

Are Small Dung Beetles (Aphodiinae) useful for monitoring neotropical forests' ecological status? Lessons from a preliminary case study in the Brazilian Amazon

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ABSTRACT

Neotropical forests are extremely diverse ecosystems, listed within the biological hotspots of our planet. However, species from these forests are threatened by diverse anthropogenic activities. Small dung beetles (Scarabaeidae, Aphodiinae) assemblages were studied within different habitats of the Brazilian Amazon. The monitored habitats encompassed the main gradients of disturbance, from pristine to highly anthropogenic situations, with the aim of supporting their use as indicators of neotropical forests' ecological status. Additionally, seasonal patterns and bait attractiveness were evaluated in the scope of more effective monitoring studies. Our main results demonstrate that the diversity and distribution of small dung beetles along disturbance gradients, represented by the monitored locations, is associated with particular habitats within the forest landscape. Although spatially and temporally restricted, the results of this study highlight the potential of using small dung beetles, due to their sensitivity and habitat specificity, as ecological indicators for assessing the extent of disturbance in neotropical forest landscapes. We also suggest specific techniques and periods to be used in order to increase captures of small dung beetles within the different habitats.

1. Introduction

Albeit neotropical forests inclusion in the biological hotspots of our planet (Foley et al., 2007; Chazdon et al., 2009), the forests and the species encompassed are threatened by local and global anthropogenic stressors (Carnus et al., 2006; Loskovtová and Horák, 2016). Scientist also highlight that the conservation of neotropical forest, such as the Brazilian Amazon (Amazonia) represents a core challenge for regulating earth's functioning and ultimately humankind (e.g. Viegas et al., 2014). In fact there is an enormous concern on the effects of anthropogenic disturbances in the biodiversity and ecosystem services provided by the Amazonia, even though for the vast majority of the region no one knows what's really happening (e.g. Verweij et al., 2009; Morris, 2010). Current land use cover changes (LUCC) could be generating effects such as isolation of populations and local extinctions that were not fully anticipated (Aerts and Honnay, 2011), resulting in massive functional

changes whose impacts are probably outreaching predictions (Aizen et al., 2012; Valiente-Banuet et al., 2015).

Predicting the socio-ecological consequences of the ongoing LUCC in this region is therefore fundamental for supporting strategic options for landscape planning and natural resources management (Turner et al., 2007). In this context the selection of the most relevant indicators for ecological assessment is crucial, namely to detect and gauge significant changes in the ecological status and possible tipping points (Cajaiba et al., 2016). Indicators and especially biological indicators have been widely used in ecosystem assessments (Gerlach et al., 2013; Lu et al., 2015). Their value increases in fast retreating biodiverse systems such as the Amazonia pristine forests where monitoring all species and processes would be logistically unfeasible (Audino et al., 2014). Additionally if the selected indicators were able to detect cause-effect socio-ecological changes in this region and tipping points' occurrence, their usefulness for managers and decision-makers would rise

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steeply (Burkhard et al., 2008).

Terrestrial invertebrates and especially insects play a central role in most ecological processes and are key components of neotropical forests' structure and functioning (Bicknell et al., 2014; Viegas et al., 2014; Campos and Hernández, 2015; Cajaiba et al., 2017a). Insects' diversity is a surrogate of other taxa diversity and abiotic conditions, representing the core biological indicators of forests' ecological status (e.g. Nichols et al., 2008). Understanding the ecological relevance of insects in the Neotropics could even support decision-making and robust management/recovery of imperiled natural and semi-natural ecosystems in the scope of the need for rapid, standardized and cost-saving assessment methodologies (Andrade et al., 2014).

Aphodiinae, also known as small dung beetles (SDB), is a diverse and widely distributed subfamily of Scarabaeidae (Dellacasa and Stebnicka, 2001; Cabrero-Sañudo et al., 2010), with more than 200 genera and 3100 species recognized, although with insufficient information for the neotropics (specially for the Amazonia) (Cabrero-Sañudo et al., 2007). This taxon has generally endocoprid behavior and coprophagous or saprophagous feeding habits, with larvae and adults occupying diverse ecological niches (Stebnicka, 2001a; Smith and Skelley, 2007; Cabrero-Sañudo and Lobo, 2009). SDB feed and nest on the ground in various types of feces and/or animal and plant debris (Stebnicka, 2001b; Smith and Skelley, 2007) facilitating the decomposition processes and nutrient cycling (Marinoni et al., 2001; Nichols et al., 2008). SDB sensitiveness to ecosystem changes, standard monitoring protocols, broad distribution, relatively well-known taxonomy and ecology has converted this group in useful ecological indicators (Jay-Robert et al., 2008; Errouissi et al., 2009; Chandra and Gupta, 2012).

In the Neotropics, SDB are considered diverse and abundant, although supported mostly by incipient works. The main purpose of this study was to evaluate the responses of SDB assemblages to anthropogenic disturbance of forests, in the scope of its usefulness as ecological indicators. In addition, we intended to increase the knowledge regarding SDB distribution and diversity in the Amazonia and to contribute to more assertive monitoring protocols. For that a gradient of habitats with increasing levels of anthropogenic stress were monitored, such as: primary forest, our reference condition, secondary forests within different stages of recovery, farmland and pasture for extensive livestock. We were particularly interested in assessing the SDB assemblages' sensitivity to anthropogenic induced structural changes. Specifically, we addressed the following questions: (1) Does the composition of SDB assemblages in the Amazonia changes through the different habitats? (2) Can we identify species/assemblages associated with specific habitats? (3) Is the diversity of SDB in the Amazonia's habitats influenced by the seasons and concomitant environmental conditions? (4) What types of baits are more effective for capturing SDB within the studied habitats?

2. Material and methods

2.1. Study sites

The study area was located in the municipality of Uruará, state of Pará, northern Brazil (−03°43'27"S; −53°44'8"W, Fig. S1). Forests comprise 69% of the municipality area while the other land uses (LULC), associated with deforested and highly degraded forests (e.g. extensive livestock and agriculture) are concentrated in the south-central part of territory and near the main roads. The selected areas covered the most representative habitats of the region, in terms of biophysical and ecological characteristics for understanding the response of SDB assemblages to forest disturbance and/or LUCC (Cajaiba et al., 2017a). The habitats include: PF (Primary forest), SF-15 (Secondary forest with 15 years of regeneration), SF-5 (Secondary forest with five years of regeneration), Agriculture (Ag, cocoa plantations, *Theobroma cacao* L.) and Pasture for extensive livestock (Pa) (For a

generic characterization of the habitats sampled, see Table S1 and Fig. S2). The climate is characterized as hot-humid (Köppen's classification), with annual average temperature and precipitation of 26 °C and 2000 mm, respectively (Peel et al., 2007).

