were found in other studies on land use in the Amazon, in which the intense use and modification of the soil caused a change in the richness and abundance of scarabaeine species (Gardner et al., 2008b; Braga et al., 2013; Cajaiba et al., 2017) as has been shown in studies comparing preserved areas with those modified for agriculture (Halffter and Matthews, 1966; Braga et al., 2013; Silva et al., 2016).

As for the faunal similarity between the areas sampled, the large difference between the two habitats may occur due to the loss of the original vegetation, changing the structural complexity of the environment and rendering it impossible to maintain some species in the area, mainly associated mammals (Halffter and Matthews, 1966; Halffter and Favila, 1993). Scarabaeinae beetles are bioindicator organisms whose community structure reflects the patterns of the vertebrate community on which they are dependent (Halffter and Matthews, 1966; Estrada et al., 1999).

The oil palm plantation alters and reduces the structure of vertebrate communities (Lima, 2013; Mendes-Oliveira et al., 2017; Pardo et al., 2018) and consequently changes that of other taxa, such as the Scarabaeinae in this case. Lees et al. (2015) and Almeida et al. (2016) in the same area found that oil palm plantations supported only impoverished avian communities and did not provide habitat for most forest-associated species, including those with restricted ranges and those of conservation concern. Knowlton et al. (2017) found that oil palm plantations disrupt mixed flocks. The functional diversity of bird communities in oil palm was greatly reduced, in spite of evidence that birds protect oil palms against herbivorous insects (Koh, 2008). Other groups affected in the same way include anurans (Corrêa et al., 2015), aquatic Hemiptera (Cunha and Juen, 2017), bees (Brito et al., 2017), and aquatic insects (Juen et al., 2016).

In the oil palm plantation, forest habitat loss results in an open niche for generalist species. These areas may be colonized by Brazilian *cerrado* or disturbance-adapted species such as *Dichotomius bos* (Blanchard, 1843), *Ontherus sulcator* (Fabricius, 1775), and *Canthon histrio* (Serville, 1828). Undisturbed forest patches are occupied by a dung beetle community constituted mainly by Amazonian species such as *Canthon proseni* (Martínez, 1949), *Coprophanaeus lancifer* (Linnaeus, 1767), *Deltochilum carinatum* (Westwood, 1837), *Dichotomius carinatus* (Luederwaldt, 1925), *Eurysternus hamaticollis* Balthasar, 1939, *Hansreia oxygona* (Perty, 1830), and *Oxysternon conspiciatum* (Weber, 1801).

To compensate for reduced biological diversity in oil palm plantations, the maintenance of forest buffers, corridors, and reserves is a partial solution, but one that requires additional experimental evidence as to its usefulness (Barlow et al., 2010; Gilroy et al., 2015). Our results indicate that the greatest number of dung beetle species was encountered at traps distant from the forest-plantation interface, at 550 m into the forest. This may well reflect the reaction of mammals to forest margins that their dung beetles faithfully mirror. A forest corridor or buffer of less than a kilometer in width or depth may not be suitable for all mammals and dung beetles, even though this is much larger than current designs.

Habitat destruction, particularly forest loss and modification to agriculture, has significant negative impacts on tropical forests (Scheffler, 2005; Gibbs et al., 2010; Sánchez-de-Jesús et al., 2016; Silva et al., 2016; Giam, 2017), and their dung beetle communities (Nichols et al., 2007, 2013; Barlow et al., 2016). Few forest-adapted dung beetle species are able to extend their activities into strongly altered forests or anthropogenic ecosystems. Our results indicate that changes in vegetation structure and complexity in oil palm plantations can lead to dramatic faunal turnover and loss of regional dung beetle richness in the eastern Amazon.

Conclusions

Dung beetle community composition was markedly different between forest and oil palm plantation habitats in the eastern Amazon. Monoculture of oil palms showed reduced ability to maintain the higher species richness found in adjacent intact forests. Oil palm plantations held fewer species and showed a higher dominance of few hyper-abundant species. This suggests that the modified and simplified habitat of the oil palm plantation adversely affects many dung beetle species while favoring generalist species. Through asymmetrical competition between native specialist species and widespread generalists, the loss of biodiversity could be exacerbated. Forests near oil palm plantations harbor more species and more rare species, some of which are found at 550 m in the forest. This indicates that forest buffers or corridors may need to have a greater width than has been generally proposed.

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Conflicts of interest

The authors declare no conflicts of interest.

Author contribution statement

LMH: Conceptualization, Data curation, Methodology, Formal analysis, Writing- Original draft preparation. ISA: Data curation, Formal analysis, Investigation, Writing- Reviewing and Editing. WLO: Conceptualization, Writing- Reviewing and Editing. FABS: Conceptualization, Methodology, Project administration, Validation, Resources, Supervision.

