

1 **Spatial and temporal shifts in functional and taxonomic diversity of dung beetles in a human-**  
2 **modified tropical forest landscape**

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24 **ABSTRACT**

25 Functional diversity is commonly used to assess the conservation value of ecosystems, but we have  
26 not yet established whether functional and taxonomic approaches are interchangeable or  
27 complementary to evaluate community dynamics over time and in response to disturbances. We used a  
28 five-year dataset of dung beetles from undisturbed forest, primary forest corridors, and *Eucalyptus*  
29 plantations to compare the sensitivity of conceptually equivalent metrics to temporal variation in  
30 different anthropogenic disturbances. We compared species richness with functional richness, Pielou's  
31 evenness with functional evenness, and Simpson's diversity with Rao's quadratic entropy. We  
32 assessed the sensitivity of the metrics to anthropogenic changes. The indices showed complex patterns  
33 among habitat types, with with similar responses in some cases and not in other, and little  
34 incongruence between the pairs within the same year. The influence of disturbance on longer-term  
35 temporal variation over the five-year period revealed lower temporal variation in functional than  
36 taxonomic metrics. Both approaches showed greater variation in plantations compared to native  
37 forests. We evaluated the variation in taxonomic and functional metrics between consecutive years and  
38 among habitats. Most metrics showed similar shifts between years in all habitats, except for species  
39 and functional richness. We demonstrate that even conceptually similar indices may not provide  
40 similar information on dung beetles responses to disturbance. However, the differences between the  
41 indices can yield key insights about the drivers of change, especially over the long-term. It is  
42 important to use taxonomic and functional diversity in tandem to better understand community  
43 responses to environmental and anthropogenic changes.

44

45 **Keywords:** Amazonia, Functional ecology, Land-use change, Scarabaeinae, Temporal dynamics.

## 46 INTRODUCTION

47         The past decade has seen a rapid increase in the use of functional metrics to quantify  
48 biodiversity responses to anthropogenic change (e.g. Elmqvist et al., 2003; Bihn et al., 2010; Barragán  
49 et al., 2011), replacing or complementing the traditional taxonomic approach, which considers each  
50 species as a unit with an equal contribution to ecosystem functioning (Mouchet et al., 2010). The  
51 functional approach is particularly important in the tropics, because the rapid rate of land-use change  
52 and the importance of biodiversity has promoted a prolific debate about the role of human-modified  
53 landscapes for ecosystem functioning and biodiversity conservation (Silver et al., 1996; Lambin et al.,  
54 2003; Gardner et al., 2008; Power, 2010; Palm et al., 2014). Additionally, the exceptionally high  
55 biological diversity of tropical environments can make it very difficult to find empirical links between  
56 biota and ecosystem functioning, which increases our reliance on functional diversity metrics (Gaston,  
57 2000; Mouillot et al., 2013).

58         Many studies have estimated the conservation value of ecosystems using either taxonomic or  
59 functional diversity, and it is well established that human-induced changes affect both sets of metrics  
60 (Braga et al., 2013; Mouillot et al., 2013; Cottee-Jones et al., 2015; Bredemeier et al., 2015). Although  
61 these metrics can complement each other and provide very different insights into mechanisms driving  
62 community changes, it is only recently that they have been assessed together in the same study (e.g.  
63 Moretti et al., 2009; Villéger et al., 2010; Baiser and Lockwood, 2011). These studies help  
64 demonstrate the importance of evaluating the sensitivity of both functional and taxonomic approaches  
65 in assessing biodiversity change, since there are valid reasons to suggest that they will show very  
66 different responses. First, most functional metrics are not related to species diversity (Villéger et al.,  
67 2008; Laliberté and Legendre, 2010), and the loss of functionally specialised species can lead to a  
68 decrease in functional diversity, even if total species richness remains high due to functionally similar  
69 species (Petchey and Gaston, 2002; Villéger et al., 2010). Second, the similarity between taxonomic  
70 and functional approaches may depend on the intensity of disturbance: low-intensity disturbance could  
71 change species composition but functional redundancy in highly diverse communities would maintain  
72 their functional structure, whereas high-intensity disturbances are likely to negatively affect both the

73 taxonomic and functional components of biodiversity (Hidasi-Neto et al., 2012; Sterk et al., 2013;  
74 Edwards et al., 2014).

75         There is currently a lack of empirical evidence to assess the sensitivity of taxonomic and  
76 functional metrics to temporal dynamics, and to determine how natural temporal variation interacts  
77 with human-induced modifications. It is important to fill this knowledge gap for two reasons: firstly,  
78 because taxonomic diversity is often a poor predictor of changes in ecosystem function (Baiser and  
79 Lockwood, 2011) and secondly, because diverse forest communities can be highly dynamic in time  
80 and the temporal variation of taxonomic or functional diversity may not show similar patterns  
81 (Villéger et al., 2010; Beiroz et al., 2017). For example, we might expect fewer changes in functional  
82 compared to taxonomic diversity over time because the traits of species within a community were  
83 selected by ecological filters (i.e. processes related to interactions among species as well as between  
84 species and the abiotic environment; Cornwell et al., 2006; Webb et al., 2010; Swenson et al., 2012),  
85 which could keep the relative frequency of traits constant even though the number of species may  
86 change. Importantly, there is little evidence of how taxonomic and functional approaches vary across  
87 time in human modified systems. We would expect the two approaches to yield more similar results as  
88 the intensity of habitat modification increases, because functional diversity declines with increasing  
89 loss of sensitive species, making it more likely that the loss of a given species will also entail a loss of  
90 function in highly disturbed areas (Leitão et al., 2016; Ricotta et al., 2016). Given the wide variation in  
91 the extent and intensity of human modifications to tropical forests, and the potential implications of  
92 disturbance for ecosystem functioning, clarifying the differences between taxonomic and functional  
93 assessments of biodiversity could provide important information for conservation and management.