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.foreco.2018.07.005>.

2.2. Aphodiinae sampling

Sampling was carried out during the year 2015, in the months of February/March (rainy season), June (final of rainy season and early dry season) and September/October (dry season), for integrating possible seasonal differences in the activity of SDB (Cajaiba et al., 2017a). In each study site (PF, SF-15, SF-5, Ag and Pa), seven sample points were placed 100 m apart. We located the sampling points at a minimum distance of 100 m from ecotones, to ensure that most beetles captured were associated to the habitat monitored (Cajaiba et al., 2017b). Each sampling point contained four pitfall traps (75 mm diameter and 110 mm deep, filled with preservative liquid) including different baits (Human faeces-HF, Rotten meat-RM, Rotten banana-RB, to attract different species according to their feeding habits and non-baited pitfalls, used as control-Co), separated by 5 m. The distance between pitfall traps by location was determined in order to select individuals according to their preferential diet, as suggested by related studies (Almeida and Louzada, 2009; Campos and Hernández, 2015; Cajaiba et al., 2017b).

This method was applied to all areas and periods of collection, totaling a sampling effort of 840 traps (see Table S2, Supplementary material, for details for the capture effort). Specimens were conserved in 70% ethanol, taken into the laboratory and identified to morphospecies or species level whenever possible. We based our identification on the keys proposed by Smith and Skelley (2007). The specimens were deposited Coleção de Zoologia, Departamento de Biologia da Universidade Federal do Pará (Zoological collection of the Biology Department of the University of Pará, Brazil). The collection authorization process was issued by SISBIO (Brazil) system under the number 50133/2015.

2.3. Environmental variables

Fourteen environmental variables, considered with potential influence on SDB communities, were measured: temperature (T), humidity (H), precipitation (P), circumference at breast height (CBH), circumference at ankle height (CAH), canopy cover (CC), richness of plants (RP), abundance of plants (AP), richness of shrubs (RS), abundance of shrubs (AS), percentage of exposed soil (PES), percentage of green (vegetation) cover (GC), percentages of leaf litter cover (LLC), height of leaf litter (HLL). Air temperature, relative humidity and rainfall of each point were measured during the traps' installation and removal by a portable weather station (model Oregon Scientific WMR200A). To assess the environmental complexity of each habitat, the quadrat-section method was adopted (Campos and Hernández, 2015). Using a cross as a reference, four quadrants (northeast, northwest, southeast, southwest) were marked and in each quadrant the following variables were measured: trees with circumference at breast height (CBH) > 15 cm, shrubs with CBH < 15 cm and with height > 1 m were selected and the distances to the centre of the cross, height, crown diameter and trunk diameter. Trunk diameter was taken at breast height (1.3 m) for the trees and ankle height (CAH = 0.1 m) for the shrubs. In each quadrant, the height of leaf litter in 1 m × 1 m marked square (using PVC pipe) was measured with a ruler, and the percentages of leaf litter layer, green and exposed soil area (no vegetation or leaf litter) were measured by visual estimation using the following classes, 0–5%, 6–25%, 26–50%, 51–75%, 76–95% and 96–100% (Campos and Hernández, 2015). Using the same classes, the percentage of canopy cover in the four quadrants was calculated with a convex

spherical Lemmon densiometer (D). Information concerning the methodology associated with each variable collection is depicted in Table S3, Supplementary material.

2.4. Assemblage analysis

Rarefaction curves were used to assess whether the sampling effort was enough to monitor all the species by habitat (Gotelli and Colwell, 2001). We performed a preliminary analysis through the Scheirer-Ray-Hare extension of the Kruskal-Wallis test (Zar, 1999), a non-parametric equivalent to the multifactorial ANOVA to verify possible interactions in the Abundance (number of individuals) and Richness (number of species) metrics of SDB: between habitat vs. season, habitat vs. baits and habitat vs. season vs. baits. The results indicate no significant interaction between habitat vs. season (Richness: $\chi^2 = 62.63$, $df = 8$, $p > 0.05$; Abundance: $\chi^2 = 49.14$, $df = 10$, $p > 0.05$) and habitat vs. baits (Richness: $\chi^2 = 116.01$, $df = 16$, $p > 0.05$; Abundance: $\chi^2 = 144.01$, $df = 16$, $p > 0.05$) and habitat vs. season vs. baits (Richness: $\chi^2 = 98.11$, $df = 24$, $p > 0.05$; Abundance: $\chi^2 = 112.29$, $df = 24$, $p > 0.05$) (see Supplementary material, Table S4). The Kruskal-Wallis test and when necessary the Dunn multi-comparisons test (Sokal and Rohlf, 1995) were applied to determine, in detail, specific differences: (i) Richness and Abundance among habitats; (ii) Richness and Abundance among seasons, and (iii) Richness and Abundance among types of baits within the studied habitats.

The taxonomic composition of SDB communities among habitats was compared by using Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson, 2001). For a better perception of PERMANOVA results, we performed a Non-Metric Multidimensional Scaling (NMDS) analysis. Considering the low degree of stress (0.09), we reduced dimensionality to two (dimensions) and fitted environmental variables to the corresponding axes using the *envfit* function (Oksanen et al., 2007) within the *vegan* package (Oksanen et al., 2013) of R 3.2.4 program (R Core Team, 2016). In order to reduce possible bias associated with correlated explanatory variables, we performed, previously to the NMDS, a non-parametric correlation test to select the least correlated variables (Spearman's $\rho < 0.75$) (Graham, 2003). This procedure selected the following environmental variables: temperature (T), humidity (H), canopy cover (CC), percentage of exposed soil (PES), LLC (percentages of leaf litter cover) and richness of shrubs (RS). We used the similarity percentages analysis (SIMPER) to quantify dissimilarity in the SDB assemblages between habitats and to identify those morphospecies/species explaining most of the dissimilarity. A similar procedure was applied – PERMANOVA / NMDS – to evaluate the taxonomic composition of SDB communities: (i) for the different

seasons (dry, intermediary and rainy) by habitat; and, (ii) for the different baits (human faeces, rotten meat, rotten banana and control bait) by habitat. The Bray-Curtis similarity index was used when performing PERMANOVA, NMDS and SIMPER (Clarke and Warwick, 2001).

