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.

INTRODUCTION

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

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

122

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^2, 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^2), and regenerating secondary

129 forest (1,000 km^2) interwoven with large primary forest corridors (c. 200 m wide), and surrounded by

130 *Terra Firme* primary forest (> 5,000 km^2; Fig. 1; Coutinho and Pires 1997; Parry et al., 2007).
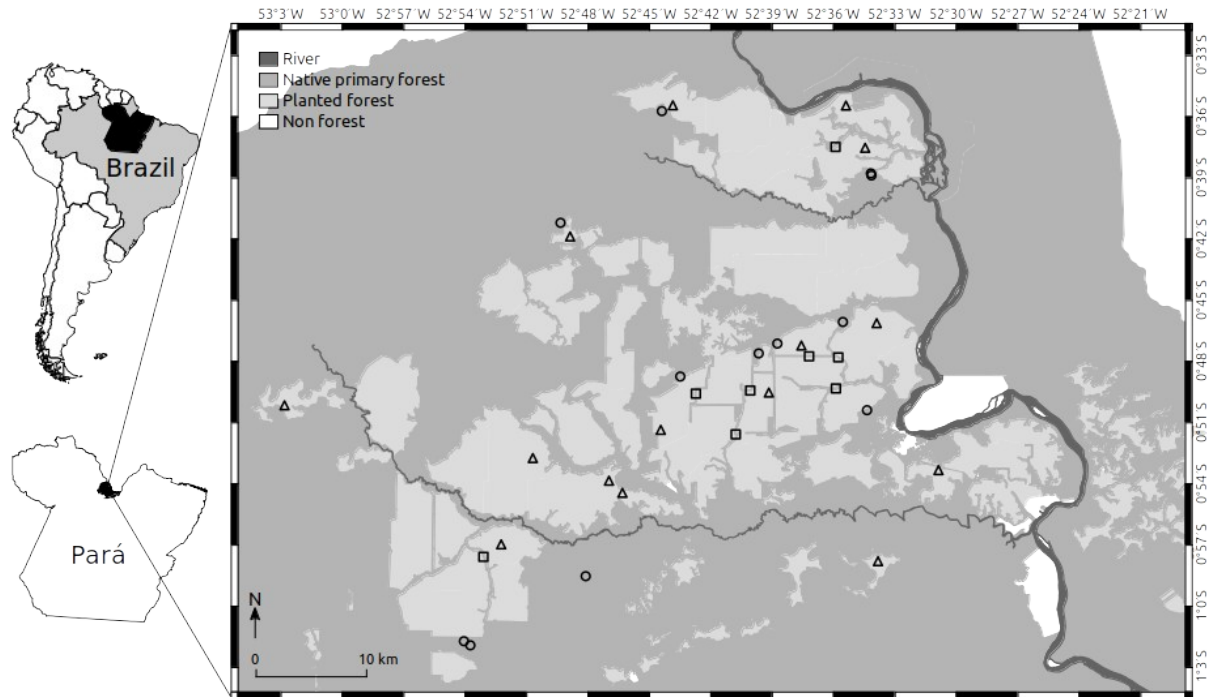
131
132 Fig. 1: Location of sampling sites in undisturbed forest (circles), primary forest corridors (squares) and
133 *Eucalyptus* plantations (triangles) within the Jari River basin in Pará State, Brazil.
134

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 ±0.6°C with monthly maxima and minima of 31.4 ±1.1°C and 22.5 ±0.2°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 β-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 Neotropicais'), 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