94         We used a five-year study of Amazonian dung beetle communities to investigate the spatial and  
95 temporal patterns of taxonomic and functional diversity, contrasting the response of conceptually  
96 similar taxonomic and functional diversity metrics between undisturbed forest (used as a baseline for  
97 comparison) and two modified habitat types: primary forest corridors, which comprise a reduction in  
98 forest extent with increased edge and isolation effects; and *Eucalyptus* plantations, which represent a  
99 highly disturbed habitat where native vegetation has been replaced by exotic trees. Dung beetles were

100 chosen as a focal group for this study because they are sensitive to changes in vegetation structure  
101 (Gardner et al., 2008; Almeida et al., 2011; Korasaki et al., 2013), their response traits are well studied  
102 (Nichols et al., 2013), and they mediate important ecosystem functions, such as seed dispersal and  
103 incorporation of nutrients into the soil (Slade et al., 2007; Nichols et al., 2008; Slade and Roslin,  
104 2016). Specifically, we addressed the following key research questions:

105 1. Which approach to measuring diversity, taxonomic or functional, shows higher sensitivity to  
106 human-induced changes?

107 As functional diversity declines with increasing loss of sensitive species, we hypothesized that  
108 functional metrics will be more sensitive to intense anthropogenic disturbance. However, as the  
109 influence of species losses varies for different taxonomic and functional metrics, the two  
110 approaches will provide complementary information.

111 2. Is the five-year temporal variation of taxonomic and functional diversity similar?

112 As functional redundancy in species-rich dung beetle communities is likely to buffer changes  
113 among years, we hypothesized that temporal variation will be greater in taxonomic diversity  
114 compared to functional diversity at low levels of human-induced change, but temporal variation  
115 will become more similar between the two approaches as disturbance intensifies.

116 3. Does anthropogenic modification affect inter-annual variation between consecutive years?

117 Previous studies have shown that inter-annual variation of dung beetle communities in undisturbed  
118 forest is mainly driven by climate (Beiroz et al., 2017), and anthropogenic disturbance often alters  
119 forest habitat structure and micro-climate (e.g. Liechty et al., 1992; Popadrit et al., 2015); we  
120 therefore hypothesised that the magnitude of differences between consecutive years will be affected  
121 by the intensity of forest modification.

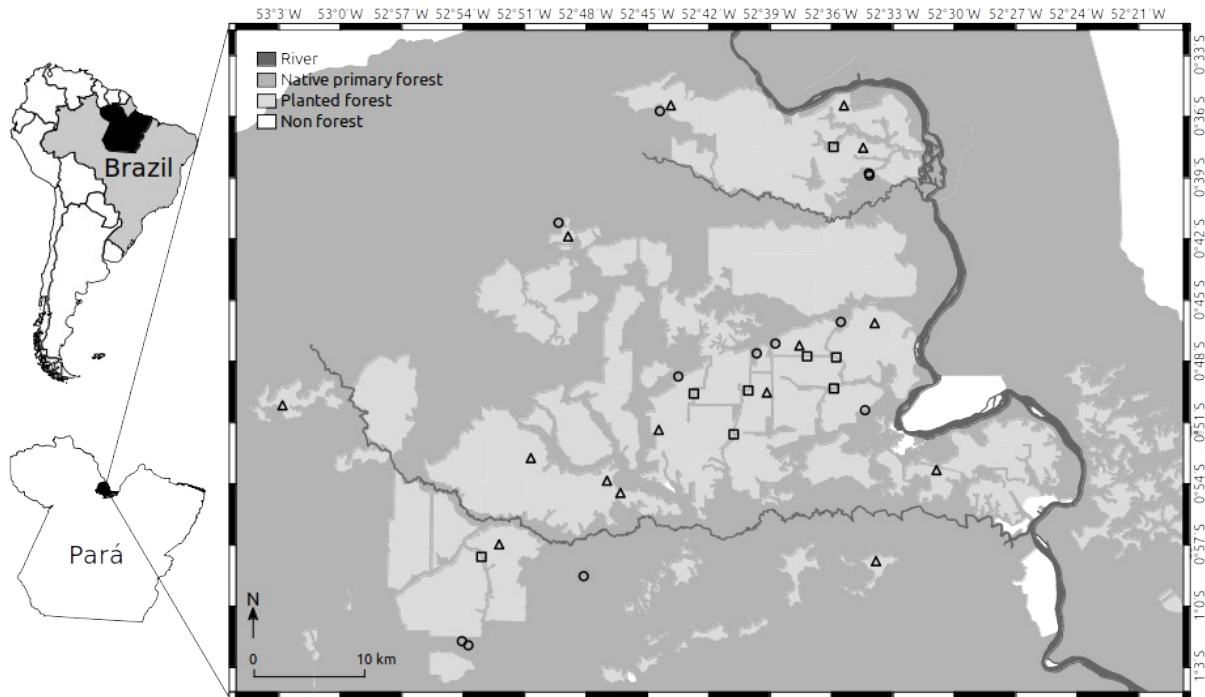
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## 123 MATERIAL AND METHODS

### 124 **Study site**

125 We conducted the study in the Jari River basin, located at north-eastern Brazilian Amazonia  
126 (00°27' - 01°30' S, 51°40' - 53°20' W; Fig. 1), an area of more than 15,000 km<sup>2</sup>, which was partially

127 converted from pristine forest to plantations of exotic trees c. 50 years ago (Coutinho and Pires 1997).  
128 Currently, the landscape comprises exotic tree plantations (450 km<sup>2</sup>), and regenerating secondary  
129 forest (1,000 km<sup>2</sup>) interwoven with large primary forest corridors (c. 200 m wide), and surrounded by  
130 *Terra Firme* primary forest (> 5,000 km<sup>2</sup>; Fig. 1; Coutinho and Pires 1997; Parry et al., 2007).



131  
132 Fig. 1: Location of sampling sites in undisturbed forest (circles), primary forest corridors (squares) and  
133 *Eucalyptus* plantations (triangles) within the Jari River basin in Pará State, Brazil.  
134

135 The region has a marked wet season from January to June, and a distinct dry season from  
136 September to November, with a tropical monsoon climate (Amw – Köppen classification), and an  
137 average annual rainfall of 2115 mm (Coutinho and Pires, 1997; Parry et al., 2007). The mean annual  
138 temperature is  $26.7 \pm 0.6^\circ\text{C}$  with monthly maxima and minima of  $31.4 \pm 1.1^\circ\text{C}$  and  $22.5 \pm 0.2^\circ\text{C}$ ,  
139 respectively (Climate Data.org, 2016).