To discriminate possible dissimilarities detected in the previous analysis, a beta diversity partition analysis was applied, using the partitioning framework proposed by Baselga (2010). The pairwise dissimilarity index (β_{sor}) was partitioned into two components: turnover (β_{sim}) and nestedness (β_{nes}): $\beta_{sor} = \beta_{sim} + \beta_{nes}$. The partitioning framework evaluates whether dissimilarities in the composition of the SDB communities occurred through the substitution of some species by others (β_{sim}) or by the formation of nested subsets of more diverse communities (β_{nes}). The β_{sor} index ranges from 0 (identical species assemblages) to 1 (dissimilar species assemblages). Using this approach with our dataset allowed testing (i) differences in the values of total dissimilarity (β_{sor}) between different sites studied, but also (ii) the relative contribution of species turnover (β_{sim}) and nestedness-resultant dissimilarity (β_{nes}) in each site. Beta diversity analysis was performed using the functions *beta.pair* from *betapart* package (Baselga et al., 2017) within R 3.2.4 program (R Core Team, 2016).

Finally, to detect the occurrence of indicator species, single value indicator (IndVal) developed by Dufrêne and Legendre (1997) was calculated, combining specificity (patterns of relative abundance) of a given species in a given habitat with its fidelity within that habitat (patterns of incidence). Species with a high specificity and high fidelity within a habitat attain the highest indicator value. This analysis was performed in R 3.2.4 program (R Core Team, 2016) using the *indicspecies* package 1.7.5 (De Cáceres and Jansen, 2015) with 9999 permutations, using SDB abundance by species.

3. Results

3.1. Small Dung Beetles assemblages' composition and habitats

A total of 867 individuals were collected, grouped within seven genera and 16 species/morphospecies (from here on species). Nine species (302 individuals) were identified in the PF, nine species (159 individuals) in the SF-15, four species (82 individuals) in SF-5, six species (93 individuals) in Ag and eight species (228 individuals) in Pa. Rarefaction curves for all sites reached their asymptotes values, supporting the sampling effort undertaken (Fig. S3, Supplementary material). The most abundant species were *Ataenius* sp1 (260 individuals), *Ataenius platensis* (134 individuals) and *Aphodius* sp1 (112 individuals), together representing approximately 59% of captures. The genus *Ataenius* (533 individuals) and *Aphodius* (203 individuals) were the

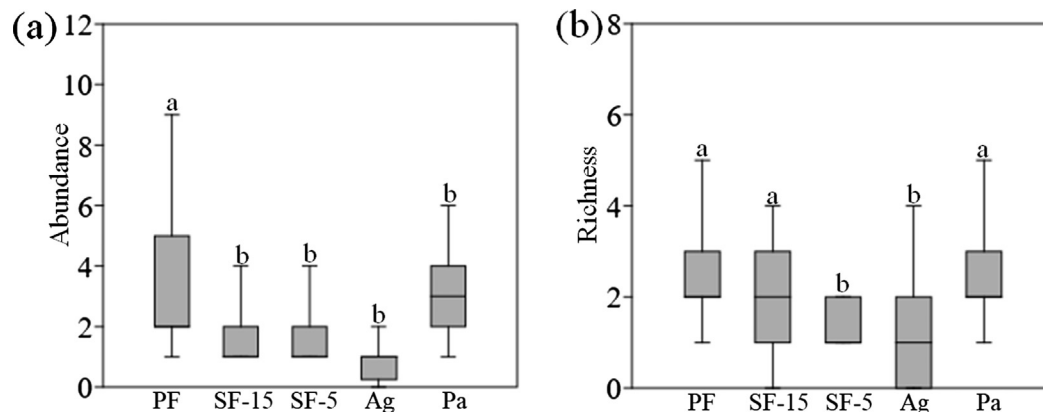


Fig. 1. Box and Whisker plots expressing the differences in (A) Abundance (number of individuals), and (B) Richness (number of species) of the Small Dung Beetles (SDB) assemblages for the different habitats considered. The values followed by the same letters are not significantly different according to Dunn multi-comparisons test. PF (Primary forest), SF-15 (Secondary forest with 15 years of regeneration), SF-5 (Secondary forest with five years of regeneration), Agriculture - Ag (cocoa plantations), Pasture.

most abundant: circa 85% of total abundance (Table S5, Supplementary Material). Of the 16 species sampled, 3 species were collected exclusively in PF; Pa also presented 3 unique species while PF and SF-15 had similar assemblages (6 common species, ~38%) (Table S5, Supplementary material). The taxonomic composition highlights species indicative of specific habitats and/or environmental conditions: *Trichiopsummobiopsis* sp, *Ataenius* sp5 and *Labarrus* sp1 were only captured in PF; *Iarupea* sp1 was captured in PF and SF-15; *Iarupea* sp2 only in SF-15; *Aphodius* sp3, *Aphodius* sp4 and *Nialaphodius* sp only in Pa (Table S5, Supplementary Material).

SDB assemblages presented significant differences between the studied habitats in terms of Abundance ($\chi^2 = 112.4$, $df = 4$, $p < 0.001$) and Richness ($\chi^2 = 96.68$, $df = 4$, $p < 0.001$). SDB Abundance in PF was significantly higher when compared with the other habitats (Fig. 1a) while SDB Richness was significantly higher in PF, SF-15 and Pa when compared with SF-5 and Ag (Fig. 1b) (see Supplementary material, Table S6, for details of the associated differences and Dunn's post-hoc values).

The Permutational Multivariate Analysis of Variance (PERMANOVA) presented significant differences in the SDB taxonomic composition between habitats ($F = 17.26$, $P < 0.001$): Ag and Pa SDB assemblages seem isolated from forest and recovering forest habitats (PF, SF-15 and SF-5) (Table 1).

