

## **Short- and long-term temporal changes in the assemblage structure of Amazonian dung beetles**

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1 **Short- and long-term temporal changes in the assemblage structure of Amazonian**  
2 **dung beetles**

3

4 **Abstract**

5 Species diversity varies in space and time. Temporal changes in the structure and  
6 dynamics of communities can occur at different scales. We investigate the temporal  
7 changes of dung beetle assemblages in the Amazonian region along seasons, years, and  
8 successional stages. We evaluated if assemblage structure changes between temporal  
9 scales and whether such changes affect the functional structure of communities. To  
10 achieve these goals, we sampled dung beetles using linear transects of baited pitfall  
11 traps during the dry and rainy seasons at two natural reserves in the Amazon region,  
12 each representing different time scales: one covering successional variations (80, 30,  
13 five, and one years of recovery from logging) and the other one encompassing three  
14 consecutive years at two successional stages (20 and 10 years from logging). We used  
15 Generalized Linear Models to analyze interannual and successional changes in  
16 diversity, described assemblage structure with a NMDS, and examined compositional  
17 variation by partitioning beta diversity into its nestedness and turnover components.  
18 Abundance and richness decrease from the rainy to the dry season and towards earlier  
19 successional stages but do not differ between years. Assemblage diversity changes  
20 differently in interannual and successional scales. During succession, dung beetle  
21 assemblages change drastically, following a nested structure due to the appearance of  
22 species and functional groups in later successional stages. In contrast, functional group  
23 composition does not show consistent changes between years, displaying a turnover  
24 structure. This pattern supports non-deterministic changes in dung beetle assemblage  
25 structure along forest succession.

26

27 **Keywords** Beta diversity, Functional groups, Interannual variations, Nestedness,  
28 Scarabaeinae, Species turnover

29

## 30 **Introduction**

31 Species diversity varies across both space and time (Rosenzweig 1995). The structure  
32 and dynamics of communities vary at multiple temporal scales, from daily and seasonal  
33 changes to variations throughout geological periods (Villéger et al. 2011; Fritz et al.  
34 2013; Grøtan et al. 2014). Within short ecological time scales, local communities show  
35 regular and, to some extent, predictable seasonal variations, coupled with seemingly  
36 stochastic interannual changes (e.g., Grimbacher and Stork 2009; Labidi et al. 2012).  
37 Such stochasticity is produced by phenological and populational processes (e.g., Tanner  
38 et al. 2009; Hodgson et al. 2010) that are in turn dependent on interannual changes in  
39 climate and temporal variations in resource availability (e.g., Voss et al. 2009; Encinas-  
40 Viso et al. 2012). Over longer time periods, the effects of large-scale processes, such as  
41 climate change, biological invasions, or land transformation, also promote different  
42 kinds of responses and changes to community dynamics (see Forister et al. 2010;  
43 Dijkstra et al. 2011).

44 Long-term changes in community composition have been traditionally studied  
45 under the umbrella of ecological succession. In general, successions can be described as  
46 the non-random changes in the structure and composition of an ecological community  
47 that take place over time after a disturbance event (e.g., Walker and Del Moral 2003).  
48 Currently, many successions take place after habitat perturbations caused directly or  
49 indirectly by human activities (e.g., logging, agricultural intensification, or cattle  
50 expansion), and they are thought to have negative effects on biodiversity and its related

51 ecological functions, as well as on ecosystem services (Nichols et al. 2007; Horgan  
52 2008; Barragan et al. 2011; Braga et al. 2013).

53         The classical view of ecological successions hypothesizes that communities in a  
54 new or post-disturbed habitat are formed by a few pioneering species that are  
55 subsequently replaced by competitively dominant ones (Connell and Slatyer 1977). This  
56 hypothesis, initially proposed by Clements (1916), has received considerable support.  
57 However, its view of temporal community dynamics as a directional deterministic  
58 process has also been traditionally questioned (Walker and Del Moral 2003). Since the  
59 first criticisms of Gleason (1927), detractors of this idea argue that community  
60 dynamics are not completely deterministic, giving more relevance to historical  
61 contingencies and large-scale processes, such as the individualistic responses of species  
62 to the environment (Hortal et al. 2012). Under this paradigm, communities assemble  
63 from the dispersal of species that are present and/or arrive in the landscape, with local  
64 interactions playing a comparatively less important role. Here, local assembly becomes  
65 a density-dependent phenomenon, where the first arrivals correspond to species that are  
66 frequent and/or abundant in the landscape, receiving comparatively less rare species.  
67 Following this idea, the core-satellite species hypothesis (Hanski 1982) states that the  
68 first colonizers would become the core species (i.e., species that make up the bulk of the  
69 individuals of the local community), whereas the satellite species (i.e., species that hold  
70 small local abundances) would be the ones arriving to the community at a later stage.  
71 Although both the pioneering species and the core-satellite species hypotheses predict  
72 similar trends of temporal increase in the richness and abundance of communities, their  
73 predictions are markedly different in terms of temporal beta diversity patterns. The  
74 pioneering hypothesis predicts a temporal turnover between pioneer and replacement  
75 (i.e., non-pioneer) species (Connell and Slatyer 1977; Denslow 1980). Whereas the

76 core-satellite hypothesis expects that temporal changes in species composition should  
77 be mostly driven by a non-random gain of species leading to increasing richness, since  
78 satellite species would be sequentially added to the community (Menéndez 1994).  
79 Therefore, a preeminence of species replacement with time will be in accordance with  
80 the pioneering hypothesis, whereas a preeminence of nestedness will provide evidence  
81 for the core-satellite hypothesis. It follows that by studying temporal trends in beta  
82 diversity components (i.e., turnover and nestedness *sensu* Baselga 2010), it should be  
83 possible to elucidate the main process governing the (re)assembly of communities along  
84 short and long time periods.

85         The Amazon rainforest is the largest contiguous and most biodiverse tropical  
86 rainforest in the world, hosting a large proportion of known diversity (Peres et al. 2010).  
87 The spatial heterogeneity, seasonal regimes (e.g., pluviosity, river pulse, seasonal  
88 humidity and temperature), and anthropic disturbances that characterize the Amazonian  
89 region result in a complex mosaic of temporal and spatial changes in its communities  
90 (Andresen 2002; Noriega et al. 2007; Korasaki et al. 2013). During the last 50 years, the  
91 Amazon may have lost up to 29% of its forest cover due to an increase in deforestation  
92 for the creation of cattle ranches, agriculture, and logging (Peres et al. 2010; INPA  
93 2017). These activities have led to the appearance of a mosaic of habitat fragments  
94 holding communities ongoing different successional stages, which provide an ideal  
95 scenario for understanding how communities reassemble after disturbance (Braga et al.  
96 2013; Franca et al. 2016; Cajaiba et al. 2017).

97         Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are an excellent study  
98 system to explore temporal variations in biodiversity. They are sensitive to  
99 environmental changes and respond quickly to habitat destruction, fragmentation or  
100 isolation (Halffter and Arellano 2002; Barlow et al. 2007; Nichols et al. 2007). Indeed,

101 dung beetle abundance and richness are affected by human disturbance, usually  
102 following a gradient of increasing negative effects when moving from natural forests to  
103 secondary forests, plantations, and pastures (e.g., Howden and Nealis 1975; Barragan et  
104 al. 2011; Braga et al. 2013). By burying and using dung as both a food and nesting  
105 resource, dung beetles provide key ecological functions and services like nutrient  
106 cycling, soil fertilization and aeration, seed dispersal, and biological pest control  
107 (Andresen 2002; Bang et al. 2005; Nichols et al. 2008), which makes them important  
108 for economy and human welfare (Losey and Vaughan 2006). Therefore, they have been  
109 widely used as indicators for evaluating and monitoring spatial and temporal changes  
110 and the impact of disturbances on natural communities (e.g., Davis et al. 2001;  
111 McGeoch et al. 2002; Gardner et al. 2008; Otavo et al. 2013; Da Silva and Hernández  
112 2018; Noriega et al. 2020).

113 In this study we evaluate both interannual and successional trends in the  
114 diversity and composition of dung beetle assemblages in the Amazonian rainforest. To  
115 do this, we use data from two dung beetle surveys with different temporal extents: one  
116 including four successional stages with a temporal extent of 80 years (using a space-for-  
117 time substitution) and another including three consecutive years of sampling with two  
118 successional stages. We address the following specific questions: 1) Do diversity and  
119 assemblage structure change in short (interannual) and long (successional) temporal  
120 scales? 2) How different are beta diversity patterns between these two temporal scales?  
121 and 3) How do temporal changes affect the functional structure of dung beetle  
122 assemblages at these two scales?