140 We sampled in 12 undisturbed primary forest sites, eight primary forest corridors, and 15  
141 *Eucalyptus* plantations separated by 0.2 – 60 km (Fig. 1). The undisturbed forest was used as a  
142 baseline, whereas primary forest corridors (100-300 m wide) were considered a low-intensity  
143 modification, with strong edge and isolation effects. *Eucalyptus* plantations represent a highly  
144 disturbed site, as the native forest has been completely replaced by exotic trees. Both modified habitat  
145 types have a distinct dung beetle species composition and community structure, mainly by species

146 replacement (turnover component of  $\beta$ -diversity in Fig. S1). However, communities in *Eucalyptus*  
147 plantations are the most dissimilar to those in undisturbed forest (Fig. S1; Barlow et al., 2010). It is  
148 also important to highlight that the *Eucalyptus* trees are harvested each 4-5 years. Thus, most of our  
149 plantations sites were harvested during the study, we are aware that this activity can strongly affect the  
150 dung beetles community but this is one of the main disturbance in fast-growing crops and was  
151 represented in this study.

152

### 153 **Dung beetle sampling**

154 We followed the protocol for dung beetle sampling in previous studies at same site (Barlow et  
155 al., 2007; Gardner et al., 2008; Barlow et al., 2010). Thus, we sampled dung beetles using pitfall traps  
156 baited with 30 g of human dung. The traps consisted of plastic containers (19 cm diameter and 11 cm  
157 deep), protected from rain with a plastic lid suspended 20 cm above the surface. Each trap was part-  
158 filled with water, salt, and detergent. Five pitfall traps were placed 150 m apart along a transect, with  
159 at least 500 m distance to the nearest edge in undisturbed forests. Collections took place once a year  
160 over a five-year period (2009 to 2013) during the wet season in each year. Beetles were sampled in  
161 exactly the same locations for 48 hours per site in each year. Due to the large number of sites and the  
162 extensive area covered by our study, sampling took place over a 2-3 month period each year between  
163 late January and early June. However, to ensure comparable data among years, sampling was  
164 concentrated in March and April each year except 2013, when most sites were sampled one month  
165 earlier (see Table S2). In addition, sites within each habitat type were visited on each sampling date.

166 Dung beetle specimens were transported from the field to the laboratory in 90% ethanol, then  
167 sorted, dried and stored in paper envelopes. Beetles were identified using a key to the New World's  
168 Scarabaeinae genera and subgenera (Vaz-de-Mello et al., 2011), a field guide for dung beetles of the  
169 Jari River basin (Louzada et al., *unpublished data*), and a reference collection held at the Universidade  
170 Federal de Lavras (CREN – UFLA; 'Coleção de Referência de Escarabeíneos Neotropicals'), Minas  
171 Gerais State, Brazil. Identifications were made to species level and, where there was uncertainty, a  
172 morphospecies number was given. Voucher specimens were deposited at CREN – UFLA.

173

#### 174 **Assessment of response traits**

175         We undertook two additional sample collections to assess dung beetle traits related to dietary  
176 preference and diel period. In January and February 2012, we collected specimens from previously  
177 selected sites with high species richness and abundance. In November and December 2013, we  
178 collected additional species for which there was scarce information about traits. The sampling sites  
179 were chosen based on data from a previous research project located within our study area and included  
180 all three studied land-use types. We set pitfall traps during the day (7:00-18:00 h) and night (19:00-  
181 6:00 h) to classify the beetles as diurnal or nocturnal. We used pitfall traps baited with either dung or  
182 carrion to assess broad dietary preferences. We classified dung beetle species as necrophagous or  
183 coprophagous based on the statistical significance ( $p < 0.05$ ) of IndVal analysis for carcass or dung  
184 baited pitfalls, respectively; or as generalist when there was no significant ( $p > 0.05$ ) association with  
185 any bait. We determined beetle nesting behaviour as rollers, tunnelers, or dwellers based on their  
186 genus (Halfpeter and Matthews, 1966; Beiroz et al., 2017). We also recorded the body mass of each  
187 species using the mean dry weight of 15 individuals (or the maximum number available) sampled  
188 during the experiments using a precision balance (0.001 g); for species with low numbers of sampled  
189 individuals, we also weighed specimens previously deposited at CREN – UFLA.

190

#### 191 **Data analysis**

192         All analyses were performed using R version 3.3.0 (R Core Team, 2016). We calculated  
193 commonly used and conceptually similar metrics of taxonomic and functional diversity for each site  
194 and collection year. The taxonomic metrics were: 1) species richness, which is the number of different  
195 species at each site; 2) Pielou's evenness, which describes the dominance/evenness in communities  
196 based on species frequency and abundance; and 3) Simpson's diversity index ( $1-D$ ), which is the  
197 probability of two individuals from a community belonging to the same species. The corresponding  
198 functional metrics were: 1) Functional richness (FRic), which is the amount of functional space  
199 occupied by species in a given community; 2) Functional evenness (FEve), which evaluates the



200 regularity of the trait distribution; 3) Rao's quadratic entropy, which is based on the probability of  
201 finding functionally similar species in a community by chance (Botta-Dukát, 2005; Villéger et al.,  
202 2008). As functional metrics depend on species trait data, all species lacking information for more  
203 than one trait were removed from the analysis (6% of species and 2% of individuals) to avoid biasing  
204 comparisons between taxonomic and functional approaches. FRic and FEve were calculated using the  
205 *dbFD* function in the *FD* package (Laliberté et al., 2014), and Rao's entropy was calculated using the  
206 *mpd* function in the *picante* package (Kembel et al., 2010). All functional indices were based on  
207 species' dietary preference, diel period, nesting behaviour, and body mass to obtain Gower's  
208 dissimilarity between species, as we had both categorical and continuous traits values (*gowdis* function  
209 in the *FD* package).