The NMDS analysis reinforced the results previously obtained with PERMANOVA: species assemblages in the studied habitats are noticeably different. The NMDS shows a partial superimposition among PF and SF-15 assemblages, also depicting a gradient from the reference PF to the most disturbed habitats such as Ag and Pa, although with divergent directions (Fig. 2). The SDB communities in PF were mostly associated with the CC (canopy cover) and H (humidity) and CBH (circumference at breast height); SF-15 was correlated with CC (canopy cover); SF-5 was correlated with RS (richness of shrubs); Pasture (Pa) was correlated with PES (percentage of exposed soil) and T (temperature); finally, Agriculture (cocoa) Ag was correlated with LLC (percentage of leaf litter cover) (Fig. 2).

Dissimilar habitat assemblages were identified by the preliminary SIMPLER analysis, showing high contrasts (above 80) between: PF vs. Pa (86.42), PF vs. Ag (85.24), PF vs. SF-5 (84.44), SF-15 vs. Ag (84.89), SF-15 vs. Pa (80.89) and Ag vs. Pa (83.38). Overall percentage values for each habitat pair and the main species that contributed to habitat dissimilarity are presented in Table S7, Supplementary material.

The beta diversity (β sd) presented relatively high values for all pairwise comparisons (β sd minimum = 0.55; β sd maximum = 0.83; β sd median = 0.69), namely for SF-5 vs. Ag (β sd = 0.89), SF-15 vs. Ag (β sd = 0.83) and Ag vs. Pa (β sd = 0.83) (Fig. 3). The β sd partition analysis additionally revealed a turnover (β sim) component with an increasing trend when inspecting the pairwise comparisons between the reference habitat (PF) and the other habitats, ordered by disturbance level: PF vs. SF-15 (β sim = 0.31), PF vs. SF-5 (β sim = 0.47), PF vs. Ag (β sim = 0.5) and PF vs. Pa (β sim = 0.61) (Fig. 3). Interestingly, β sd presents a similar trend to β sim for the same comparisons,

Table 1

PERMANOVA results (based on Bray-Curtis similarity) comparing the composition of Small Dung Beetles (SDB) assemblages between the studied habitats ($F = 17.26$, $P < 0.001$). PF (Primary forest), SF-15 (Secondary forest with 15 years of regeneration), SF-5 (Secondary forest with five years of regeneration), Agriculture - Ag (cocoa plantations), Pasture. NS = Not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

	PF	S-15	SF-5	Ag
PF	0	–	–	–
SF-15	14.19 ^{NS}	0	–	–
SF-5	30.00 ^{NS}	8.74 ^{NS}	0	–
Ag	19.32 [*]	2.69 [*]	16.49 [*]	0
Pa	14.17 ^{***}	12.87 ^{**}	6.08 ^{NS}	15.11 ^{NS}

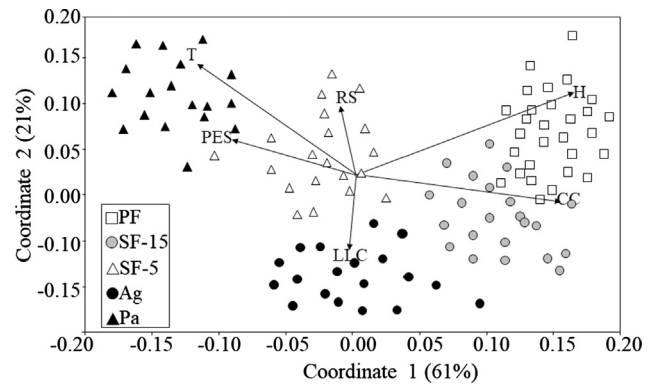


Fig. 2. Non-metric multidimensional scaling (NMDS) showing Small Dung Beetles (SDB) assemblages grouped in accordance with the habitats (using Bray-Curtis similarity; Stress: 0.09). PF (Primary forest), SF-15 (Secondary forest with 15 years of regeneration), SF-5 (Secondary forest with five years of regeneration), Agriculture - Ag (cocoa plantations), Pasture. T = Temperature; H = Humidity; CC = Canopy cover; PES = Percentage of exposed soil; LLC = Percentage of leaf litter cover; RS = Richness of shrubs.

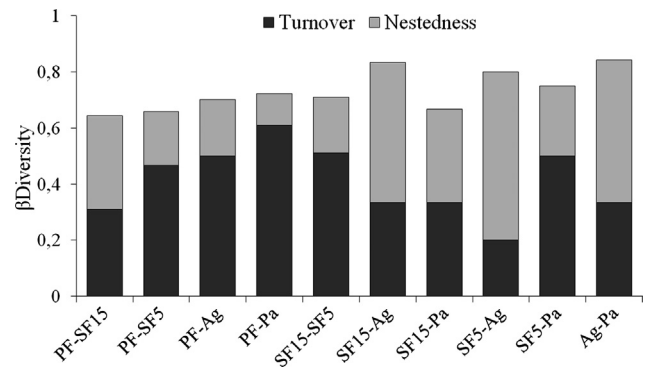


Fig. 3. Comparison of dissimilarity values for β sd (overall dissimilarity), β nes (dissimilarity resulting from nestedness), and β sim (turnover) for the Small Dung Beetles (SDB) assemblages associated with the different habitats. PF (Primary forest), SF-15 (Secondary forest with 15 years of regeneration), SF-5 (Secondary forest with five years of regeneration), Agriculture - Ag (cocoa plantations), Pasture.

whereas nestedness (β nes) depicts a negative one: PF vs. SF-15 (β nes = 0.33), PF vs. SF-5 (β nes = 0.19), PF vs. Ag (β nes = 0.20) and PF vs. Pa (β nes = 0.11) (Fig. 3). High turnover values (β sim) were found, in general, when comparing disturbed habitats with recovered ones, such as PF vs. Pa (β sim = 0.61), SF-15 vs. SF-5 (β sim = 0.51) and SF-5 vs. Pa (β sim = 0.50). On the other hand, habitats with similar structure and disturbance presented low β sim values: SF-5 vs. Ag (β sim = 0.20) and PF vs. SF-15 (β sim = 0.31) (Fig. 3). High nestedness values (β nes) were found when comparing Ag vs. Pa (β nes = 0.51), SF-15 vs. Ag (β nes = 0.50) and SF-5 vs. Ag (β nes = 0.60) while the lowest nestedness was found when comparing PF vs. Pa (β nes = 0.11) and PF vs. SF-15 (β nes = 0.19) (Fig. 3). If we consider all the studied habitats, Pa seems to be most divergent in term of species composition while Ag seems to retain less diversity, i.e. a small subset of the other habitats (Fig. 3).