123

## 124 **Materials and methods**

125 *Study sites*

126 Surveys were conducted in two nearby Natural Reserves of the Amazon basin, Palmari  
127 (Brazil) and Monilla (Colombia) (Fig. 1). The climate is humid with a mean rainfall of  
128 2500 mm and a mean annual temperature of 25 °C. The area has a monomodal  
129 pluviometric regime with two seasons: rainy – November to May ( $\geq 300$  mm/month  
130 average), and dry – June to October ( $\leq 100$  mm/month average). The two Natural  
131 Reserves are contiguous to indigenous human settlements, so they are subject to  
132 significant anthropic pressures that vary with their distance from the villages. These  
133 human settlements affect the forest in different ways and intensities: from cutting small-  
134 medium areas for “slash and burn” shifting cultivation (see below), to extracting big  
135 trees for construction and wood, to the collection of fruits and seeds, and occasionally  
136 hunting for food.

137 The first study area, used to characterize long-term successional changes, was  
138 located in the Palmari Natural Reserve (home of the Marubo indigenous community) in  
139 the municipality of Atalaia do Norte (4°17'1" S - 70°17'0" W, 77 m a.s.l.), 22 km from  
140 the city of Benjamin Constant, in the Brazilian state of Amazonas (Fig. 1). Here we  
141 sampled four types of habitats, representing a long-term successional recovery from  
142 human-induced disturbances: *primary forest*, with ~80 years of recovery after logging;  
143 *secondary forest*, with ~30 years of recovery after logging; an *old chagra*, abandoned  
144 approximately 5 years before sampling; and a *new chagra*, abandoned the same year of  
145 the sampling. Here, “*chagras*” are forest areas that were completely cut and burn in a  
146 “slash and burn” shifting cultivation regime used for different types of crops like  
147 cassava, maize, rice, sugarcane, soybean, and plantain (see van Vliet et al. 2013).

148 The second study area, used to characterize both short-term yearly variations and  
149 short-term successional changes, was located in the Monilla Amena Natural Reserve  
150 (herein Monilla; home of Ticuna indigenous community), in the municipality of Leticia

151 (4°06'46" S - 69°55'52" W, 60 m a.s.l.), 9.5 km from the city of Leticia, in the  
152 Colombian state of Amazonas (Fig. 1). We assessed differences in short-term temporal  
153 variations (i.e., between sampling years, see below) by sampling this locality during  
154 three consecutive years. In addition, we evaluated whether these between-year  
155 differences are similar in different moments of long-term community evolution by  
156 doing these surveys in two different successional stages, *secondary old forest* and  
157 *secondary new forest*, with approximately 20 and 10 years of recovery after logging,  
158 respectively. This also allows us to evaluate whether the successional changes  
159 eventually identified in the Palmari dataset hold up in other similar communities, rather  
160 than responding to local idiosyncrasies.

161

#### 162 *Dung beetle sampling and processing*

163 Dung beetle assemblages were sampled in Palmari in April (herein dry season) and  
164 September (herein rainy season) 2009. Surveys were conducted using one linear  
165 transect of 10 pitfall traps in each type of habitat (primary forest, secondary forest, old  
166 chagra, and new chagra) with 50 m between traps (following Larsen and Forsyth 2005).  
167 The pitfall traps were baited with 30 g of a 1:1 mixture of human and pig dung (a  
168 combination that allows high quantities of bait with a high attraction level). In Monilla,  
169 dung beetle assemblages were sampled during three consecutive years (2002, 2003, and  
170 2004), in the same months and seasons than in Palmari (April, dry season; and  
171 September, rainy season). In this case, because of the large extension of the forest, the  
172 sampling was conducted using 10 linear transects of 10 pitfall traps in each type of  
173 habitat (secondary old forest and secondary new forest) with 10 m between each trap  
174 and 20 m between transects (see Noriega et al. 2007). The pitfall traps were baited with  
175 30 g of carrion or human dung. Due to the short distance between traps, and in order to



176 make both datasets more comparable, the sampling unit was considered to be the trap in  
177 the case of Palmari and the entire transect in Monilla (n=10 per habitat type and  
178 season).

179         The model of the pitfall trap (plastic containers with the bait hanging above the  
180 trap; see Noriega and Fagua 2009) and the time that the traps were active in the field (48  
181 hours) were the same in both localities. The dung beetle specimens collected were  
182 stored in 70% alcohol and identified to species level using several taxonomic keys  
183 (Edmonds 1994; Genier 1996; Cook 2002; Edmonds and Zidek 2004, 2010; Camero  
184 2010; Vaz-de-Mello et al. 2011; Cupello and Vaz-de-Mello 2013) and expert support.  
185 After identifying and labelling all the specimens, the ones from Palmari were deposited  
186 at the Natural History Museum of Los Andes University, Bogotá (EANDES), and those  
187 from Monilla at the Natural History Museum of the Pontificia Javeriana University,  
188 Bogotá (MPUJ).

189         All individuals were assigned to functional groups based on the dung beetle  
190 functional classification proposed by Doube (1990), which combines their main food  
191 relocation strategies (i.e., guilds) with the size of the individuals. We inferred dung  
192 beetle guilds from the food relocation behavior known for each genus, assigning each  
193 species to one of the three distinct guilds: paracoprids (or tunnelers), which dig under  
194 the dung pile and make tunnels where they relocate a brood mass of dung; telecoprids  
195 (or rollers), which construct a brood ball in the dung pile, roll it apart from the main  
196 source, and bury it; and endocoprids (or dwellers), which nest and feed exclusively  
197 inside the dung pats or build their nests right beneath the resource in the dung-soil  
198 interface (Halffter and Matthews 1966; Halffter and Edmonds 1982; Cambefort and  
199 Hanski 1991). Average body size was measured from the captured individuals as the  
200 total length from the external border of the clypeus to the pygidium for each species,

201 with recourse to the literature for species with low abundances. These measurements  
202 were performed using an electronic digital caliper (Powerfix – Z22855,  $\pm 0.01$  mm).  
203 Each species was assigned to one of the three size categories (defined by the gaps in  
204 species' body size; see Appendix S1): Large ( $>18$  mm), Medium (10–18 mm), and  
205 Small ( $<10$  mm). We combined guilds and average body size into nine functional  
206 groups (Appendix S1): large paracoprids, medium paracoprids, small paracoprids, large  
207 telecoprids, medium telecoprids, small telecoprids, large endocoprids, medium  
208 endocoprids and small endocoprids.

209

#### 210 *Data analysis*

211 We described dung beetle assemblages for each year, season, and type of forest by total  
212 abundance, richness, and the abundance of each species and functional group. We  
213 assessed inventory completeness as the percentage of the estimated total species  
214 richness that were observed in each locality (Lobo 2008) to ensure that the surveys  
215 attained a fair description of the studied assemblages. We estimated total species  
216 richness with four nonparametric estimators (ACE, ICE, Chao 1, and Jackknife 1) that  
217 are commonly used to characterize dung beetle communities for the ease of comparison  
218 with other studies. All estimators were calculated with EstimateS v 9.1.0 (Colwell  
219 2016).

220 We explored whether dung beetle species richness and abundance vary through  
221 time using generalized linear models (GLMs) on each one of these diversity attributes at  
222 the sampling unit level, as a function of successional stages in the Palmari dataset, and  
223 as a function of sampling year and successional stage in the Monilla dataset. In both  
224 datasets we also included the season as a predictor variable. We conducted this analysis  
225 separately for the diversity attributes related with species diversity and functional group

226 diversity. We assumed a Poisson error distribution to fit richness and abundance  
227 models, following a backward model selection based on Akaike Information Criterion  
228 corrected by sample size (Burnham and Anderson 2002; AICc).

229         We described temporal variations in assemblage composition with a non-metric  
230 multidimensional scaling ordination (NMDS) performed on matrices of sampling sites  
231 by species and by functional groups. To avoid an excessive influence of rare taxa,  
232 species with less than 5% occurrences were excluded from the NMDS analysis (see  
233 McCune and Grace 2002). Data were subject to Wisconsin double standardization,  
234 where each value is first standardized by the column maximum (i.e., for each species or  
235 functional group), abundance is divided by its largest value in the surveys before being  
236 standardized by the row total (i.e., for each trap), and species or functional group  
237 abundance is divided by the total abundance of all species or functional groups in that  
238 sampling unit. We used the Bray-Curtis index to measure the dissimilarity in species or  
239 functional groups between the two datasets. We assessed the goodness of fit of the  
240 ordination through the percentage of variance represented (see McCune and Grace 2002  
241 for details). To select the main factor affecting assemblage composition, we performed  
242 Spearman correlations between the NMDS axes resulting from previous analyses and  
243 the potential explanatory variables (Matos et al. 2015). We also analyzed the  
244 relationship between the NMDS ordination and the explanatory variables through vector  
245 fitting. Then, those variables presenting significant correlations were overlaid in the  
246 NMDS ordination (McCune and Grace 2002; Oksanen 2009).