References

Almeida, S. M., Silva, L. C., Cardoso, M. R., Cerqueira, P. V., Juen, L., de Santos, M. P., 2016. The effects of oil palm plantations on the functional diversity of Amazonian birds. *J. Trop. Ecol.* 32 (6), 510-525.

Andrade, R. B., Barlow, J., Louzada, J., Vaz-de-Mello, F. Z., Silveira, J. M., Cochrane, M. A., 2014. Tropical forest fires and biodiversity: dung beetle community and biomass responses in a northern Brazilian Amazon forest. *J. Insect Conserv.* 18 (6), 1097-1104.

Barlow, J., Lennox, G. D., Ferreira, J., Berenguer, E., Lees, A. C., Mac Nally, R., Thomson, J. R., Ferraz, S. F., Louzada, J., Oliveira, V. H., Parry, L., Solar, R. R., Vieira, I. C., Aragao, L. E., Begotti, R. A., Braga, R. F., Cardoso, T. M., Oliveira Junior, R. C., Souza Junior, C. M., Moura, N. G., Nunes, S. S., Siqueira, J. V., Pardini, R., Silveira, J. M., Vaz-de-Mello, F. Z., Veiga, R. C., Venturieri, A., Gardner, T. A., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* 535 (7610), 144-147.

Barlow, J., Louzada, J., Parry, L., Hernández, M. I. M., Hawes, J., Peres, C. A., Vaz-de-Mello, F. Z., Gardner, T. A., 2010. Improving the design and management of forest strips in human-dominated tropical landscapes: a field test on Amazonian dung beetles. *J. Appl. Ecol.* 47 (4), 779-788.

Barlow, J., Mestre, L. A. M., Gardner, T. A., Peres, C. A., 2007. The value of primary, secondary and plantation forests for Amazonian birds. *Biol. Conserv.* 136, 212-231.

Beroz, W., Slade, E. M., Barlow, J., Silveira, J. M., Louzada, J., Sayer, E., 2017. Dung beetle community dynamics in undisturbed tropical forests: implications for ecological evaluations of land-use change. *Insect Conserv. Divers.* 10 (1), 94-106.

Bicknell, J. E., Phelps, S. P., Davies, R. G., Mann, D. J., Struebig, M. J., Davies, Z. G., 2014. Dung beetles as indicators for rapid impact assessments: evaluating best practice forestry in the neotropics. *Ecol. Indic.* 43, 154-161.

Braga, R. F., Korasaki, V., Andresen, E., Louzada, J., 2013. Dung beetle community and functions along a habitat-disturbance gradient in the Amazon: a rapid assessment of ecological functions associated to biodiversity. *PLoS One* 8 (2), e57786.

Brito, T. F., Phifer, C. C., Knowlton, J. L., Fiser, C. M., Becker, N. M. C., Barros, F., Contrera, F. A. L., Maués, M. M., Juen, L., Montag, L. F. A., Webster, C. R., Flaspohler, D. J., Santos, M. P. D., Silva, D. P., 2017. Forest reserves and riparian corridors help maintain orchid bee (Hymenoptera: Euglossini) communities in oil palm plantations in Brazil. *Apidologie* 48 (5), 575-587.

Butler, R., 2011. In Brazil, palm oil plantations could help preserve the Amazon. *Yale Environment* 360, New Haven, CT. Available in: <https://e360.yale.edu> (accessed 20 September 2019).

Butler, R., Laurance, W. F., 2009. Is oil palm the next emerging threat to the Amazon? *Trop. Conserv. Sci.* 2 (1), 1-10.

Cajaiba, R. L., Périco, E., Dalzochio, M. S., da Silva, W. B., Bastos, R., Cabral, J. A., Santos, M., 2017. Does the composition of Scarabaeidae (Coleoptera) communities reflect the extent of land use changes in the Brazilian Amazon? *Ecol. Indic.* 74, 285-294.

Clarke, K. R., Gorley, R. N., 2006. *Primer Version 6: User Manual/Tutorial*. Plymouth Marine Laboratory, Plymouth, UK.

Chown, S. L., Klok, J., 2011. The ecological implications of physiological diversity in dung beetles, in: Simmons, L. W. & Ridsdill-Smith, T. J. (eds.). *Ecology and evolution of dung beetles*. John Wiley & Sons, Oxford, U.K. & Hoboken, NJ, pp. 200-219.

Colwell, R. K. 2013. *EstimateS: Statistical Estimation of Species Richness and Shared Species From Samples*. Version 9.1: User's Guide and Application. Storrs, Connecticut, University of Connecticut.