210 To compare the magnitude of taxonomic and functional differences in dung beetle communities  
211 between different habitat types, we calculated Hedge's *g* for each taxonomic and functional metric  
212 individually in the *compute.es* package. The *g*-values represent the magnitude of changes in diversity  
213 metrics based on the mean of the baseline (undisturbed forest) subtracted from the mean of the  
214 modified habitat type (Del Re 2013). Subsequently, we multiplied the values by '-1', such that a  
215 positive *g*-value represents an increase in a given diversity metric for each modified habitat type  
216 compared to the baseline, a negative *g*-value represents a decrease, and a *g* of zero represents no  
217 response. We then used paired t-tests to compare the mean values of Hedge's *g* between pairs of  
218 conceptually similar diversity metrics in each modified habitat type; comparisons were made between  
219 species richness and FRic, Pielou's evenness and FEve, Simpson's diversity and Rao's entropy. We  
220 also ran the Pearson's correlation to test the correlation between the equivalent metrics in taxonomic  
221 and functional approach.

222 To assess the sensitivity of diversity metrics to temporal variation over the five sampled years  
223 for each habitat type, we calculated the coefficient of variation (the ratio between the standard  
224 deviation and the mean for each taxonomic and functional metric) for each site over the five sampled  
225 years. We then assessed whether the coefficient of variation differed between approaches for each  
226 habitat type and pair of metrics (Species richness and FRic, Pielou's evenness and FEve, and

227 Simpson's diversity and Rao's entropy) using linear models (Gaussian error distribution; *lm* function)  
228 with the coefficient of variation as the response variable and the type of metric (taxonomic or  
229 functional) as the explanatory variable. We tested the explanatory variable significance using the F-  
230 test to perform an analysis of variance with *anova* function (R Core Team, 2016).

231 To test whether forest modification influences the variation in dung beetle communities  
232 between consecutive years, described by taxonomic and functional diversity approaches, we built  
233 generalized linear mixed models. Each diversity metric was used as a response variable with a  
234 Gaussian error distribution, except for species richness (count data), for which we used a Poisson error  
235 distribution (*glmer* function in the *lme4* package; Bates et al., 2015). Our models included the  
236 categorical variables of habitat type, sampling year, and their interaction as fixed effects, and sampling  
237 site as a random effect to reduce the effect of temporal dependency (pseudo-replication). We tested the  
238 significance of fixed effects with type II Wald Chi-square tests, using the *Anova* function in the  
239 package *car* (Fox and Weisberg, 2011), as it considers the sums of squares for each main effect  
240 conditional on the other main effects. Finally, for those models with significant fixed effects, we ran  
241 Chi-square tests for multiple pairwise comparisons among habitat types in each year and between  
242 consecutive years within each human-modified habitat type using the *testInteractions* function in the  
243 *phia* package followed by Holm-Bonferroni correction of *p*-values to control the family-wise error rate  
244 (Rosario-Martinez, 2015).

245

## 246 RESULTS

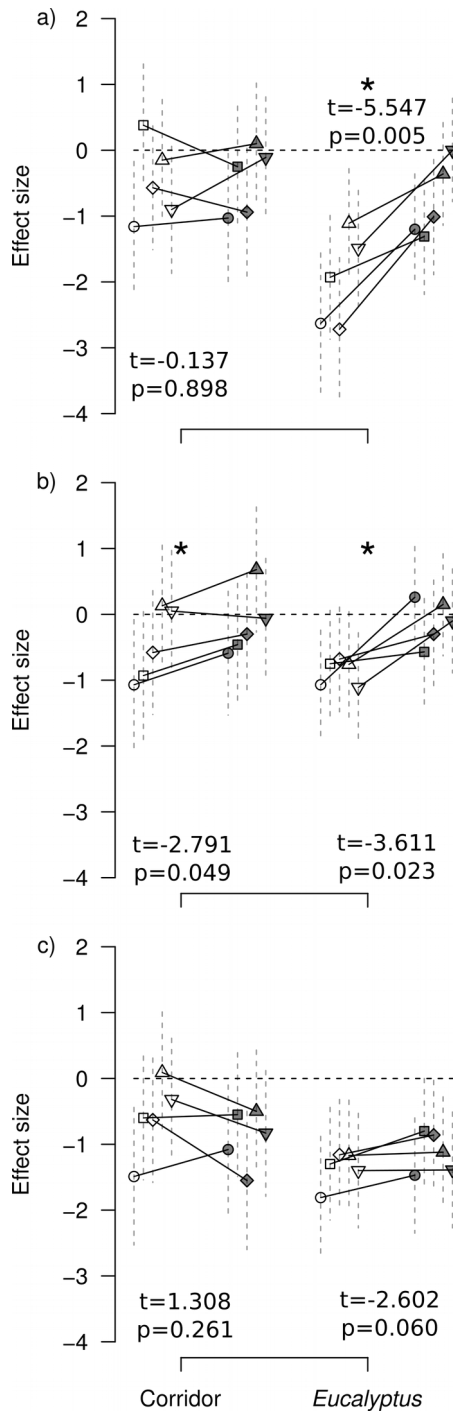
247 We sampled 27,192 dung beetles individuals and 102 species in total, recording 10,240  
248 individuals of 70 species in undisturbed forest, 8,163 individuals of 64 species in corridors, and 8,125  
249 individuals of 65 species in *Eucalyptus* plantations. We obtained trait information for 75 species (74%  
250 of the 102 species sampled), which represents 26,528 (98%) of the individuals sampled. In terms of  
251 nesting behaviour, most were classified as tunnelers (44 spp; 59%), followed by rollers (20 spp; 17%),  
252 and dwellers (11 spp; 15%). The majority of species were either classified as coprophagous or  
253 generalist (34 spp. for both; 45.3% each), whereas necrophagous beetles represented only 9.3% (7

254 spp.) of all species. We recorded the diel period for 66 species (65%) represented by 25,545  
255 individuals (94%). Most species were classified as diurnal (38 spp; 58%), compared to nocturnal (28  
256 spp; 42%).