247         Compositional variations in assemblage structure were evaluated based on the  
248 nestedness and turnover components of beta diversity patterns using the indices  
249 proposed by Baselga (2010):  $\beta_{SIM}$  (Simpson dissimilarity – spatial turnover),  $\beta_{NES}$   
250 (nestedness dissimilarity), and  $\beta_{SOR}$  (Sørensen dissimilarity – total Beta diversity).

251 These dissimilarity measures are additive fractions, so  $\beta_{\text{SOR}} = \beta_{\text{SIM}} + \beta_{\text{NES}}$ . Specifically, we  
252 measured nestedness and turnover for each pair of sampling units belonging to different  
253 time periods. Then, we measured beta diversity between consecutive periods and for  
254 each season and successional stage (in the case of Monilla dataset) independently.  
255 Finally, we used a Wilcoxon matched-pairs test to explore if nestedness and turnover  
256 measures differ between different pairs of time periods.

257 All analyses were performed in R v. 3.1.1 environment (R Development Core  
258 Team 2016), through different packages: *lsmeans* package (Lenth 2016) for the least-  
259 squares means; the functions *metaMDS* and *envfit* of *vegan* package (Oksanen et al.  
260 2013) for NMDS; and *betapart* package (Baselga and Orme 2012) in the case of beta  
261 diversity components.

262

## 263 **Results**

264 A total of 1,073 individuals were collected in Palmari, representing 34 species from 12  
265 genera and six tribes (Table 1). The most abundant species in this site were *Dichotomius*  
266 cf. *boreus* (Olivier, 1789), *Dichotomius* cf. *fortestriatus* (Luederwaldt, 1923), and  
267 *Onthophagus haematopus* Harold, 1875, which altogether encompass about a third of  
268 total abundance. In Monilla surveys rendered 822 individuals from 35 species belonging  
269 to 13 genera and six tribes (Table 1). In this case, the most abundant species were  
270 *Sylvicanthon aequinoctialis* (Harold, 1868), *O. haematopus*, and *Canthon luteicollis*  
271 Erichson, 1847, together constituting more than 40% of all individuals. The percentages  
272 of total species covered by the surveys were between 85.2 and 100% for Palmari and  
273 73.6–98.9% for Monilla, indicating that sampling effort was sufficient to cover most of  
274 the assemblage (Appendix S2).

275

276 *Abundance and species richness*

277 Regarding successional variations, both richness and abundance increased along  
278 successional stages. In Palmari, primary forest held the highest recorded species  
279 richness and abundance (33 species, 14 of them unique, and 699 individuals), followed  
280 by secondary forest (19 species, one of them unique, 249 individuals), old chagra (10  
281 species, 99 individuals) and new chagra (7 species, 26 individuals); neither of the two  
282 chagras had unique species (Table 1). In Monilla, richness and abundance were also  
283 higher at the secondary old forest (31 species, 17 of them unique, and 671 individuals),  
284 compared with the secondary new forest (18 species, five of them unique, and 151  
285 individuals) (Table 1).

286 When considering yearly variations, in general, abundance did not differ  
287 substantially between years within neither habitat (i.e., successional stage) nor season in  
288 the Monilla dataset; however, it varied in the rainy season of one of the years for both  
289 habitats, remaining nonetheless similar between years for both habitats during the dry  
290 season (Fig. 2b, Appendix S3). Richness did not vary significantly between years for  
291 each combination of habitat and season (Fig. 2d, Appendix S3).

292 Both seasons show similar patterns of variation in abundance and species  
293 richness in both datasets (Fig. 2). In general, abundance and species richness decreased  
294 from rainy to dry season, when dung beetle faunas seemingly tend to homogenize along  
295 successional stages. During the dry season all stages presented low abundances in  
296 Palmari, and the two chagras did not differ in neither abundance nor richness (Fig.  
297 2a,c). These patterns were similar in Monilla, where the differences in abundance and  
298 richness between the old and the new forest were lower, though significant during the  
299 dry season (Figs. 2b,d, Appendix S4). Indeed, the interaction between season and  
300 successional stage was the best supported model for richness, and a model describing

301 the joint effects of seasons and successional stages was in both datasets the best model  
302 for abundance (Appendix S3).

303

#### 304 *Assemblage composition*

305 The main variations in species composition described by NMDM ordinations can be  
306 summarized by axes related to successional and seasonal gradients in both datasets (Fig.  
307 3a and 3b). At Palmari, the two first axes (final stress = 0.17, total variability explained  
308 = 56%; Fig. 3a) identify a seasonal gradient between the rainy and the dry season, and a  
309 successional gradient from the new chagra to the primary forest (see Appendix S4). In  
310 Monilla, the obtained NMDS axes (final stress = 0.16, total variability explained = 52%;  
311 Fig. 3b) were not related with variations throughout sampling years, but rather with  
312 easily-identifiable successional and seasonal gradients like the Palmari dataset—  
313 although in this case these changes are summarized by the combination of both NMDS  
314 axes (Appendix S4).

315         Nestedness and turnover (i.e.,  $\beta_{\text{NES}}$  and  $\beta_{\text{SIM}}$ ) markedly changed between long  
316 and short temporal scales, showing that compositional changes are fundamentally  
317 different for these two distinct time scales. Nestedness is influential in the long  
318 successional gradient of Palmari (Figs. 4a,c), driven by a steep reduction of richness  
319 along the habitat disturbance gradient mainly due to the loss of rare species (while 14  
320 species are unique to the primary forest, only one is unique for the new chagra). On the  
321 contrary, in the shorter temporal scales of the interannual variations at Monilla, beta  
322 diversity is mainly driven by a true turnover of species (Figs. 4b,d). Nonetheless,  
323 compositional differences are attenuated in both datasets during the dry season, a period  
324 when there were almost no differences of beta diversity between years (see Appendix  
325 S5 for results regarding the dry season and total  $\beta_{\text{SOR}}$ ).

326

327 *Functional diversity and structure*

328 Both study sites presented all nine functional groups, defined according to resource  
329 allocation behavior and body size, but their patterns of diversity along temporal changes  
330 differ between datasets (Table 1). In Palmari, more than half of the functional groups  
331 (small paracoprids and endocoprids, and all telecoprids) appear towards the latter stages  
332 of the succession, while the composition of functional groups is maintained between  
333 years in Monilla, corroborating that responses to succession are fundamentally different  
334 from interannual variations. In general, paracoprids were dominant in Palmari, although  
335 some functional groups appear with increasing successional maturity: large paracoprids  
336 are exclusive of the primary forest, small telecoprids and small endocoprids appear only  
337 on the secondary forest, and medium telecoprids and small paracoprids do so at the old  
338 chagra (Table 1). This contrasts with Monilla, which is dominated by small paracoprids  
339 and medium and small telecoprids, and only the former functional group appears in the  
340 older successional stage, while the only large endocoprid species (*Eurysternus velutinus*  
341 Bates, 1887) appears just in the secondary new forest (Table 1).

342         The abundance of all functional groups (except large telecoprids) increased  
343 significantly with habitat succession in Palmari in the rainy season, while small and  
344 large paracoprids and medium endocoprids were the only groups showing abundance  
345 differences between successional stages in Monilla (Fig. 5j, 5l, 5q). Also, there was an  
346 important decrease in abundance—accompanied with a functional homogenization of  
347 the successional stages—from the rainy to the dry season in most functional groups in  
348 both datasets, except for large telecoprids in Palmari and small telecoprids in Monilla  
349 (Fig. 5f and 5j, respectively). Such successional and seasonal variability contrasts with  
350 the interannual similarity in the abundance of functional groups found in the Monilla

351 dataset, which holds up for all groups except for medium telecoprids and endocoprids in  
352 the secondary old forest during the rainy season (Fig. 5n and 5q). In fact, medium  
353 telecoprids were the only functional group showing a distinct response, with changes in  
354 abundance between years, successional stages, and seasons (Fig. 5n).