Corrêa, F. S., Juen, L., Rodrigues, L. C., Silva-Filho, H. F., Santos-Costa, M. C., 2015. Effects of oil palm plantations on anuran diversity in the eastern Amazon. *Anim. Biol. Leiden Neth.* 65 (3-4), 321-335.

Cultid-Medina, C. A., Escobar, F., 2016. Assessing the ecological response of dung beetles in an agricultural landscape using number of individuals and biomass in diversity measures. *Environ. Entomol.* 45, 310-319.

Cunha, E. J., Juen, L., 2017. Impacts of oil palm plantations on changes in environmental heterogeneity and Heteroptera (Gerromorpha and Nepomorpha) diversity. *J. Insect Conserv.* 21 (1), 111-119.

Englund, O., Berndes, G., Persson, U. M., Sparovek, G., 2015. Oil palm for biodiesel in Brazil: risks and opportunities. *Environ. Res. Lett.* 10 (4), 044002.

Estrada, A., Anzures, A., Coates-Estrada, R., 1999. Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*), and dung beetles at Los Tuxtlas, Mexico. *Am. J. Primatol.* 48 (4), 253-262.

Feer, F., 2008. Responses of dung beetle assemblages to characteristics of rain forest edges. *Ecotropica* 14, 49-62.

Filgueiras, B. K., Tabarelli, M., Leal, I. R., Vaz-de-Mello, F. Z., Peres, C. A., Iannuzzi, L., 2016. Spatial replacement of dung beetles in edge-affected habitats: biotic homogenization or divergence in fragmented tropical forest landscapes? *Divers. Distrib.* 22 (4), 400-409.