257

### 258 **Magnitude of taxonomic and functional diversity responses to forest modification**

259       The taxonomic and functional metrics used to describe dung beetle communities were highly  
260 correlated both across and within different habitat types (Fig. S3). The analysis of the mean effect size  
261 (changes relative to the undisturbed forest baseline) showed that taxonomic and functional diversity  
262 metrics might not respond similarly when describing changes in beetle communities in forest corridors  
263 and *Eucalyptus* plantations (Fig. 2). We found that species richness was more affected than FRic in  
264 plantation and Pielou's evenness more than FEve in both human-modified habitats (Fig. 2a-b).  
265 However, species richness and FRic showed similar effect sizes in forest corridors, and Simpson's  
266 diversity and Rao's entropy showed similar effect sizes in both modified habitat types (Fig. 2b-c).



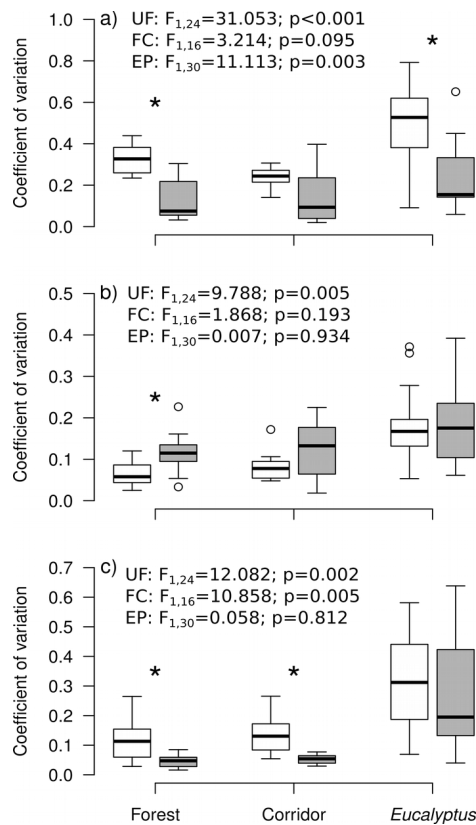
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268 Fig. 2: Hedge's  $g$ -value for taxonomic (white symbols) and functional (grey symbols) diversity  
 269 metrics describing changes in dung beetle communities in modified forest sites (corridors and  
 270 *Eucalyptus*) relative to undisturbed forest; a) species richness and functional richness; b) Pielou's  
 271 evenness and functional evenness, and c) Simpson's diversity index and Rao's quadratic entropy.  
 272 Solid lines connect the values for both approaches in the same year, dashed horizontal lines represent  
 273 no change ( $g = 0$ ) and vertical dashed lines show the 95% confidence intervals; geometric symbols  
 274 represent the years, as following: circles = 2009, squares = 2010, diamonds = 2011, triangles = 2012  
 275 and inverted triangles = 2013.

276

277 **Sensitivity of taxonomic and functional diversity metrics to temporal variation within habitat**  
 278 **types**

279 There were substantial differences between conceptually equivalent taxonomic and functional  
 280 diversity metrics when they were used to assess five-year temporal variation in dung beetle  
 281 communities within habitat types (Fig. 3). In undisturbed forests and *Eucalyptus* plantation, species  
 282 richness varied significantly more among years than FRic (Fig. 3a), whereas Pielou’s evenness varied  
 283 less than FEve in both undisturbed forest and native forest corridors – although the latter was not  
 284 statistically significant (Fig. 3b). We also found higher variation in Simpson’s diversity than Rao’s  
 285 entropy for undisturbed forest and forest corridors (Fig. 3c).



286  
 287 Fig. 3: Coefficient of temporal variation for pairs of conceptually similar taxonomic (white) and  
 288 functional (grey) metrics of dung beetle communities in different habitat types over a five-year study  
 289 period, showing a) species richness and Functional richness, b) Pielou’s evenness and Functional  
 290 evenness, and c) Simpson’s diversity index and Rao’s quadratic entropy; where ‘UF’ = undisturbed  
 291 forest, ‘FC’ = primary forest corridor, and ‘EP’ = *Eucalyptus* plantation; stars indicate significant  
 292 differences ( $p < 0.05$ ) between taxonomic and functional diversity approaches within a given habitat  
 293 type.  
 294

295 **Inter-annual variation between consecutive years and anthropogenic effects on taxonomic and**  
 296 **functional diversity**