355         The NMDS ordinations describing variations in functional group composition  
356 for both datasets identified similar gradients of joint successional and seasonal change,  
357 from the young stages in dry season to old stages in the rainy season. In Palmari, the  
358 two axes selected (final stress = 0.17, total explained variability = 61%) show an  
359 increasing trend in all types of telecoprids and small endocoprids in both the rainy  
360 season and the older stages of the successional gradient (Fig. 3c, Appendix S4). In  
361 Monilla (two NMDS axes, final stress = 0.19, total explained variability = 52%), the  
362 first axis selected was not correlated with any of the explanatory variables studied, but  
363 the second was clearly related with both successional and seasonal variations, showing a  
364 gradient of functional change from new forest assemblages in the dry season to old  
365 forest assemblages in the rainy season (Appendix S4). Here, small and medium  
366 telecoprids and small endocoprids are related with secondary old forest, while large  
367 endocoprids and telecoprids and medium paracoprids are related with the rainy season  
368 (Fig. 3d).

369

## 370 **Discussion**

371 Our results show that changes in assemblage structure are fundamentally different  
372 between interannual and successional temporal scales, but they also show that there is  
373 some coherence between seasonal and successional variations. Amazon dung beetles  
374 present relatively similar trends towards higher abundance, richness, and functional  
375 diversity both in the older successional stages and during the rainy season. Another



376 important result is the almost negligible effect of interannual variations for the overall  
377 diversity and structure of the assemblage, which is limited to significant species  
378 turnover between years. In contrast, composition and diversity change in a more  
379 estimated way throughout the succession, as variations between successional stages  
380 show a clear nested structure. Indeed, changes in functional group structure are also  
381 different between time scales, with drastic shifts throughout succession and seasonally  
382 (with some groups disappearing from assemblages), which contrast with the  
383 maintenance of functional structure at short temporal scales despite changes in the  
384 identity of some of the species.

385

#### 386 *Successional variations in assemblage diversity, composition and structure*

387 The increase of perturbation in Amazon forests generates poor dung beetle assemblages  
388 in terms of both abundance and species richness (Barragan et al. 2011; Braga et al.  
389 2013; Beiroz et al. 2017), a well-known trend that we also identify in both Palmari and  
390 Monilla. This decay in diversity could be related to the loss of vegetation cover,  
391 changes in soil texture, and the disappearance of vertebrate fauna that affects resource  
392 availability and drastically changes the microclimatic conditions for dung beetles  
393 (Andrade et al. 2011; Beiroz et al. 2017; Cajaiba et al. 2017; Ferreira et al. 2019). Many  
394 low-intensity anthropogenic disturbances (e.g., reduced-impact logging, moderate  
395 hunting, or logging roads) may also affect negatively dung beetle assemblage structure  
396 (Bicknell et al. 2014; Feer and Boissier 2015; Edwards et al. 2017) and alter ecological  
397 functions (Hosaka et al. 2014). This result is a clear nested pattern of compositional  
398 change over the long temporal scales of succession, contrasting with the turnover that  
399 defines the compositional variation at the short interannual time scales studied in the  
400 Monilla dataset (Fig. 6; see below).

401           This nested pattern along successional stages suggests an effect of a non-random  
402 species loss towards increasingly disturbed habitats. Indeed, some eurytopic species  
403 (i.e., species with wide habitat requirements, such as *Dichotomius mamillatus* (Felsche,  
404 1901), *Dichotomius* cf. *boreus*, or *Sylvicanthon aequinoctialis*) seem to be able to  
405 pioneer the recovery of dung beetle assemblages after disturbance by persisting in the  
406 majority of successional stages. In contrast, some stenotopic species (i.e., species with a  
407 narrow habitat requirement, such as *Canthon luteicollis*, *Deltochilum* aff. *pseudoparile*  
408 Paulian, 1938, or *Onthophagus rubrescens* Blanchard, 1843) are probably more  
409 sensitive and restricted to the less disturbed habitats of the later successional stages. The  
410 ability of colonizing habitats at different levels of disturbance may be the result of  
411 several local factors that constrain assemblage structure, whose importance decreases  
412 along the succession. These include loss of vegetation cover, abundance, diversity of the  
413 available resources, and a significant change in microclimatic conditions related to open  
414 areas (i.e., loss of humidity, increase of temperature, changes in soil texture, etc.; Beiroz  
415 et al. 2017).

416           The anthropic pressure represented along the succession gradient also affected  
417 the functional structure of the assemblages. Functional group richness is known to  
418 decrease in disturbed areas as a result of changes in land use (Barragan et al. 2011,  
419 Beiroz et al. 2018). In our study, some functional groups are absent or rare in the most  
420 perturbed successional stages, especially those that include larger species. The loss of  
421 large dung beetles is a common trend that occurs in several ecosystems and regions due  
422 to the increase in anthropic perturbations (e.g. Lobo 2001, Tonelli et al. 2018). These  
423 changes result in the existence of gradients in the composition of functional groups  
424 found in our NDMS analyses. Interestingly, while the different functional groups of  
425 telecoprids and endocoprids show a successional (and seasonal, see below) replacement,

426 paracoprids show no evident correlation with the succession. Under Hanski's (1982)  
427 core-satellite hypothesis (see below), this could be attributed to many species with this  
428 nesting behavior being "core" elements of the community that are present since the  
429 beginning of assembly after the disturbance occurs.

430 Different responses of dung beetle functional groups to ecological pressures are  
431 commonly found in the studies addressing the (generally negative) effects of habitat  
432 disturbance on dung beetle diversity in the Neotropics (Andresen 2005; Horgan 2008;  
433 Barragan et al. 2011; Braga et al. 2013; Nichols et al. 2013; Da Silva and Hernández  
434 2015; Beiroz et al. 2017). Indeed, Audino et al. (2014) established that more than 18  
435 years of recovery are needed to restore the functional diversity of dung beetle  
436 assemblages in tropical rain forests. Here, it is essential to include the identity of species  
437 and functional groups to understand restoration processes (Tonelli et al. 2020).  
438 Following our results and taking into consideration the successional process in Palmari,  
439 it is evident that, although some species from mature forest communities may endure  
440 disturbance, full recovery of species richness, abundance, and functional group diversity  
441 may take more than 30 years. Nonetheless, it is important to note that the analyses of  
442 succession based on space-for-time substitution may underestimate the negative  
443 consequences of human impact on local species diversity (Franca et al. 2016).

444

#### 445 *Interannual turnover*

446 In general, our results indicate that the diversity, composition, and structure of dung  
447 beetle assemblages change significantly more between successional stages and seasons  
448 than between years. Indeed, beta diversity between years in Palmari is mainly due to the  
449 turnover component of compositional variation. This pattern of apparently random  
450 species replacement can be related with the existence of climatic or biotic factors (such

451 as unpredictable start of rains, strong variations in dry season rainfall, or a big reduction  
452 in food resources) that might affect the phenological cycles or generate local population  
453 declines and/or peaks. Besides the intrinsic environmental stochasticity of small time  
454 periods, these factors can include: species of longer phenological cycles (i.e., supra-  
455 annual cycles; cycles that took more than a year for the larvae to become an adult),  
456 explosive population outbursts (i.e., species that appear in high numbers during a brief  
457 window of time associated with complex life history cycles), or the presence of rare  
458 species that are active during very narrow windows of time (Wolda 1988; Ribeiro and  
459 Freitas 2011; Kishimoto-Yamada and Itioka 2015). Other groups like butterflies have  
460 life cycles longer than a year (Grøtan et al. 2014), evidencing the importance of  
461 sampling during longer time periods.

462         The differences between interannual and successional changes in Amazonian  
463 dung beetle communities have been seldom studied. The only study also addressing  
464 both temporal scales that we are aware of also reports large interannual oscillations  
465 during five years at an Amazonian primary forest (Beiroz et al. 2017), contrasting with  
466 the relatively constant turnover between years we found in Monilla. However, in this  
467 same study, dry season fauna in poorer years were comparable between primary forest  
468 and disturbed areas (Beiroz et al. 2017), showing a pattern of biotic homogenization of  
469 early and late successional stages with seasonality that coincides with the coherent  
470 successional-seasonal gradient we found. Indeed, despite the relatively short time period  
471 of our study in Monilla, the turnover between these three years could also be related to a  
472 small forest recovery that translates into an increase in the number of species between  
473 2002 and 2004 (from 30 to 34 species, 5 new species appear and one disappears),  
474 similar to Beiroz et al. (2017) findings for their study area. Actually, the number and  
475 composition of functional groups in the Monilla dataset do not vary between years,

476 which is congruent with the remarkable interannual stability in the relative abundance  
477 of functional groups found by these authors (Beiroz et al. 2017). Indeed, other studies  
478 exploring functional diversity trends after long temporal periods (i.e. 34 or 35 years; see  
479 Escobar et al. 2008 and Cuesta & Lobo 2019) did not find significant shifts in the  
480 composition of functional groups, reporting only changes in the proportion of  
481 individuals of each group, possibly connected with the effect of human activities.