Of the 16 species found in the present study, 9 species ($\approx 56\%$) were considered habitat indicators by the IndVal analysis (Dufrêne and Legendre, 1997). According to IndVal, 3 SDB species were significantly associated with PF, 2 with SF-15, 1 with SF-5 and 3 with Pa. No SDB species was indicative for Ag (Table 2).

3.2. Small Dung Beetles assemblages' diversity and seasonality

Regarding seasonal differences, 331 individuals were collected in

Table 2

Small Dung Beetles (SDB) select by the IndVal method. PF (Primary forest), SF-15 (Secondary forest with 15 years of regeneration), SF-5 (Secondary forest with five years of regeneration), Agriculture - Ag (cocoa plantations), Pasture - Pa (only taxa with IndVal $\geq 25\%$ were considered).

SDB species	Indicator value	p value	Habitat
<i>Trichiopammobius</i> sp1	0.87	0.001	PF
<i>Labarrus</i> sp1	0.80	0.001	PF
<i>Ataenius</i> sp5	0.77	0.001	PF
<i>Iarupea</i> sp2	0.81	0.05	SF-15
<i>Labarrus</i> sp2	0.65	0.01	SF-15
<i>Ataenius</i> sp4	0.71	0.01	SF-5
<i>Nialaphodius</i> sp1	0.85	0.001	Pa
<i>Aphodius</i> sp3	0.55	0.05	Pa
<i>Aphodius</i> sp4	0.54	0.05	Pa

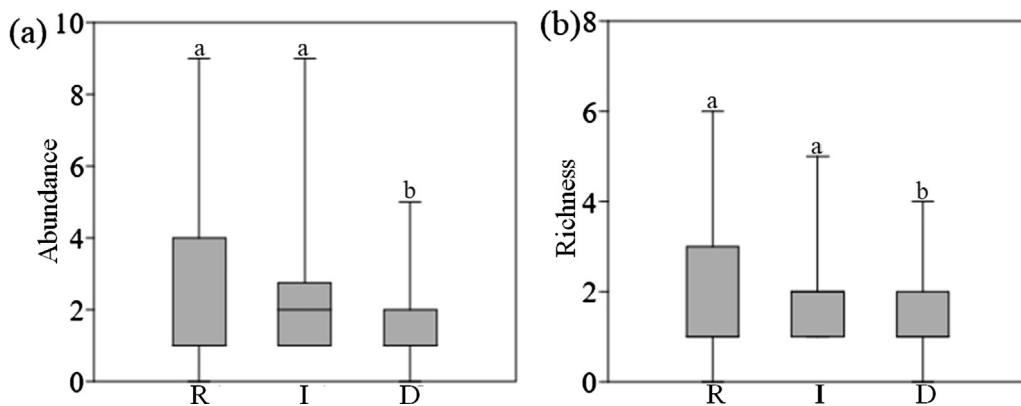


Fig. 4. Box and Whisker plots expressing the differences in (A) Abundance (number of individuals), and (B) Richness (number of species) of the Small Dung Beetles (SDB) assemblages for the different seasons. The values followed by the same letters are not significantly different according to Dunn multi-comparisons test. D = Dry; I = Intermediary; R = Rainy.

the rainy season, followed by the intermediate season with 317 individuals and the dry season with 219 individuals. Of the 16 species sampled, 5 (31.25%) were captured during all monitoring seasons. On the other hand, the rainy season presented exclusive species (4 species = 25%) (Table S5, Supplementary material). Statistical differences in Abundance and Richness of SDB were identified between seasons ($\chi^2 = 12.84$, $df = 2$, $p < 0.0001$; $\chi^2 = 18.59$, $df = 3$, $p < 0.001$, respectively). Abundance and Richness presented statistical significant

differences between the rainy and dry seasons, and the intermediary and dry seasons (Fig. 4a and 4b) (see Supplementary material, Table S8, for details of the associated differences and Dunn's post-hoc values). Even though the statistical significant higher scores of Abundance and Richness depicted in the rainy season, this seasonal trend was not even for all habitats: in SF-15, these metrics presented higher values in the dry period and, for Ag and Pa, in the intermediate season. SF-5 showed no statistical significant differences in Abundance and Richness within the different seasons (Fig. 5; see Supplementary material, Table S9, for details of the associated differences and Dunn multi-comparisons test).

The results of the NMDS showed that the SDB assemblages of the different seasons could be separated from each other by ordination in the species composition. The composition of the SDB assemblages from the rainy and intermediary seasons were more similar to each other