Assessment of response traits

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

Data analysis

All analyses were performed using R version 3.3.0 (R Core Team, 2016). We calculated commonly used and conceptually similar metrics of taxonomic and functional diversity for each site and collection year. The taxonomic metrics were: 1) species richness, which is the number of different species at each site; 2) Pielou's evenness, which describes the dominance/evenness in communities based on species frequency and abundance; and 3) Simpson's diversity index (1-*D*), which is the probability of two individuals from a community belonging to the same species. The corresponding functional metrics were: 1) Functional richness (FRic), which is the amount of functional space 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).
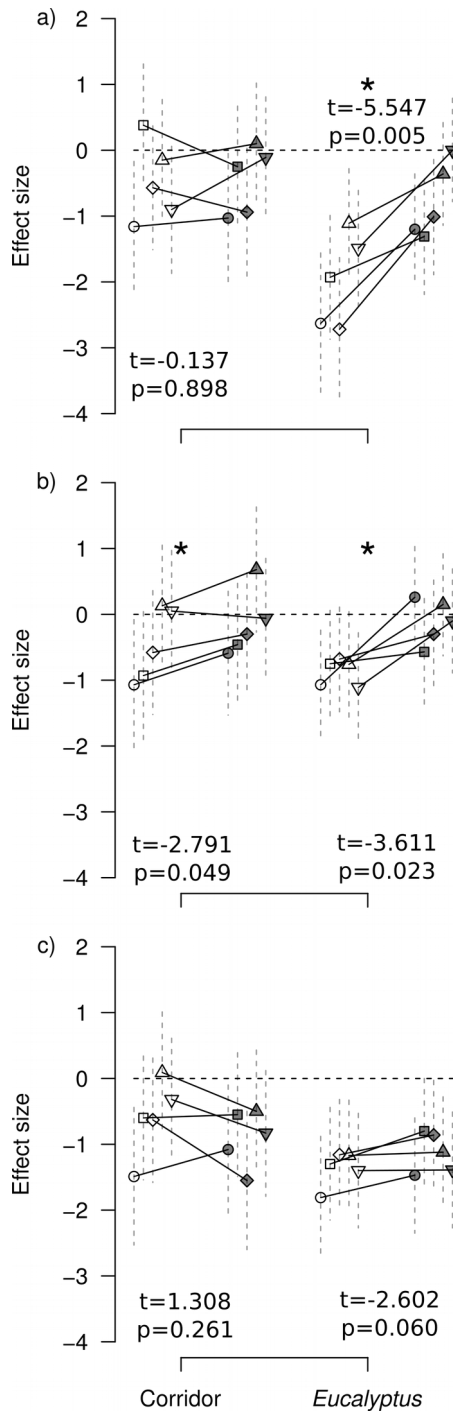
Fig. 2: Hedge's *g*-value for taxonomic (white symbols) and functional (grey symbols) diversity metrics describing changes in dung beetle communities in modified forest sites (corridors and *Eucalyptus*) relative to undisturbed forest; a) species richness and functional richness; b) Pielou's evenness and functional evenness, and c) Simpson's diversity index and Rao's quadratic entropy. Solid lines connect the values for both approaches in the same year, dashed horizontal lines represent no change ($g = 0$) and vertical dashed lines show the 95% confidence intervals; geometric symbols represent the years, as following: circles = 2009, squares = 2010, diamonds = 2011, triangles = 2012 and inverted triangles = 2013.

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

There were substantial differences between conceptually equivalent taxonomic and functional diversity metrics when they were used to assess five-year temporal variation in dung beetle communities within habitat types (Fig. 3). In undisturbed forests and *Eucalyptus* plantation, species richness varied significantly more among years than FRic (Fig. 3a), whereas Pielou's evenness varied less than FEve in both undisturbed forest and native forest corridors – although the latter was not statistically significant (Fig. 3b). We also found higher variation in Simpson's diversity than Rao's entropy for undisturbed forest and forest corridors (Fig. 3c).
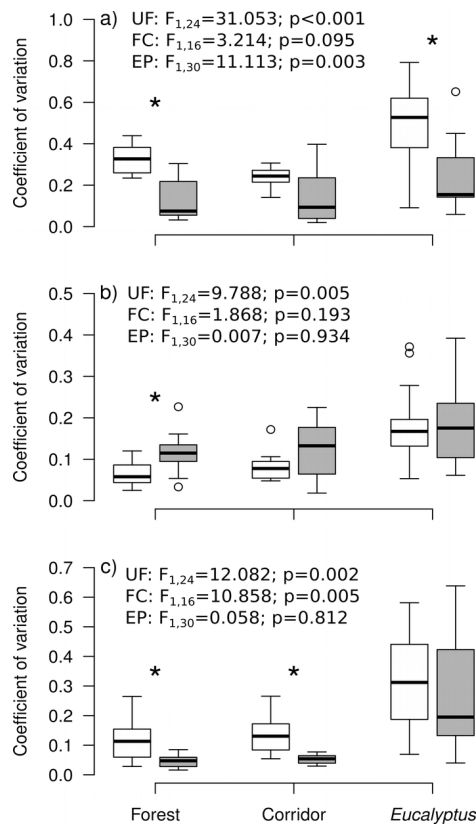
Fig. 3: Coefficient of temporal variation for pairs of conceptually similar taxonomic (white) and functional (grey) metrics of dung beetle communities in different habitat types over a five-year study period, showing a) species richness and Functional richness, b) Pielou's evenness and Functional evenness, and c) Simpson's diversity index and Rao's quadratic entropy; where 'UF' = undisturbed forest, 'FC' = primary forest corridor, and 'EP' = *Eucalyptus* plantation; stars indicate significant differences ($p < 0.05$) between taxonomic and functional diversity approaches within a given habitat type.