482

#### 483 *Similarities between seasonal and successional gradients*

484 Strikingly, the importance of the community enrichment along the successional process  
485 is relatively similar to that of the seasonal gradient towards more abundant and diverse  
486 assemblages in the rainy season. This common trend is particularly consistent for  
487 functional structure and is likely related with the biotic homogenization promoted by  
488 the low productivity characteristic of both disturbed habitats (see above) and the dry  
489 season (see Hernández and Vaz-de-Mello 2009). Dung beetle assemblages are  
490 characterized by a strong seasonality (e.g., Hernández and Vaz-de-Mello 2009; Andrade  
491 et al. 2011; Lopes et al. 2011; Labidi et al. 2012; Viega et al. 2014), where the species  
492 active during the dry season represent an impoverished sample (i.e., a subsample) of  
493 those found during the rainy season (Agoglitta et al. 2012). In tropical rain forests, fruit  
494 and green leaf production peaks during the hot-humid season, increasing the amount of  
495 resources available for mammals and consequently the amount of excrements available  
496 for dung beetles (Estrada et al. 1993). In contrast, during the dry season, dung  
497 production is lower and its distribution is less spatially aggregated, with fewer dung  
498 pads being available and becoming drier faster due to climatic conditions (Andresen  
499 2005). However, some studies have found little seasonal variation in dung beetle  
500 abundance, richness, and assemblage structure in the humid forests of the Amazon

501 region (Gardner et al. 2008; Korasaki et al. 2013). Following the results of Berioz et al.  
502 (2017), such small seasonal variations may be an effect of the stochastic interannual  
503 variations in climate, where climatically milder years allow the maintenance of richer  
504 faunas throughout the whole year (see also Ferreira et al. 2019).

505

506 *A matter of core and satellite species and functional groups*

507 Our results point to the importance of core rather than pioneering species along the  
508 successional gradients. The pioneering hypothesis predicts a strong temporal turnover  
509 between early successional stages and later stages, following a sequence of species over  
510 time (i.e., a deterministic process from few pioneer species to competitively dominant  
511 non-pioneering species: “Pioneer hypothesis”; Connell and Slatyer 1977). In contrast,  
512 dung beetle assemblages from Palmari indicate a negligible turnover and strong  
513 nestedness along the successional gradient, with early stages acting as species-poor sub-  
514 samples of the later and richer stages (Fig. 6). This nested structure is consistent with  
515 the core-satellite species hypothesis proposed by Hanski (1982) and found in the few  
516 studies that analyzed this hypothesis in dung beetle assemblages (e.g., Menendez 1994).  
517 This hypothesis states that communities are primarily formed by an initial assembly of  
518 core species, which are widely distributed, locally frequent and/or abundant, and better  
519 adapted to environmental changes; satellite species, which present a patchy distribution  
520 and are locally rare and less adapted to environmental changes, are sequentially added  
521 to the assemblage (Hanski 1982). This consistency with a core-satellite pattern suggests  
522 that changes in dung beetle assemblage composition in the Amazon are not only a  
523 consequence of deterministic successional processes but also of context-dependent  
524 historical contingencies and neutral assembly of the species that are more abundant in  
525 the landscape.

526           Although patterns of successional change are seemingly not deterministic, they  
527 may have consequences for the functional structure of the assemblages. The species that  
528 could be playing the role of “core species” are medium-large paracoprids (such as *D.*  
529 *mamillatus*, *D. cf. boreus*, or *D. cf. fortistriatus* in the Palmari dataset) and medium-  
530 large endocoprids (e.g., *Eurysternus* spp.), whereas those seemingly acting as “satellite  
531 species” are small-large telecoprids (e.g., *Canthon smaragdulus* (Fabricius, 1781),  
532 *Deltochilum amazonicum* Bates, 1887, or *D. aff. pseudoparile*) and small paracoprids  
533 (e.g., *Ateuchus* and *Uroxys* spp.). Large paracoprids show the highest performance in  
534 terms of dung removal in the ecosystem (Slade et al. 2007), so their presence from the  
535 beginning would guarantee the maintenance of an important part of ecosystem  
536 functionality. In contrast, large telecoprids, which are more important for seed dispersal  
537 (Andresen 2002; Vulinec 2002), may be more vulnerable to habitat transformations  
538 (Lobo 2001; Nichols et al. 2013), appearing only in the later successional stages and  
539 well-preserved patches. This is congruent with our results which show a perceptible  
540 sequence in the dominance of different functional groups along successional stages,  
541 shifting first from paracoprids to endocoprids, and then towards large telecoprids. These  
542 sequences may relate to either species’ specific ecological and physiological  
543 requirements or some type of guild facilitation in terms of assemblage structuring,  
544 which may affect ecosystem functionality. However, these hypotheses need to be tested  
545 in the field with a mesocosm experimental design. Regardless of the existence of a  
546 succession or not, a complete set of all functional groups is required in order to  
547 maximize ecosystem functioning (Slade et al. 2007; Braga et al. 2013; Milotic et al.  
548 2018).

549

550 *Caveats*

551 Although Palmari and Monilla are located nearby (approx. 30 km, see Fig. 1), they  
552 show small differences in species composition. However, we believe that despite such  
553 differences these two localities provide accurate representations of the variability in  
554 central Amazonian dung beetle assemblages at different temporal scales. Note that  
555 Korasaki et al. (2013) collected more species than us in a compositionally similar  
556 locality near Palmari, possibly due to the lower numbers of traps (80 vs. ~450),  
557 sampling points (4 vs. ~14-18), and habitats (4 vs. 6) sampled in our study. In any case,  
558 the differences between Palmari and Monilla study sites could be related to eventual  
559 variations in the soil and forest composition, because they belong to different  
560 geomorphological plates (Pebas formation at Palmari and Nauta formation at Monilla)  
561 with different evolutionary histories (Higgins et al. 2011). Differences could also be  
562 related with some distinctive methodological aspects between the two datasets, such as  
563 sampling years and types of bait. We believe that the effects of these differences are  
564 small, so the dissimilarities in the assemblages captured in this study correspond to the  
565 different temporal factors that we studied, allowing the comparison in terms of the  
566 magnitude of compositional change in the two datasets. Note that the differences  
567 between sampling designs in the two study sites are due to the specific questions  
568 addressed in each site (either successional or interannual changes). Despite these  
569 differences, the clear contrast between successional and interannual scales found in this  
570 study give us confidence about the reliability of our results.

571

## 572 **Conclusions**

573 In summary, dung beetle richness, abundance, and composition of functional groups  
574 differ between short and long temporal scales. In long-term successional scales, dung  
575 beetle assemblage structure changes significantly through time, following a nested



576 structure and causing many species and some of the functional groups to disappear in  
577 highly disturbed areas. Seasonal changes may follow the same structure, at least to some  
578 extent. On the contrary, in short interannual temporal stages richness and functional  
579 group composition remain stable, as the turnover between years only affects the identity  
580 of some species. Indeed, our results show that dung beetle assemblages in the Amazon  
581 region are highly dynamic in time but with contrasting structural beta diversity patterns  
582 depending on the processes involved in temporal changes. This evidence stresses the  
583 importance of promoting long-term studies (especially long-term trapping) that include  
584 temporal beta diversity analysis in order to elucidate insect community dynamics. The  
585 inclusion of temporal dynamics in sampling protocols and monitoring studies could  
586 favor the confidence and completeness of biodiversity inventories, positively affecting  
587 conservation planning strategies (Hewitt et al. 2016). Moreover, it is necessary to study  
588 the recovery process of ecological functions in restoration chronosequences,  
589 incorporating functional trait data to fully understand the re-establishment and resilience  
590 capacity of Amazon rain forests. This enhanced knowledge on the functional dynamics  
591 of this hyperdiverse biome will eventually aid specific management and long-term  
592 conservation strategies.

593

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615

## 616 **References**

- 617 Agoglitta R, Moreno CE, Zunino M, Bonsignori G, Dellacasa M (2012) Cumulative  
618 annual dung beetle diversity in Mediterranean seasonal environments. *Ecol Res*  
619 27:387-395.
- 620 Andrade RB, Barlow J, Louzada J, Vaz-de-Mello FZ, Souza M, Silveira JM, Cochrane  
621 MA (2011) Quantifying responses of dung beetles to fire disturbance in tropical  
622 forests: the importance of trapping method and seasonality. *PlosOne* 6:e26208.
- 623 Andresen E (2002) Dung beetles in a Central Amazonian rainforest and their ecological  
624 role as secondary seed dispersers. *Ecol Entomol* 27:257-270.

625 Andresen E (2005) Effects of season and vegetation type on community organization of  
626 dung beetles in a tropical dry forest. *Biotropica* 37:291-300.