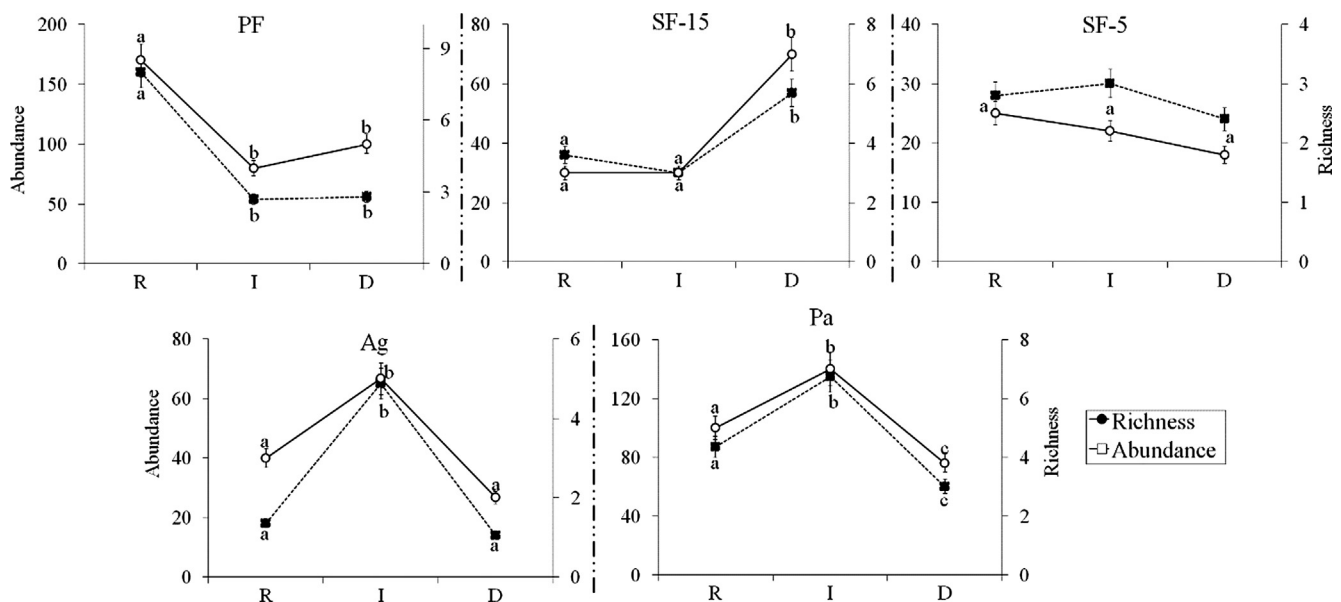


Fig. 5. Graphical representation of the seasonal variation of the Abundance and Richness of Small Dung Beetles (SDB) by habitat. The values followed by the same letters are not statistically significantly different according to the Dunn post-hoc test. PF (Primary forest), SF-15 (Secondary forest with 15 years of regeneration), SF-5 (Secondary forest with five years of regeneration), Agriculture - Ag (cocoa plantations), Pasture - Pa (only taxa with IndVal $\geq 25\%$ were considered). D = Dry; I = Intermediary; R = Rainy.

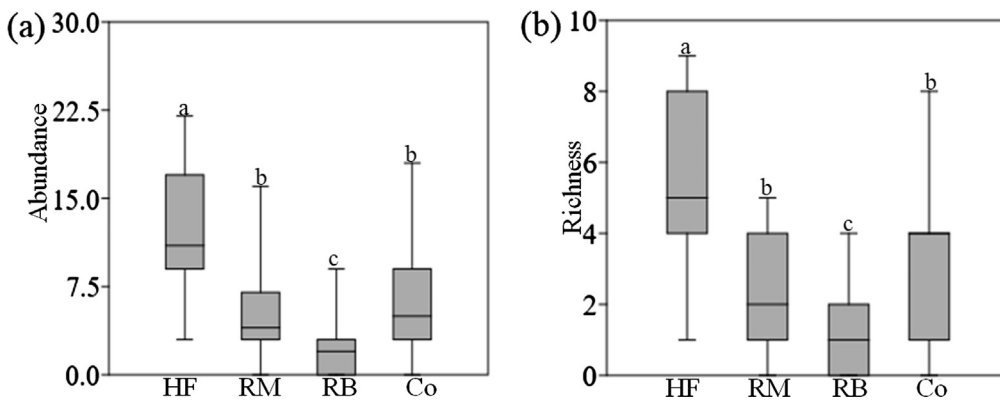


Fig. 6. Box and Whisker plots expressing the differences in (A) Abundance (number of individuals), and (B) richness (number of species) of the Small Dung Beetles (SDB) assemblages of the SDB studied in accordance with the type of bait. The values followed by the same letters are not significantly different according to Dunn multi-comparisons test. HF = Human faeces; RM = Rotten meat; RB = Rotten banana; Co = Control bait.

NMDS results produced a pattern consistent with the species composition between the seasons, indicating that the SDB assemblages' composition changes gradually from the rainy towards the dry period (Fig. S5, Supplementary material).

3.3. Small Dung Beetles assemblages' diversity and bait attractiveness

Significant statistical differences in capturing individuals (Abundance) by types of baits were encountered ($\chi^2 = 65.84$, $df = 3$, $p < 0.01$). According to a posteriori Dunn multi-comparisons test, human faeces bait (HF) presented a statistically significantly greater Abundance by comparison with all other baits while RB depicted a statistically significantly lower Abundance by comparison with all other baits (Fig. 6a and Tables S12 and S13, Supplementary material). Similar results were obtained for richness ($\chi^2 = 58.19$, $df = 3$, $p < 0.01$) (Fig. 6b). See Supplementary material, Table S13, for details of the associated differences and Dunn multi-comparisons test.

HF bait traps were, in general, able to capture significantly more species and individuals (Abundance and Richness) (Fig. 7; Table S14, Supplementary material for details of the associated differences and Dunn's posthoc values). Anyhow, SF-5 presented significantly higher richness with Control bait (Co) while in Ag, Abundance and Richness were significantly higher using Co. In Pa greater richness was obtained with Co and HF (Fig. 7; Table S14, Supplementary material for details

of the associated differences and Dunn's posthoc values).

In relation to the taxonomic composition of the SDB assemblages' collected by type of bait, the NMDS showed mostly an overlap (Fig. S6). Anyway, HF and Co seem to present some divergence (Fig. S6). The PERMANOVA analysis showed a statistically significant difference between the baits ($F = 6.25$, $p < 0.001$), with the exception of HF vs. RM and RM vs. RB (Table S15, supplementary material). Taxonomic composition of the SDB captured by habitat presented significant differences between types of baits, as demonstrated by PERMANOVA and NMDS (see Table S16 and Fig. S7 for differences associated with between baits in each studied habitat).

4. Discussion

4.1. Neotropical Small Dung Beetles assemblages' composition as indicators of land use change in forest landscapes

Small dung beetles (SDB) diversity (Abundance and Richness) was generally superior in the Primary forest (PF), which suggests SDB assemblages' dependence on complex and pristine habitats with more resources (e.g., carrion, faeces and even leaf litter; Driscoll and Weir, 2005; Cajaiba et al., 2017b). This result might also be associated with a range of environmental characteristics created by vegetation structure that are favorable for SDB survival and reproduction: e.g. canopy cover,