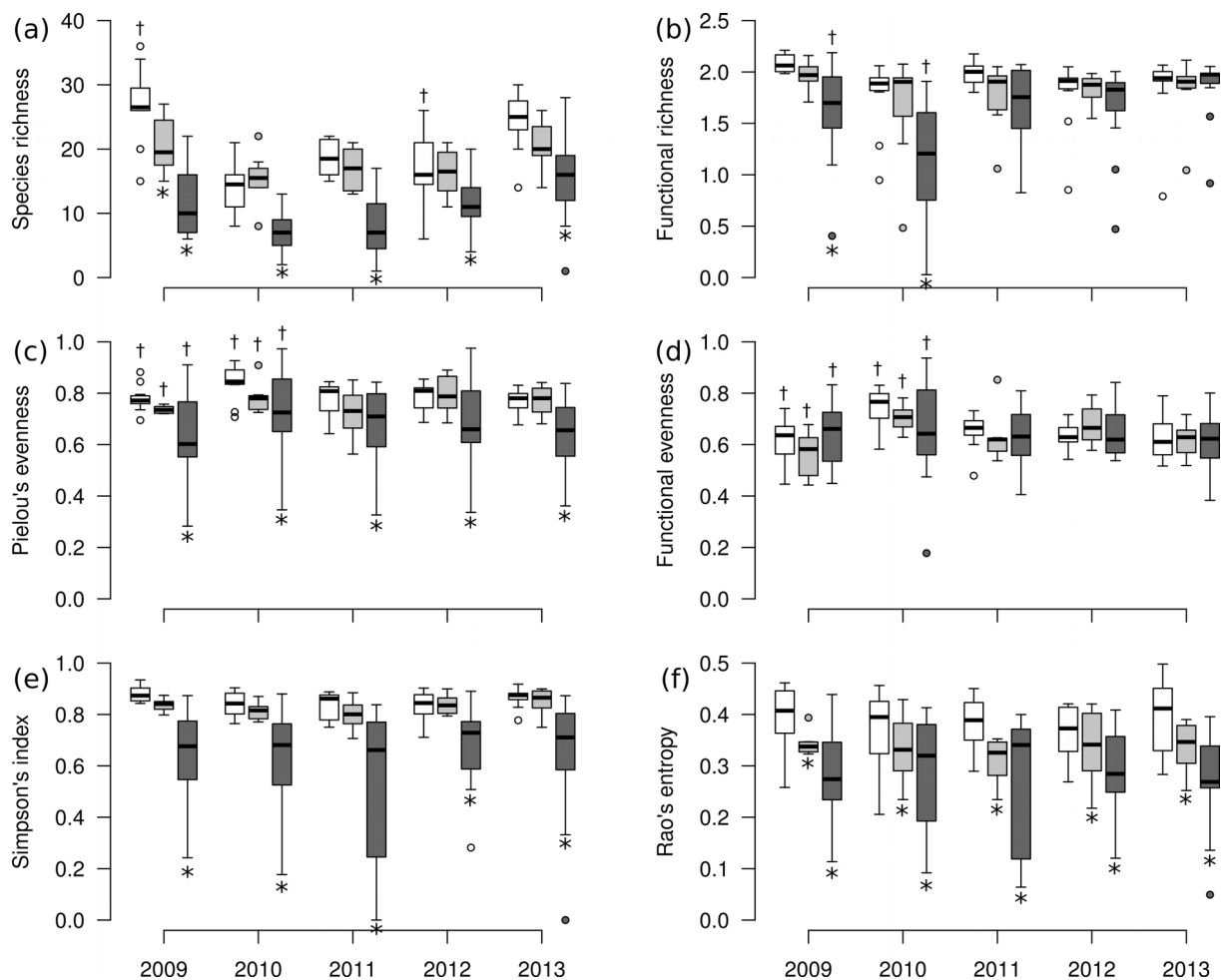
297 Most of the functional and taxonomic metrics exhibited variation between consecutive years,  
 298 except for Simpson's diversity and Rao's entropy, which differed among habitat types but not between  
 299 consecutive years (Figs 4 and 5; Table S4). It is important to highlight that we evaluated differences  
 300 between consecutive years and not among all years. Only species richness and FRic had distinct  
 301 patterns of inter-annual variation among habitat types, indicated by a significant interaction between  
 302 habitat type and year (Figs 4 and 5a; Tables S4, S5 and S6). There was a marked decrease in species  
 303 richness in all habitat types from 2009 to 2010 (but it was only statistically significant for undisturbed  
 304 forest), followed by a slight increase in subsequent years (Fig. 5a; Table S5). We also found higher  
 305 values of species richness in 2013 compared to the 2012 in undisturbed forest (Fig. 5a; Table S5) and  
 306 FRic in *Eucalyptus* plantation was lower in 2010 than 2009 (Fig. 5b; Table S6). Pielou's evenness and  
 307 FEve were higher in in 2010 compared to 2009 and 2011 for all habitat types (Fig. 5; Table S7).

308

| Year                | Year*Habitat type   | Habitat type              |
|---------------------|---------------------|---------------------------|
| Species richness    | Species richness    | Species richness          |
| Functional richness | Functional richness | Functional richness       |
| Pielou's evenness   |                     | Pielou's evenness         |
| Functional evenness |                     |                           |
|                     |                     | Simpson's diversity index |
|                     |                     | Rao's quadratic entropy   |

309

310 Fig. 4: Summarized results of global models showing the statistically significant variables ( $p < 0.05$ ).  
 311 The metrics displayed in the boxes are those which we found difference among years ('Year' box),  
 312 habitat types ('Habitat type' box) and the pattern of inter-annual variation was different among habitat  
 313 type ('Year\*Habitat type' box shows the interaction between explanatory variables).



314

315 Fig. 5: Differences in diversity metrics for dung beetle communities among habitat types and between  
 316 consecutive years for undisturbed forest (baseline; white boxes), forest corridors (light-grey boxes),  
 317 and *Eucalyptus* plantations (dark-grey boxes) over five years, showing a) species richness, b)  
 318 functional richness, c) Pielou's evenness, d) functional evenness, e) Simpson's diversity index, and f)  
 319 Rao's quadratic entropy. Asterisks ("\*") indicate significant differences ( $p < 0.05$ ) between human-  
 320 modified habitats and undisturbed forest in a given year; crosses ("†") represent significant  
 321 dissimilarity between consecutive years within the same habitat type.  
 322

323

Despite the inter-annual variation, we found consistent differences among habitat types for most  
 324 of the metrics (Figs 4 and 5; Table S4). Across all years, communities in *Eucalyptus* plantations had  
 325 the lowest values of species richness, Pielou's evenness, Simpson's diversity and Rao's entropy (Figs  
 326 4 and 5; Tables S5 and S6). We also found lower values of FRic in plantations in 2009 and 2010 (Figs  
 327 4 and 5b; Table S7). Only FEve did not differ significantly among habitat types (Figs 4 and 5d; Table  
 328 S4). We also found that the metrics describing dung beetle communities in corridors were similar to

329 undisturbed forest, apart from species richness in 2009 and Rao's entropy across all years, which were  
330 lower in corridors (Figs 4 and 5; Table S5 and S7).

331

## 332 DISCUSSION

333 We assessed taxonomic and functional diversity metrics simultaneously as tools to investigate  
334 changes in dung beetle biodiversity over time in three different habitat types. We found that the  
335 sensitivity of conceptually similar metrics to human-induced changes may not always be similar, with  
336 higher sensitivity in taxonomic metrics compared to functional metrics (Fig. 2). However, there were  
337 inconsistencies between approaches within years, even for pairs of metrics with similar sensitivity  
338 (Fig. 2) and the temporal variation across the five-year period tended to be higher for taxonomic  
339 compared to functional diversity (Fig. 3). Although we found higher temporal variation in taxonomic  
340 metrics, the interannual variation in taxonomic and functional metrics between consecutive years was  
341 similar among habitat types (Fig. 5), indicating that interannual variation during the sampling period is  
342 unlikely to influence biodiversity assessments among habitat types. Our findings provide important  
343 insights for interpreting anthropogenic disturbance and temporal stability in tropical forests, which  
344 will inform further research and monitoring.