627 Audino LD, Louzada J, Comita L (2014) Dung beetles as indicators of tropical forest  
628 restoration success: Is it possible to recover species and functional diversity? *Biol*  
629 *Conserv* 169:248-257.

630 Bang HS, Lee JH, Kwon OS, Na YE, Jang YS, Kim WH (2005) Effects of paracoprid  
631 dung beetles (Coleoptera: Scarabaeidae) on the growth of pasture herbage and on  
632 the underlying soil. *App Soil Ecol* 29:165-171.

633 Barlow J, Gardner TA, Araujo IS, Avila-Pires TC, Bonaldo AB, Costa JE, Esposito  
634 MC, Ferreira LV, Hawes J, Hernandez MIM, Hoogmoed MS, Leite RN, Lo-Man-  
635 Hung NF, Malcolm JR, Marins MB, Mestre LAM, Miranda-Santos R, Nunes-  
636 Gutjahr AL, Overal WL, Parry L, Peters SL, Ribeiro-Junior MA, Da Silva MNF,  
637 Motta CS, Peres CA (2007) Quantifying the biodiversity value of tropical  
638 primary, secondary and plantation forests. *Proc Nat Acad Sci USA* 104:18555-  
639 18560.

640 Barragan F, Moreno CE, Escobar F, Halffter G, Navarrete D (2011) Negative impacts  
641 of human land use on dung beetle functional diversity. *PlosOne* 6:e17976.

642 Baselga A (2010) Partitioning the turnover and nestedness components of beta  
643 diversity. *Global Ecol Biogeogr* 19:134-143.

644 Baselga A, Orme CDL (2012) betapart: an R package for the study of beta diversity.  
645 *Methods Ecol Evol* 3:808-812.

646 Beiroz W, Sayer E, Slade EM, Audino L, Braga RF, Louzada J, Barlow J (2018) Spatial  
647 and temporal shifts in functional and taxonomic diversity of dung beetles in a  
648 human-modified tropical forest landscape. *Ecol Indic* 95:518-526.

649 Beiroz W, Slade EM, Barlow J, Silveira JM, Louzada J, Sayer E (2017) Dung beetle  
650 community dynamics in undisturbed tropical forests: implications for ecological  
651 evaluations of land-use change. *Insect Conser Diver* 10:94-106.

652 Bicknell JE, Phelps SP, Davies RG, Mann DJ, Struebig MJ, Davies ZG (2014) Dung  
653 beetles as indicators for rapid impact assessments: Evaluating best practice  
654 forestry in the neotropics. *Ecol Indic* 43:154-161.

655 Braga RF, Korasaki V, Andresen E, Louzada J (2013) Dung beetle community and  
656 functions along a habitat-disturbance gradient in the Amazon: A rapid assessment  
657 of ecological functions associated to biodiversity. *PlosOne* 8:e57786.

658 Burnham KP, Anderson DR (2002) Model selection and multimodel inference: A  
659 practical information-theoretic approach. (2nd Ed), Springer-Verlag, New York,  
660 488 p.

661 Cajaiba RL, Perico E, Dalzochio MS, da Silva WB, Bastos R, Cabral JA, Santos M  
662 (2017) Does the composition of Scarabaeidae (Coleoptera) communities reflect  
663 the extent of land use changes in the Brazilian Amazon? *Ecol Indic* 74:285-294.

664 Camero E (2010) Los escarabajos del género *Eurysternus* Dalman, 1824 (Coleoptera:  
665 Scarabaeidae) de Colombia. *Bol Soc Entomol Aragonesa (S.E.A.)* 46:147-179.

666 Cambefort Y, Hanski I (1991) Dung beetle population biology. In: Hanski I, Cambefort  
667 Y (Eds) *Dung beetle ecology*, Princeton University, Princeton, New Jersey, USA,  
668 pp 37-50.

669 Clements FE (1916) *Plant succession. An analysis of the development of vegetation.*  
670 Carnegie Institution of Washington, Publ 242, Washington DC, 512 p.

671 Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and  
672 their role in community stability and organization. *Am Nat* 111:119-44.

673 Colwell RK (2016) EstimateS: Statistical estimation of species richness and shared  
674 species from samples. Version 9.1.0. User's guide and applications available at:  
675 <http://viceroy.eeb.uconn.edu/estimates>.

676 Cook J (2002) A revision of the neotropical genus *Cryptocanthon*. Coleop Soc Monog  
677 1:1-96.

678 Cuesta E, Lobo JM (2019) A comparison of dung beetle assemblages (Coleoptera,  
679 Scarabaeoidea) collected 34 years apart in an Iberian mountain locality. J Insect  
680 Conserv 23:101-110.

681 Cupello M, Vaz-de-Mello FZ (2013) Taxonomic revision of the South American dung  
682 beetle genus *Gromphas* Brullé, 1837 (Coleoptera: Scarabaeidae: Scarabaeinae:  
683 Phanaeini: Gromphadina). Zootaxa 3722:439-482.

684 Da Silva PG, Hernández MIM (2015) Scale-dependence of processes structuring dung  
685 beetle metacommunities using functional diversity and community deconstruction  
686 approaches. PLoS ONE 10(3):e0123030.

687 Da Silva PG, Hernández MIM (2018) Spatial but not temporal dung beetle  $\beta$ -diversity  
688 components are scale-dependent in a mainland-island scenario. Austr Ecol  
689 43:915-925.

690 Davis AJ, Holloway JD, Huijbregts H, Krikken J, Kirk-Spriggs AH, Sutton SL (2001)  
691 Dung beetles as indicators of change in the forests of northern Borneo. J Appl  
692 Ecol 38:593-616.

693 Denslow JS (1980) Patterns of plant species diversity during succession under different  
694 disturbance regimes. Oecologia 46:18-21.

695 Dijkstra JA, Westerman EL, Harris LG (2011) The effects of climate change on species  
696 composition, succession and phenology: a case study. Global Change Biol  
697 17:2360-2369.

698 Doube B (1990) A functional classification for analysis of the structure of dung beetle  
699 assemblages. *Ecol Entomol* 15:371-383.

700 Edmonds WD (1994) Revision of *Phanaeus* Macleay, a new world genus of  
701 Scarabaeine dung beetles (Coleoptera: Scarabaeidae, Scarabaeinae). *Contr Sci*  
702 *NHM Angeles County* 443:1-105.

703 Edmonds WD, Zidek J (2004) Revision of the Neotropical dung beetle genus  
704 *Oxysternon* (Scarabaeidae: Scarabaeinae: Phanaeini). *Folia Heyrovskyana Suppl*  
705 11:1-58.

706 Edmonds WD, Zidek J (2010) A taxonomic review of the neotropical genus  
707 *Coprophanæus* Olsoufieff, 1924 (Coleoptera: Scarabaeidae, Scarabaeinae). *Insec*  
708 *Mundi* 0129:1-111.

709 Edwards FA, Finan J, Graham LK, Larsen TH, Wilcove DS, Hsu WW, Chey VK,  
710 Hamer KC (2017) The impact of logging roads on dung beetle assemblages in a  
711 tropical rainforest reserve. *Biol Conser* 205:85-92.

712 Encinas-Viso F, Revilla TA, Etienne RS (2012) Phenology drives mutualistic network  
713 structure and diversity. *Ecol Lett* 15:198-208.

714 Escobar F, Halffter G, Solis A, Halffter V, Navarrete D (2008) Temporal shifts in dung  
715 beetle community structure within a protected are of tropical wet forest: a 35-year  
716 study and its implications for long-term conservation. *J App Ecol* 45:1584-1592.

717 Estrada A, Halffter G, Coates-Estrada R, Merrit DA (1993) Dung beetles attracted to  
718 mammalian hervibore (*Alouatta palliata*) and omnivore (*Nasua narica*) dung in  
719 the tropical rain forest of Los Tuxtlas, Mexico. *J Trop Ecol* 9:45-54.

720 Feer F, Boissier O (2015) Variations in dung beetle assemblages across a gradient of  
721 hunting in a tropical forest. *Ecological Indicators* 57:164-170.

722 Ferreira SC, Da Silva PG, Paladini A, Di Mare RA (2019) Climatic variables drive  
723 temporal patterns of  $\alpha$  and  $\beta$  diversities of dung beetles. Bulletin of Entomological  
724 Research 109:390-397.

725 Forister ML, McCall AC, Sanders NJ, Fordyce JA, Thorne JH, O'Brien J, Waetjen DP,  
726 Shapiro AM (2010) Compounded effects of climate change and habitat alteration  
727 shift patterns of butterfly diversity. PNAS 107:2088-2092.