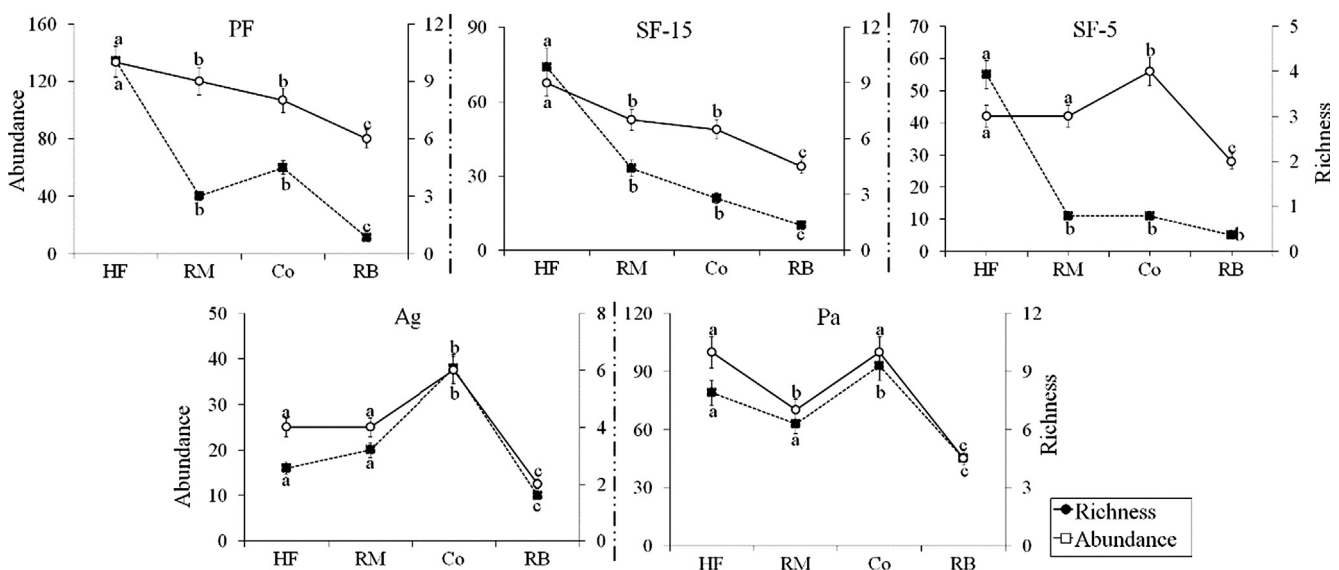


Fig. 7. Graphical representation of the differences between Abundance and Richness of the Small Dung Beetles (SDB) with different types of baits by habitat. The values followed by the same letters are not different according to Dunn test. PF (Primary forest), SF-15 (Secondary forest with 15 years of regeneration), SF-5 (Secondary forest with five years of regeneration), Agriculture - Ag (cocoa plantations), Pasture - Pa. HF = Human faeces; RM = Rotten meat; RB = Rotten banana; Co = Control bait.

understory vegetation, deeper and softer soils, soil moisture content, more stable air and soil temperature, lower insolation, and higher concentration of food resources (Horgan, 2007; Audino et al., 2014).

Anthropogenic disturbance reduces the populations of several mammalian species (Culot et al., 2013) and, therefore, the food resources for SDB. Anyhow, no linear trend in diversity could be associated with anthropogenic disturbance: highly disturbed habitats depicted equivalent values of diversity to less-disturbed ones, disagreeing from several publications (e.g. Gardner et al., 2008; Viegas et al., 2014). In fact the results of Rey Benayas et al. (2009), showing that restoration efforts tend to increase species richness, diversity, abundance and biomass relative to degraded systems was only partially substantiated by our work. Moreover Nichols et al. (2007) results demonstrating that land-use systems with a high degree of forest cover (such as SF-15) could harbor similar SDB assemblages, in terms of species richness and abundance, to those found in intact tropical forest was not entirely factual in our case study.

Even though the diversity (Abundance and Richness) of SDB assemblages associated with highly disturbed habitats (such as Pa) was comparable to pristine or recovered ones (PF and SF-15), their composition was rather dissimilar, as demonstrated by PERMANOVA and β sor partition results. The β sor partition indicates Pa (Pasture) as the more divergent in composition while Ag (Agriculture) as the poorest with a subset of the other habitats diversity. We found a relatively high percentage of species turnover between the studied habitats, which represented an average of approximately 73% of the overall beta diversity: each habitat presents a distinct subset of species, although agroecosystems (agriculture and pastures) typically retaining a non-random set of species that often replaces core forest specialists (Lyra-Jorge et al., 2010). The obtained results also seem to show agroecosystems act, in this region, as a selective filter on SDB across the landscape (Chiarello, 2000), affecting matrix fluxes according to the dispersal capacity of each species (Lees and Peres, 2009). The conversion of the pristine habitats into Pastures (Pa) or monocultures (Ag) is associated with dramatic changes in abiotic and biotic factors, with detrimental effects on the structure and composition of the SDB communities (Medri and Lopes, 2001). These changes seem also to decrease evenness in the assemblages, leading to the dominance of some species and to the disappearance of forest specialists, unable to tolerate the conditions of disturbed habitats (Liberal et al., 2011).

The high value of undisturbed Primary forest (PF) was also supported by our indicator species analysis. We identified 3 SDB species that are significant indicators of mature forest, and other 2 that are indicators of Secondary forest (SF-15), therefore, especially sensitive to disturbance. These species present important ecosystem functions when consuming mammalian excrements or detritus, fungi, decaying plants or roots (Cabrero-Sañudo, 2012). They also increase soil permeability and recycle organic matter, favoring the fertility of pastures (Ridsdill-Smith and Edwards, 2011; Cabrero-Sañudo, 2012). Indicator species analysis further highlights the importance of considering species identity by revealing that widespread, generalist species with little conservation value are characteristic of heavily disturbed areas (Cabrero-Sañudo, 2012). Thus, the results obtained with the IndVal signals indicator SDB for pristine and/or anthropogenic systems and might guide the management and recovery of imperilled Neotropical ecosystems. Our results support the applicability of SDB metrics as ecological indicators for the management of forests in the region under study, demonstrating that several forest-dependent species could disappear if the forests are replaced by an agricultural landscape (e.g. Pa or Ag) (Cajaiba et al., 2018).

4.2. Neotropical Small Dung Beetles assemblages' seasonality and monitoring programs

Seasonality is an important component in the dynamics of arthropods' communities. If the goal of the study is to perform a complete

inventory of SDB communities, the researcher should not only decide where (e.g. altitudinal gradient, location) and how (e.g. collection methods), but also when (e.g. time of year) collections should take place (Maveety et al., 2014). In our study, the abundance and richness of SDB collected at different times of the year (rainy season, intermediate season and dry season) depicted a decreasing trend towards aridity, corroborating the hypothesis that the abundance and richness are associated with seasons and concomitant environmental conditions (Andresen, 2005). However, according to Cajaiba and Silva (2017), biotic responses to seasonal changes are not easily understood or predictable because the responses contrast between species. This suggests that disturbance history may be an important determinant in the species occurrence. I.e. prior knowledge of SDB communities is required to understand the concomitant responses to possible new conditions (Cajaiba and Silva (2017)).