345

### 346 **Does the similarity between taxonomic and functional diversity responses depend on the** 347 **intensity of anthropogenic disturbances?**

348 Our findings partially support the hypothesis that taxonomic metrics are more sensitive than  
349 functional metrics at detecting the effects of strong habitat modification on dung beetle communities  
350 (*Eucalyptus* plantations), but we also found that most paired taxonomic and functional approaches  
351 performed similarly in detecting the lower level of disturbance imposed by greater edge and isolation  
352 effects in primary forest corridors. Usually, studies comparing taxonomic to functional diversity  
353 evaluate metrics that are not directly comparable, which can make the findings and discussion  
354 excessively complex (Mlambo, 2014). By contrast, we selected conceptually similar metrics to assess  
355 taxonomic and functional diversity, and we found clear correlations between each pair of metrics (Fig.



356 S3). However, the two approaches showed a similar response of dung beetle communities across the  
357 gradient of human modification only in some cases (Fig. 2), indicating that careful selection of  
358 conceptually similar metrics is likely to give complementary results.

359 The significant differences between taxonomic and functional approaches must be interpreted  
360 with caution, as they could either be a result of functional redundancy among species in undisturbed  
361 and modified habitats or the replacement by functionally different species, which could keep similar  
362 FRic values but with different trait attributes (Villegger et al., 2008; Magnago et al., 2014). In our case,  
363 functional redundancy is the most likely explanation, as the sampled habitats have low values of  
364 functional originality (the highest value was *c.* 5% in undisturbed forest; Fig. S8), and some of the  
365 functional attributes were frequently assigned to many species (e.g. coprophagous and generalist diet  
366 preference).

367 Species richness declined much more strongly as a result of conversion from undisturbed forest  
368 into *Eucalyptus* plantation than it did in response to the reduction in habitat area in forest corridors  
369 (Fig. 2a) but there was no corresponding reduction in the occupied functional space (represented by  
370 FRic). This suggests that species loss was compensated by the presence of other species with similar  
371 functional trait attributes, which allowed the dung beetle communities in *Eucalyptus* plantations to  
372 maintain a similar functional structure to the undisturbed forest. The lower effects on FEve compared  
373 to Pielou's evenness (Fig. 2b) provide further evidence that the loss of taxonomic diversity in  
374 disturbed habitats had little effect on the functional differences among the remaining species.

375 When we considered the magnitude of changes in dung beetle communities (Hedge's *g*-values)  
376 in each year, we observed a mismatch between some of the pairs of metrics in some years but not in  
377 others, even those with similarities in overall response (Fig. 2). Different components of biodiversity  
378 can display distinct variation across sampling sites, regions or through time, depending on e.g. the  
379 attributes of the organisms and environmental conditions (see Moretti et al., 2009; Devictor et al.,  
380 2010 for a full discussion). Thus, studies based on a single sampling year or a small number of sites  
381 could show greater incongruence between functional and taxonomic metrics. Our work highlights the  
382 value of integrating both approaches to assess changes in biodiversity over multiple years. The

383 assessment of both approaches to evaluate ecological mechanisms and processes (e.g. habitat filtering,  
384 species loss) can help to clarify the consequences of anthropogenic disturbance. The taxonomic  
385 metrics address the loss or replacement of species individually, whereas the functional approach is  
386 related to the communities disassembly and assesses whether species losses or replacement change the  
387 previous functional space. For instance, the decrease in species number and the reduction of functional  
388 space can shed light on the potential effects of local species extinction on the shifts of functional  
389 attributes and species sensitivity under disturbance.

390

391 **In hyper-diverse tropical communities, is functional diversity more stable than taxonomic**  
392 **diversity over time?**

393 Two of the three taxonomic metrics showed greater temporal variation over the five years than  
394 the equivalent functional metrics in undisturbed forests and primary forest corridors, whereas  
395 functional and taxonomic approaches showed similarly high levels of inter-annual variation in  
396 *Eucalyptus* plantations, except species richness and FRic (Fig. 3). This finding supports our hypothesis  
397 that functional metrics will show greater temporal stability compared to taxonomic metrics at low  
398 levels of disturbance, but that the two approaches will yield similar results as forest modification  
399 intensifies. Low temporal variation in functional metrics in the primary forest corridors suggests that  
400 ecosystems subjected to edge and isolation effects can keep their functional structure in the face of  
401 external pressures, as long as those pressures do not change the trait-environment relationship (Webb  
402 et al., 2010). In contrast, the plantations at our study site are intensively managed for timber extraction  
403 (e.g. harvesting, fertilization, pest control) and these activities do not happen in all areas at the same  
404 time. Although the interpretation of biodiversity metrics can be influenced by sampling effort (e.g. if  
405 sampling is biased towards common species and attributes; van der Plas et al., 2017), our sampling  
406 design was consistent over the five years of the study and we were able to assign taxonomic identities  
407 and functional traits to a high proportion of individuals. The relative comparisons between years and  
408 among habitat types are therefore unlikely to be biased by sampling effort. Hence, disturbances due to

409 management activities likely explain the high between-year and between-site variation in dung beetle  
410 communities in the *Eucalyptus* plantations.

411 Our results suggest that functional metrics might be more appropriate in long-term research  
412 programmes evaluating changes in dung beetle community assembly and structure, whereas  
413 taxonomic approaches appear to be more sensitive to shifts in community dynamics. We found that  
414 conceptually similar taxonomic and functional metrics can differ over time even when both  
415 approaches show low overall temporal variation; for example, the temporal variation of Simpson's  
416 diversity was significantly higher than the limited variation of Rao's entropy (Fig. 2c; Flynn et al.,  
417 2009; Mason and De Bello, 2013). In some cases, the functional metric varied more in time than the  
418 taxonomic equivalent: the higher temporal variation in functional evenness (FEve) compared to its  
419 taxonomic counterpart (Pielou's evenness; Fig. 2b) could be due to the loss of a few functionally  
420 unique species, which would increase the sensitivity of FEve without changing Pielou's index of  
421 taxonomic evenness (Pakeman, 2011). Hence, the combination of the two approaches provides  
422 valuable information about different aspects of community change, which occur over different time-  
423 frames.