728 Franca F, Louzada J, Korasaki V, Griffiths H, Silveira JM, Barlow J (2016) Do space-  
729 for-time assessments underestimate the impacts of logging on tropical  
730 biodiversity? An Amazonian case study using dung beetles. J App Ecol 53:1098-  
731 1105.

732 Fritz SA, Schnitzler J, Eronen JT, Hof C, Bohning-Gaese K, Graham CH (2013)  
733 Diversity in time and space: wanted dead and alive. Trends Ecol Evol 28:509-516.

734 Gardner TA, Hernández MIM, Barlow J, Peres CA (2008) Understanding the  
735 biodiversity consequences of habitat change: the value of secondary and  
736 plantation forests for neotropical dung beetles. J Appl Ecol 45:883-893.

737 Genier F (1996) A revision of the neotropical genus *Ontherus* Erichson (Coleoptera:  
738 Scarabaeidae, Scarabaeinae). Mem Entomol Soc Canada 170:1-168.

739 Gleason HA (1927) Further views on the succession concept. Ecology 8: 299-326.

740 Grimbacher PS, Stork NE (2009) Seasonality of a diverse beetle assemblage inhabiting  
741 lowland tropical rain forest in Australia. Biotropica 41:328-337.

742 Grøtan VR, Lande R, Engen S, Sæther BE, DeVries PJ (2014) Seasonal cycles of  
743 diversity and similarity in a Central American rainforest butterfly community.  
744 Ecography 37:509-516.

745 Halffter G, Arellano L (2002) Response of dung beetle diversity to human-induced  
746 changes in a tropical landscape. Biotropica 34:144-154.

- 747 Halffter G, Edmonds WD (1982) The nesting behaviour of dung beetles (Scarabaeinae):  
748 An ecological and evolutive approach. *Inst Ecol Mex* 10:1-176.
- 749 Halffter G, Matthews EG (1966) The natural history of dung beetles of the subfamily  
750 Scarabaeinae. *Folia Entom Mex* 12-14:1-312.
- 751 Hanski I (1982) Dynamics of regional distribution: the core and satellite species  
752 hypothesis. *Oikos* 38:210-221.
- 753 Hernández MIM, Vaz-de-Mello FZ (2009) Seasonal and spatial species richness  
754 variation of dung beetle (Coleoptera, Scarabaeidae s. str.) in the Atlantic forest of  
755 southeastern Brazil. *Rev Brasil Entom* 53(4):607-613.
- 756 Hewitt JE, Thrush SF, Ellingsen KE (2016) The role of time and species identities in  
757 spatial patterns of species richness and conservation. *Conserv Biol* 30(5):1080-  
758 1088.
- 759 Higgins MA, Ruokolainen K, Tuomisto H, Llerena N, Cardenas G, Phillips OL,  
760 Vásquez R, Räsänen M (2011) Geological control of floristic composition in  
761 Amazonian forests. *J Biogeog* 38:2136-2149.
- 762 Hodgson JA, Thomas CD, Oliver TH, Anderson BJ, Brereton TM, Crone EE (2010)  
763 Predicting insect phenology across space and time. *Global Change Biol* 17:1289-  
764 1300.
- 765 Horgan FG (2008) Dung beetle assemblages in forests and pastures of El Salvador: a  
766 functional comparison. *Biodiv Conserv* 17:2961-2978.
- 767 Hortal J, De Marco P, Santos AMC, Diniz-Filho AF (2012) Integrating biogeographical  
768 processes and local community assembly. *J Biogeog* 39:627-628.
- 769 Hosaka T, Niino M, Kon M, Ochi T, Yamada T, Fletcher C, Okuda T (2014) Effects of  
770 logging road networks on the ecological functions of dung beetles in Peninsular  
771 Malaysia. *Forest Ecology and Management* 326:18-24.



- 772 Howden HF, Nealis VG (1975) Effects of clearing in a tropical rain forest on the  
773 composition of the coprophagous scarab beetle fauna (Coleoptera). *Biotropica*  
774 7:77-83.
- 775 INPA (2017) PRODES—Monitoramento da Floresta Amazônica Brasileira por Satélite.  
776 Instituto Nacional de Pesquisas Espaciais, São José dos Campos, São Paulo,  
777 Brasil. Available online: [http://www.obt.inpe.br/prodes/dashboard/prodes-](http://www.obt.inpe.br/prodes/dashboard/prodes-rates.html)  
778 [rates.html](http://www.obt.inpe.br/prodes/dashboard/prodes-rates.html) (accessed on 30 January 2018).
- 779 Kishimoto-Yamada K, Itioka T (2015) How much have we learned about seasonality in  
780 tropical insect abundance since Wolda (1988)? *Entomol Sci* 18:407-419.
- 781 Korasaki V, Vaz-De-Mello FZ, Braga RF, Zanetti R, Louzada J (2013) Conservation  
782 value of alternative land-use systems for dung beetles in Amazon: valuing  
783 traditional farming practices. *Biodiv Conserv* 22:1485-1499.
- 784 Larsen TH, Forsyth A (2005) Trap spacing and transect design for dung beetle  
785 biodiversity studies. *Biotropica* 37:322-325.
- 786 Labidi I, Erroussi F, Noura S (2012) Spatial and temporal variation in species  
787 composition, diversity, and structure of mediterranean dung beetle assemblages  
788 (Coleoptera: Scarabaeidae) across a bioclimatic gradient. *Environ Entomol*  
789 41:785-801.
- 790 Lenth RV (2016) Least-squares means: The R package lsmeans. *J Stat*  
791 *Software* 69(1):1-33.
- 792 Lobo JM (2001) Decline of roller dung beetle (Scarabaeinae) populations in the Iberian  
793 península during the 20th century. *Biol Conserv* 97:43-50.
- 794 Lobo JM (2008) Database records as a surrogate for sampling effort provide higher  
795 species richness estimations. *Biodiv Conserv* 17:873-881.
- 796 Lopes J, Korasaki V, Catelli L, Marcai VVM, Nunes MPBP (2011) A comparison of

797 dung beetle assemblage structure (Coleoptera: Scarabaeidae: Scarabaeinae)  
798 between an Atlantic forest fragment and adjacent abandoned pasture in Paraná,  
799 Brazil. *Zoologia* 28:72-79.

800 Losey JE, Vaughan M (2006) The economic value of ecological services provided by  
801 insects. *BioScience* 56:311-323.

802 Matos P, Pinho P, Aragón G, Martínez I, Nunes A, Soares AMVM, Branquinho C  
803 (2015) Lichen traits responding to aridity. *J Ecol* 103:451-458.

804 McCune B, Grace JB (2002) Analysis of ecological communities. MS Design (ed),  
805 MjM Software Design, Gleneden Beach, Oregon.

806 McGeoch MA, van Rensburg BJ, Botes A (2002) The verification and application of  
807 bioindicators: a case study of dung beetles in a savanna ecosystem. *J Appl Ecol*  
808 39:661-72.

809 Menéndez R (1994) Patrones de distribución y abundancia en especies de escarabajos  
810 coprófagos. *Studia Oecol* 10-11:395-400.

811 Milotic T, Blatzinger C, Eichberg C, Eycott AE, Heurich M, Müller J, Noriega JA,  
812 Menendez R, Stadler J, Ádám R, Bargamnn T, Bilger I, Buse J, Calatayud J,  
813 Ciubuc C, Boros G, Jay-Robert P, Kruus M, Merivee E, Miessen G, Must A,  
814 Ardali E, Preda E, Rahimi I, Rohwedder D, Rose R, Slade EM, Somay L,  
815 Tahmasebi P, Ziani S, Hoffman M (2018) Functionally richer communities  
816 improve ecosystem functioning: Dung removal and secondary seed dispersal by  
817 dung beetles in the Western Palaearctic. *J Biogeog* 46(1):70-82.

818 Nichols E, Larsen T, Spector S, Davies AL, Escobar F, Favila M, Vulinec K, The  
819 Scarabaeinae Research Network (2007) Global dung beetle response to tropical  
820 forest modification and fragmentation: A quantitative literature review and meta-  
821 analysis. *Biol Conserv* 137:1-19.

822 Nichols E, Spector S, Louzada J, Larsen T, Amezquita S, Favila ME, The Scarabaeinae  
823 Research Network (2008) Ecological functions and ecosystem services provided  
824 by Scarabaeinae dung beetles. *Biol Conserv* 141:1461-1474.

825 Nichols E, Uriarte M, Bunker DE, Favila ME, Slade EM, Vulinec K, Larsen T, Vaz-de-  
826 Mello FZ, Louzada J, Naeem S, Spector SH (2013) Trait-dependent response of  
827 dung beetle populations to tropical forest conversion at local and regional scales.  
828 *Ecology* 94:180-189.