- Filgueiras, B. K. C., Tabarelli, M., Leal, I. R., Vaz-de-Mello, F. Z., Iannuzzi, L., 2015. Dung beetle persistence in human-modified landscapes: combining indicator species with anthropogenic land use and fragmentation-related effects. *Ecol. Indic.* 55, 65-73.
- Fitzherbert, E. B., Struebig, M. J., Morel, A., Danielsen, F., Brühl, C. A., Donald, P. F., Phalan, B., 2008. How will oil palm expansion affect biodiversity? *Trends Ecol. Evol.* 23, 538-545.
- Gardner, T. A., Barlow, J., Araújo, I. S., Avila-Pires, T. C., Bonaldo, A. B., Costa, J. E., Esposito, M. C., Ferreira, L. V., Hawes, J., Hernández, M. I., Hoogmoed, M. S., Leite, R. N., Lo-Man-Hung, N. F., Malcolm, J. R., Martins, M. B., Mestre, L. A., Miranda-Santos, R., Overal, W. L., Parry, L., Peters, S. L., Ribeiro-Júnior, M. A., Silva, M. N., Silva Motta, C., Peres, C. A., 2008a. The cost-effectiveness of biodiversity surveys in tropical forests. *Ecol. Lett.* 11 (2), 139-150.
- Gardner, T. A., Hernández, M. I. M., Barlow, J., Peres, C. A., 2008b. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *J. Appl. Ecol.* 45 (3), 883-893.
- Gardner, T. A., Ribeiro-Júnior, M. A., Barlow, J., Avila-Pires, T. C. S., Hoogmoed, M. S., Peres, C. A., 2007. The value of primary, secondary, and plantation forests for a neotropical herpetofauna. *Conserv. Biol.* 21, 775-787.
- Génier, F., 1996. A revision of the Neotropical genus *Ontherus* Erichson (Coleoptera: Scarabaeidae, Scarabaeinae). *Mem. Entomol. Soc. Can.* 128 (S170), 3-170.
- Génier, F., 2009. Le Genre *Eurysternus* Dalman, 1824 (Scarabaeidae: Scarabaeinae: Oniticellini): Révision Taxonomique et Clés de Détermination Illustrées. Pensoft, Sofia, Bulgaria.
- Giam, X., 2017. Global biodiversity loss from tropical deforestation. *Proc. Natl. Acad. Sci. USA* 114 (23), 5775-5777.
- Gibbs, H. K., Ruesch, A. S., Achard, F., Clayton, M. K., Holmgren, P., Ramankutty, N., Foley, J. A., 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proc. Natl. Acad. Sci. USA* 107, 16732-16737.
- Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J., Laurance, W. F., Lovejoy, T. E., Sodhi, N. S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478 (7369), 378-381.
- Gilroy, J. J., Prescott, G. W., Cardenas, J. S., Castañeda, P. G. P., Sánchez, A., Rojas-Murcia, L. E., Medina Uribe, C. A., Haugaasen, T., Edwards, D. P., 2015. Minimizing the biodiversity impact of Neotropical oil palm development. *Glob. Change Biol.* 21 (4), 1531-1540.
- Griffiths, H. M., Louzada, J., Bardgett, R. D., Barlow, J., 2016. Assessing the importance of intraspecific variability in dung beetle functional traits. *PLoS One* 11 (3), e0145598.
- Griffiths, H. M., Louzada, J., Bardgett, R. D., Beiroz, W., França, F., Tregidgo, D., Barlow, J., 2015. Biodiversity and environmental context predict dung beetle mediated seed dispersal in a tropical forest field experiment. *Ecology* 96 (6), 1607-1619.
- Hayes, L., Mann, D. J., Monastyrskii, A. L., Lewis, O. T., 2009. Rapid assessments of tropical dung beetle and butterfly assemblages: contrasting trends along a forest disturbance gradient. *Insect Conserv. Divers.* 2 (3), 194-203.
- Halffter, G., Favila, M. E., 1993. The Scarabaeinae (Insecta: Coleoptera), an animal group for analysing, inventorying and monitoring biodiversity in tropical rainforest and modified landscapes. *Biol. Internat.* 27, 15-21.
- Halffter, G., Matthews, E. G., 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). *Folia Entomol. Mex.* 12-14, 1-312.
- Hanski, I., Cambefort, Y., 1991. *Dung Beetle Ecology*. Princeton University Press, Princeton, NJ.
- Hernández, M. I., Monteiro, L. R., Favila, M. E., 2011. The role of body size and shape in understanding competitive interactions within a community of Neotropical dung beetles. *J. Insect Sci.* 11, 13.
- Hsieh, T. C., Ma, K. H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecol. Evol.* 7, 1451-1456.
- Hueck, K., 1972. *As florestas da América do Sul*. Ed. Polígono, São Paulo.
- Juen, L., Cunha, E. J., Carvalho, F. G., Ferreira, M. C., Begot, T. O., Andrade, A. L., Shimano, Y., Leão, H., Pompeu, O. S., Montag, L. F., 2016. Effects of oil palm plantations on the habitat structure and biota of streams in Eastern Amazon. *River Res. Appl.* 32 (10), 2081-2094.
- Knowlton, J. L., Phifer, C. C., Cerqueira, P. V., Barro, F. C., Oliveira, S. L., Fiser, C. M., Becker, N. M., Cardoso, M. R., Flaspohler, D. J., Dantas Santos, M. P., 2017. Oil palm plantations affect movement behavior of a key member of mixed-species flocks of forest birds in Amazonia, Brazil. *Trop. Conserv. Sci.* 10. In press.
- Koh, L. P., 2008. Birds defend oil palms from herbivorous insects. *Ecol. Appl.* 18 (4), 821-825.
- Köppen, W., Geiger, R., 1928. *Klimate der Erde (Map)*. Gotha, Verlag Justus Perthes.
- Larsen, T. H., Forsyth, A., 2005. Trap spacing and transect design for dung beetle biodiversity studies. *Biotropica* 37, 322-325.
- Larsen, T. H., Lopera, A., Forsyth, A., 2008. Understanding trait-dependent community disassembly: dung beetles, density functions, and forest fragmentation. *Conserv. Biol.* 22 (5), 1288-1298.
- Lees, A. C., Moura, N. G., Almeida, A. S., Vieira, I. C. G., 2015. Poor prospects for avian biodiversity in Amazonian oil palm. *PLoS One* 10 (5), e0122432.
- Lima, R. C. S. 2013. Efeito da monocultura da palma de dendê (*Elaeis guineensis* Jacq.) sobre a fauna de pequenos mamíferos não voadores na Amazônia. Thesis, Universidade Federal do Pará & Museu Paraense Emílio Goeldi.
- Lucey, J. M., Tawatao, N., Senior, M. J., Chey, V. K., Benedick, S., Hamer, K. C., Woodcock, P., Newton, R. J., Bottrell, S. H., Hill, J. K., 2014. Tropical forest fragments contribute to species richness in adjacent oil palm plantations. *Biol. Conserv.* 169, 268-276.
- Marsh, C. J., Louzada, J., Beiroz, W., Ewers, R. M., 2013. Optimising bait for pitfall trapping of Amazonian dung beetles (Coleoptera: scarabaeinae). *PLoS One* 8 (8), e73147.
- Mendes-Oliveira, A. C., Peres, C. A., Maués, P. C. R. A., Oliveira, G. L., Mineiro, I. G. B., de Maria, S. L. S., Lima, R. C. S., 2017. Oil palm monoculture induces drastic erosion of an Amazonian forest mammal fauna. *PLoS One* 12 (11), e0187650.
- Nichols, E., Gardner, T. A., 2011. Dung beetles as a candidate study taxon in applied biodiversity conservation research. In: Simmons, L.W., Ridsdill-Smith, T.J. (Eds.), *Ecology and Evolution of Dung Beetles*. John Wiley & Sons, Chichester, U.K., pp. 267-291.
- Nichols, E., Larsen, T., Spector, S., Davis, A.F., Escobar, F., Favila, M., Vulinec, K., 2007. Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. *Biol. Conserv.* 137, 1-19.
- Nichols, E., Spector, S., Louzada, J., Larsen, T., Amezcuita, S., Favila, M. E., 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol. Conserv.* 141, 1461-1474.
- Nichols, E., Uriarte, M., Bunker, D. E., Favila, M. E., Slade, E. M., Vulinec, K., Larsen, T., Vaz-de-Mello, F. Z., Louzada, J., Naeem, S., Spector, S. H., 2013. Trait-dependent response of dung beetle populations to tropical forest conversion at local and regional scales. *Ecology* 94 (1), 180-189.
- Pardo, L. E., Campbell, M. J., Edwards, W., Clements, G. R., Laurance, W. F., 2018. Terrestrial mammal responses to oil palm dominated landscapes in Colombia. *PLoS One* 13 (5), e0197539.