424

#### 425 **Is there an effect of anthropogenic modification in the inter-annual dynamic of dung beetles?**

426 Although temporal variation over the five-year study period was higher for taxonomic metrics  
427 of dung beetle communities than their functional equivalents in the undisturbed forest (Fig. 3), human  
428 modification of tropical forests did not consistently affect the variation in diversity metrics between  
429 consecutive years, which contrasts with our initial hypothesis. One potential explanation is that the  
430 core structure of the dung beetle communities is shaped by internal filters (e.g. micro-environmental  
431 and density-dependent processes; Webb et al., 2010; Violle et al., 2012), which are habitat-specific,  
432 whereas interannual variation is mainly driven by external conditions, such as climate and extreme  
433 weather events. The severe dry season that took place from 2009 to 2010 at our study site, would have  
434 affected dung beetle communities across all habitat types, and was the most likely cause of temporal  
435 variation in the undisturbed forest (see Beiroz et al., 2017 for details).

436 The lack of significant changes in taxonomic and functional diversity during the drought period,  
437 and the rapid recovery of both species and functional richness and evenness post-drought, indicates  
438 that dung beetle communities in hyper-diverse Amazonian forests are highly resilient to drought (Fig.  
439 5). However, the increasing dominance of human-modified habitats in tropical landscapes has already  
440 caused strong shifts in regional hydroclimate, and more frequent extreme events, such as severe  
441 drought and fires, could jeopardise the ability of communities to recover from adverse conditions  
442 (Franklin and Lindenmayer, 2009; Butt et al., 2011; Chen et al., 2011; Spracklen and Garcia-Carreras,  
443 2015; Khanna et al., 2017). The combination of taxonomic and functional approaches can help to  
444 identify changes in the resilience of ecosystems to constant negative pressures and to determine  
445 critical levels of biodiversity in the face of growing changes.

446 Despite the clear negative impact of the drought on dung beetles sampled in 2010, we found  
447 higher values of Pielou's evenness and FEve in 2010. Functional and taxonomic evenness can increase  
448 following climatic anomalies, as sensitive specialist species with rare combinations of traits are the  
449 first to disappear (Pakeman, 2011; Luck et al., 2013; Hitt and Chambers, 2015), resulting in greater  
450 taxonomic and functional similarity of the remaining species (Pakeman, 2011). Indeed, functional  
451 specialization was highly positively correlated to species richness, which indicates that there are more  
452 dung beetle species with unique sets of functional attributes in species-rich habitats, such as native  
453 forests in our study site (Fig. S8).

454 Only species richness and FRic showed different patterns of inter-annual variation across land-  
455 use types: inter-annual variation in species richness was similar in human-modified land-use types but  
456 differed strongly from undisturbed forest, whereas FRic only decreased in 2010 for *Eucalyptus*  
457 plantations (Fig. 5a and b). In contrast to the other metrics, species richness is highly sensitive to the  
458 loss of species with few individuals, which suggests that the differences between undisturbed and  
459 modified forests could occur due to systematic loss of rare species that are particularly sensitive to  
460 disturbance or changes in climate. FRic can be maintained by redundant species (Villegger et al., 2008)  
461 in which case, we would observe lower FRic if there was much fewer species compared to the  
462 reference sites (e.g. in *Eucalyptus* plantation compared to native forest habitats in 2009; Fig. 5a and b).

463 A decrease in FRic could also be explained by a large disturbance in a species-poor community; this  
464 could account for the lower FRic we observed in *Eucalyptus* communities in 2010, which was likely a  
465 response to a drought in 2009 (Fig. 5b; Beiroz et al., 2017). However, these decreases in species  
466 richness and FRic did not substantially alter the temporal dynamic of other metrics, even though forest  
467 modification has already altered dung beetle communities through the loss of vulnerable species (for  
468 further explanation of disturbance and species loss affecting functional diversity see Mouillot et al.,  
469 2013; Leitão et al., 2016).

470

#### 471 **Final considerations**

472 The taxonomic and functional metrics used here revealed a complex response of dung beetle  
473 diversity between years and among habitat types over the five-year study. Thus, our study  
474 demonstrates that conceptually similar indices do not necessarily represent more convergent results  
475 than other commonly used indices that are not directly comparable (Mlambo, 2014). Even when the  
476 overall effect size was more similar between approaches we found some inconsistent results in  
477 individual years, as taxonomic and functional metrics are related to different mechanisms underlying  
478 community shifts. Furthermore, as severely impacted habitats (e.g. *Eucalyptus* plantation) can show  
479 high temporal variation, it is still important to consider changes over several years in land-use studies,  
480 even in relatively aseasonal humid tropics. Hence, studies of community dynamics using one set of  
481 diversity metrics or approach to identify responses to anthropogenic changes could differ markedly  
482 from studies using other metrics or approaches. Thus, we propose that the use of both taxonomic and  
483 functional metrics will provide a more complete picture of biological responses to disturbance, and  
484 this may be particularly important for long-term evaluation of the effects of anthropogenic change  
485 (Mouchet et al., 2010; Villéger et al., 2010; Gagic et al., 2015).

486 Even though we did not directly compare the consequences of anthropogenic changes on the  
487 studied systems, it is important to highlight the consistent reduction of both taxonomic and functional  
488 diversity in plantations compared to undisturbed native forests, which has been previously reported for  
489 our study site (Gardner et al., 2008; Louzada et al., 2010; Beiroz et al., 2017), as well as other tropical

490 forests around the world (e.g. Harvey et al., 2006; Edwards et al., 2014; Campos and Hernández,  
491 2015). Much has been discussed about the importance of restoring landscape features (e.g.  
492 surrounding native vegetation, matrix permeability) to increase the conservation value of tree  
493 plantations (Audino et al., 2014; 2017; Gray et al., 2014; 2016). Thus, despite the potential effect of  
494 management on temporal and spatial variation of dung beetle communities in plantations, we  
495 recommend that future studies account for the high variation in both taxonomic and functional  
496 diversity within the same year. The ability of dung beetle communities to maintain functional structure  
497 in *Eucalyptus* plantation might indicate specific ecological conditions that increase the conservation  
498 value of plantations.

499

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506

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508

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513

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