13

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

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

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

Fig. 4: Summarized results of global models showing the statistically significant variables (p<0.05). The metrics displayed in the boxes are those which we found difference among years ('Year' box), habitat types ('Habitat type' box) and the pattern of inter-annual variation was different among habitat type ('Year*Habitat type' box shows the interaction between explanatory variables).
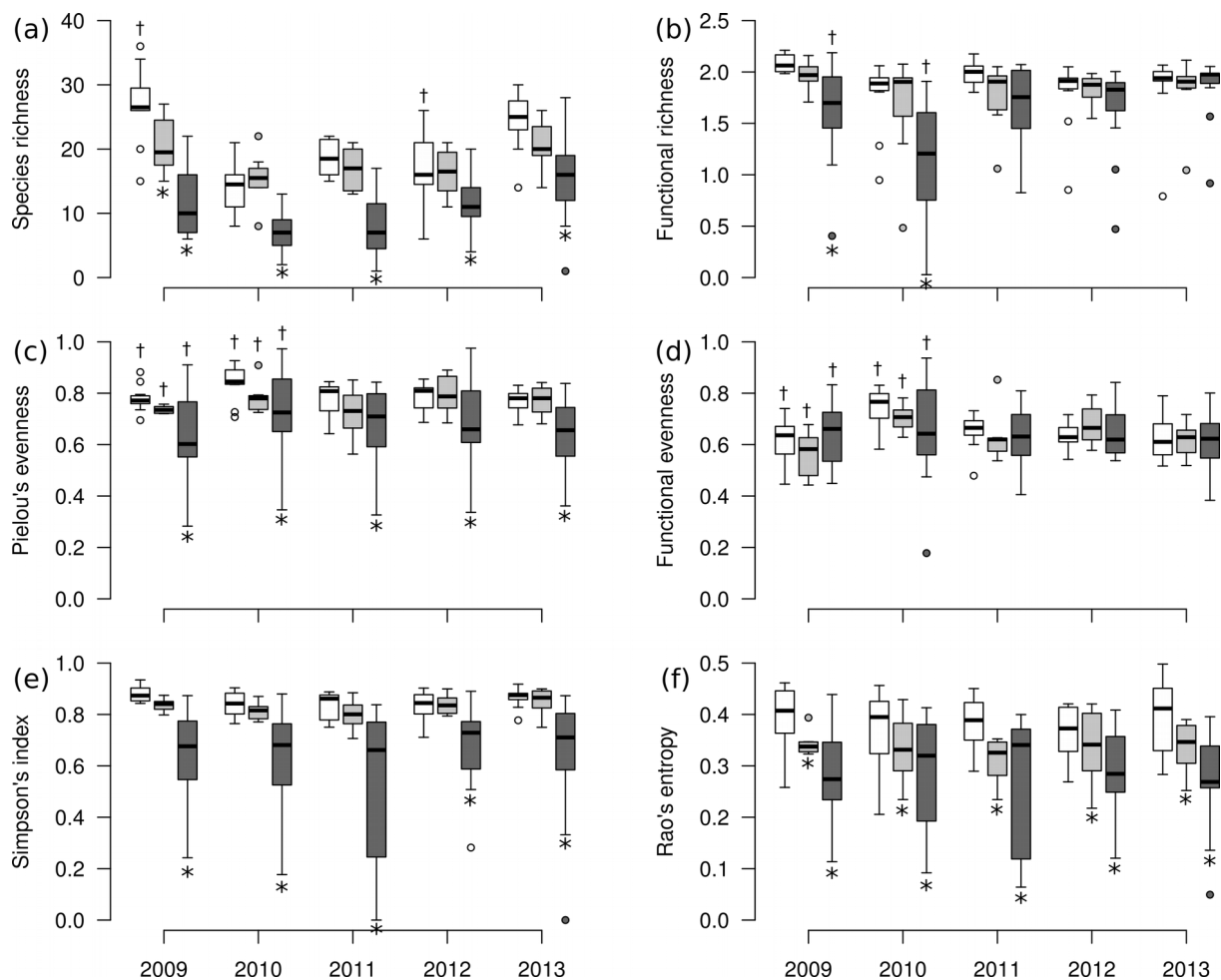
Fig. 5: Differences in diversity metrics for dung beetle communities among habitat types and between consecutive years for undisturbed forest (baseline; white boxes), forest corridors (light-grey boxes), and *Eucalyptus* plantations (dark-grey boxes) over five years, showing a) species richness, b) functional richness, c) Pielou's evenness, d) functional evenness, e) Simpson's diversity index, and f) Rao's quadratic entropy. Asterisks ('*') indicate significant differences ($p < 0.05$) between human-modified habitats and undisturbed forest in a given year; crosses ('†') represent significant dissimilarity between consecutive years within the same habitat type.

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

15

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 (Vílleger 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 (Vílleger 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

506

507　Conflict of interest: The authors declare that they have no conflict of interest.

508

509　Author Contributions: All authors contributed to the conception of ideas and hypotheses, and the

510　interpretation of results. Additionally, W.B. J.B. and J.L. designed the fieldwork; W.B. analysed the

511　data with input from E.J.S., E.M.S., J.B. and J.L. All authors contributed critically to the drafts and

512　gave final approval for publication.

513

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