- Ridsdill-Smith, T. J., Edwards, P. B., 2011. Biological control: ecosystem functions provided by dung beetles. In: Simmons, L.W. & Ridsdill-Smith, T.J. (Eds.), *Ecology and Evolution of Dung Beetles*. John Wiley & Sons, Oxford, UK, pp. 245-266.
- Sánchez-de-Jesús, H. A., Arroyo-Rodríguez, V., Andresen, E., Escobar, F., 2016. Forest loss and matrix composition are the major drivers shaping dung beetle assemblages in a fragmented rainforest. *Landsc. Ecol.* 31 (4), 843-854.
- Scheffler, P. Y., 2005. Dung beetle (Coleoptera: Scarabaeidae) diversity and community structure across three disturbance regimes in eastern Amazonia. *J. Trop. Ecol.* 21 (1), 9-19.
- Silva, P. G., Hernández, M. I. M., 2015. Spatial patterns of movement of dung beetle species in a tropical forest suggest a new trap spacing for dung beetle biodiversity studies. *PLoS One* 10 (5), e0126112.
- Silva, R. J., Coletti, F., Costa, D. A., Vaz-de-Mello, F. Z., 2014. Rola-bostas (Coleoptera: Scarabaeidae: Scarabaeinae) de florestas e pastagens no sudoeste da Amazônia brasileira: Levantamento de espécies e guildas alimentares. *Acta Amazon.* 44 (3), 345-352.
- Silva, R. J., Pelissari, T. D., Krinski, D., Canale, G., Vaz-de-Mello, F. Z., 2017. Abrupt species loss of the Amazonian dung beetle in pastures adjacent to species-rich forests. *J. Insect Conserv.* 2017, 1-8.
- Silva, R. J., Storck-Tonon, D., Vaz-de-Mello, F. Z., 2016. Dung beetle (Coleoptera: Scarabaeinae) persistence in Amazonian forest fragments and adjacent pastures: biogeographic implications for alpha and beta diversity. *J. Insect Conserv.* 20 (4), 549-564.
- Spector, S., 2006. Scarabaeine dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. *Coleopt. Bull.* 60 (sp5), 71-83.
- Spector, S., Forsyth, A. B., 1998. Indicator taxa for biodiversity assessment in the vanishing tropics, in: Mace, G. M., Balmford, A. & Ginsberg, J. R. (ed.). *Conservation in a changing world*. Cambridge University Press, Cambridge, U.K., pp. 181-209.
- StatSoft Inc., 1996. *Statistica for Windows*. Available in: <http://www.statsoftinc.com> (accessed 20 September 2019).
- Van Schalkwyk, J., Pryke, J. S., Samways, M. J., 2017. Wide corridors with much environmental heterogeneity best conserve high dung beetle and ant diversity. *Biodivers. Conserv.* 26 (5), 1243-1256.
- Viegas, G., Stenert, C., Schulz, U. H., Maltchik, L., 2014. Dung beetle communities as biological indicators of riparian forest widths in southern Brazil. *Ecol. Indic.* 36, 703-710.
- Zar, J. H. 2010. *Biostatistical Analysis*. Pearson/Prentice Hall, Upper Saddle River, New Jersey.