Previous studies demonstrated that vegetation structure and its effects on microclimate (e.g. temperature and air moisture) might be one of the most important factors controlling and structuring the distribution of SDB (Magura et al., 2000). Apparently, the evolutionary life cycle strategy of SDB is optimized and synchronized with seasonal changes of microclimatic environmental conditions (Wang et al., 2014). However, additional studies are necessary to document the extent and sensitivity to microclimate, particularly relevant in the light of the potential effects of climate change (Maveety et al., 2014). Understanding seasonal patterns of SDB in a given region could be valuable for several reasons. Seasonal variations in abundance, richness, and species composition could uncover the role of phenology and the effect of survey timing on the results obtained namely in studies associating SDB with habitats. Moreover, seasonal information of SDB might be a relevant ecological indicator, which might be fundamental for the management of habitats and landscapes.

4.3. The interplay between baits, habitats and neotropical Small Dung Beetles

SDB species collected in this study demonstrated preferences for specific types of baits. Human faeces' (HF) baits, as expected, presented the highest diversity of captures (e.g. abundance and richness). The high coprophagy specialization in the SDB seems to be related to the regular and diverse availability of mammal dung (Cajaiba et al., 2017b). However, this preference was not linear for all habitats. Disturbed habitats (e.g. Pa and Ag) depicted higher diversity of SDB in non-baited traps. Although highly specialized in mammalian excrement due to evolutionary processes, many neotropical species of SDB show plasticity in their diet (Larsen et al., 2006). This process seems to be linked with the local availability of the habitats to provide food, i.e. when the preferred food is not available, many SDB may use other resources in similar state of decomposition (Cajaiba et al., 2017b). It is obvious that saprophages and coprophages adults have less specialized diets (Stebnicka, 2001b): for example, the adults of a given species imbibe the liquid that seeps from vegetable masses undergoing fermentation. Others also occasionally consume the liquid contents of dung or exhibit other feeding habits, such as consuming various waste materials discarded by ants and termites (Stebnicka, 2001b). The SDB occurring in Agriculture might not prefer faeces or rotten meat (coprophagia or saprophagia, respectively) probably to the absence of large mammals in this habitat. This perspective suggests that loss of mammals (i.e., and their faeces as a food resource) may alter competitive interactions between SDB and may even cause local extinction of highly specialized species (Bogoni and Hernández, 2014). However, it is not clear the low preference for faeces baits in areas of Pa, given that this habitat presents large numbers domestic animals (cattle). According to Andresen (2002), human actions reduce the diversity of mammals and of SDB associated, which in turn may alter nutrient cycling processes and secondary dispersion of seeds. In addition, the biological effects of a poorer diversity may affect processes (e.g.

behavioural/physiological, ecological, and evolutionary) at different scales (e.g., local, regional, ecosystemic, and global) (Galetti and Dirzo, 2013; Bogoni and Hernández, 2014).

4.4. Perspectives and challenges on using neotropical Small Dung Beetles metrics for environmental management of forest landscapes

The change and degradation of natural landscapes by humans is the primary cause of global biodiversity loss across all major taxonomic groups (Reid et al., 2005) and is expected to increase in severity over the coming decades as human populations continue to grow exponentially (Sala et al., 2000). Understanding the response of biotic communities to the modification of natural habitat is essential for predicting and mitigating further biodiversity loss (Nichols et al., 2007). A strong, synthetic understanding of insect response to human activity is necessary to both support conservation policy decisions and assess the functional consequences of human disturbance (Balmford and Bond, 2005; Rocha et al., 2011). Because of their dependence on vertebrate dung, SDB communities are likely to be influenced by changes in mammal communities (Salomão et al., 2018), which are often themselves affected by the synergistic effects of forest modification, fragmentation and elevated hunting pressure that can accompany increased forest access. Importantly, SDB community structure can be rapidly determined using simple, standardized trapping methods (Larsen and Forsyth, 2005), allowing efficient comparative evaluation of human impacts around the world. Thus, we believe that SDB can provide a broader, taxonomic representation in the development of conservation practice and policies and can therefore be used as model species of disturbance indicators. Despite their wide global distribution, high diversity and their abundance in both tropical and warm temperate ecosystems, they are also sensitive to changes at local and landscape scales (Nichols et al., 2007) because they are linked to specific habitats (Davis et al., 2001) and form part of specific intertrophic associations (Andresen and Laurance, 2007). They are particularly useful for ecological surveys because the required methods are cheaper than for many other taxa (Gardner et al., 2008) and they have a relatively stable taxonomy (Philips et al., 2004). Studies show that changes in the composition and availability of dung resources, as a result of the decline or local extinction of medium and large bodied mammals, severely disrupts the diversity and abundance of dung beetles (e.g. Nichols et al., 2009 and associated references). Studies already carried out with the SDB show that, despite the different SDB species pool of particular regions, the general patterns of their functional responses to anthropogenic disturbances were very similar (Jay-Robert et al., 2008; Cabrero-Sañudo et al., 2010; Chandra and Gupta, 2012). This suggests the possibility of using SDB universally to monitor changes in terrestrial habitats. Inherent to a preliminary case study, our work presents insights on using ecological indicators for gauging functional changes associated to anthropogenic disturbance in a forest landscape of Amazonia.

5. Final remarks

Small Dung Beetles (SDB) assemblages in the Amazonia seem to be particularly sensitive to land use changes, highlighting the groups' feasibility in indicating the ecological status of habitats, useful for monitoring the forest remnants and/or restoration of disturbed habitats. The obtained results suggest that SDB assemblages' composition undergoes major changes when responding to disturbance even with minor shifts in diversity.

Although spatially and temporally restricted, the field methodologies disentangled here, namely concerning types of bait and season, provide remarks to improve the detection and description of the responses of SDB assemblages to disturbance and anthropogenic pressures. Surveying SDB communities within different seasons and using diverse baits seems fundamental to estimate diversity in neotropical

forests. This result should guide optimal sampling strategies, fundamental to support decision-making and robust management and or recovery of imperiled ecosystems.

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