829 Noriega JA, Botero JP, Viola M, Fagua G (2007) Dinámica estacional de la estructura  
830 trófica de un ensamblaje de Coleoptera en la Amazonía Colombiana. *Rev Colomb*  
831 *Entomol* 33(2):157-164.

832 Noriega JA, Fagua G (2009) Monitoreo de escarabajos coprofagos (Coleoptera:  
833 Scarabaeidae) en la región neotropical. In: *Técnicas de campo en ambientes*  
834 *tropicales. Manual para el monitoreo en ecosistemas acuáticos y artrópodos*  
835 *terrestres*. Acosta A, Fagua G, Zapata AM (eds), Pontificia Universidad Javeriana,  
836 Bogotá, Colombia, pp 165-188.

837 Noriega JA, Zapata-Prisco C, García H., Hernández E, Hernández J, Martínez R,  
838 Santos-Santos JH, Pablo-Cea JD, Calatayud J (2020) Does ecotourism impact  
839 biodiversity? An assessment using dung beetles (Coleoptera: Scarabaeinae) as  
840 bioindicators in a tropical dry forest natural park. *Ecol Indic* 117:106580.

841 Oksanen J (2009) Ordination and analysis of dissimilarities: Tutorial with R and vegan.  
842 1-25.

843 Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR,  
844 O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2013)  
845 *Vegan: Community Ecology Package*. R package version 2.0-7.

846 Otavo S, Parrado-Rosselli A, Noriega JA (2013) Superfamilia Scarabaeoidea (Insecta:  
847 Coleoptera) como elemento bioindicador de perturbación antropogénica en un  
848 parque nacional amazónico. *Rev Biol Trop* 61:735-752.

849 Peres CA, Gardner TA, Barlow J, Zuanon J, Michalski F, Lees AC, Vieira ICG,  
850 Moreira FMS, Feeley KJ (2010) Biodiversity conservation in human-modified  
851 Amazonian forest landscapes. *Biol Conserv* 143:2314-2327.

852 R Core Team (2016) R: A Language and Environment for Statistical Computing. R 707  
853 Foundation for Statistical Computing, Vienna <http://www.r-project.org/>.

854 Ribeiro DB, Freitas AVL (2011) Large-sized insects show stronger seasonality than  
855 small-sized ones: a case study of fruit-feeding butterflies. *Biol J Linn Soc*  
856 104:820-827.

857 Rosenzweig ML (1995) Species diversity in space and time. Cambridge University  
858 Press, UK, 436 p.

859 Slade EM, Mann DJ, Villanueva JF, Lewis OT (2007) Experimental evidence for the  
860 effects of dung beetle functional group richness and composition on ecosystem  
861 function in a tropical forest. *J Anim Ecol* 76:1094-1104.

862 Tanner JE, Hughes TP, Connell JH (2009) Community-Level Density Dependence: An  
863 Example from a Shallow Coral Assemblage. *Ecology* 90:506-516.

864 Tonelli M, Verdú JR, Zunino M (2018) Effects of the progressive abandonment of  
865 grazing on dung beetle biodiversity: body size matters. *Biodiversity and*  
866 *Conservation* 27:189-204.

867 Tonelli M, Verdú JR, Morelli F, Zunino M (2020) Dung beetles: functional identity, not  
868 functional diversity, accounts for ecological process disruption caused by the use  
869 of veterinary medical products. *Journal of Insect Conservation* 24:643-654.

- 870 Vaz-de-Mello FZ, Edmonds WD, Ocampo FC, Schoolmeesters P (2011) A multilingual  
871 key to the genera and subgenera of the subfamily Scarabaeinae of the New World  
872 (Coleoptera: Scarabaeidae). *Zootaxa* 2854:1-73.
- 873 Viega G, Stenert C, Schulz UH, Maltchik L (2014) Dung beetle communities as  
874 biological indicators of riparian forest widths in southern Brazil. *Ecol Indic*  
875 36:703-710.
- 876 Villéger S, Novack-Gottshall PM, Mouillot D (2011) The multidimensionality of the  
877 niche reveals functional diversity changes in benthic marine biotas across  
878 geological time. *Ecol Lett* 14:561-568.
- 879 van Vliet N, Adams C, Vieira ICG, Mertz O (2013) “Slash and Burn” and “Shifting”  
880 cultivation systems in forest agriculture frontiers from the Brazilian Amazon. *Soc*  
881 *Nat Resour* 26:1454-1467.
- 882 Voss SC, Spafford H, Dadour IR (2009) Annual and seasonal patterns of insect  
883 succession on decomposing remains at two locations in Western Australia. *Forest*  
884 *Sci Inter* 193:26-36.
- 885 Vulinec K (2002) Dung beetle communities and seed dispersal in primary forest and  
886 disturbed land in Amazonia. *Biotropica* 34:297-309.
- 887 Walker LR, Del Moral R (2003) Primary succession and ecosystem rehabilitation.  
888 Cambridge University Press, Cambridge, UK, 456 p.
- 889 Wolda H (1988) Insect seasonality: why? *Ann Rev Ecol System* 19:1-18.

## Figure captions

**Fig. 1** Map of the study region. Location of the two sampling localities: Palmari (Brazil - Natural Reserve Palmari) and Monilla (Colombia - Natural Reserve Monilla Amena) in the Amazon region

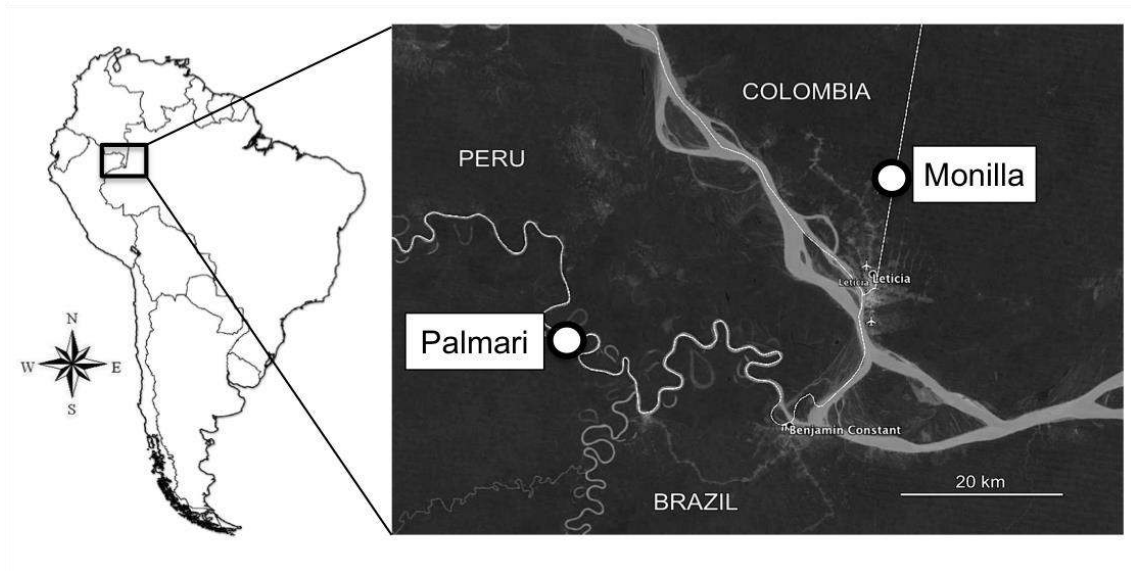
**Fig. 2** Abundance (a,b) and richness (c,d) of the two sampling localities in the Amazon region: Palmari (Brazil - successional) and Monilla (Colombia - interannual) in each year (2002, 2003, 2004), sampling season (R: Rainy and D: Dry) and type of habitat (ChN: new abandoned “chagra”, ChA: old abandoned “chagra”, SF: secondary forest, PF: primary forest, SNF: secondary new forest and SOF: secondary old forest). Different letters, above bars, indicate statistically significant differences (Wilcoxon’s test;  $p < 0.05$ ) among years/seasons/forests. Error bars represent average  $\pm$  SE

**Fig. 3** Non-metric multidimensional scaling (NMDS) analyses of species (a,b) and functional groups (c,d) composition in Palmari (Brazil) and Monilla (Colombia) in the Amazon region. Season (Rainy and Dry) and type of habitat (ChN: new abandoned “chagra”, ChA: old abandoned “chagra”, SF: secondary forest, PF: primary forest, SNF: secondary new forest and SOF: secondary old forest). Vectors represent significant correlations between assemblage composition and significant explanatory variables: Successional and Rainy (rainy season of the year). Functional groups and species code correspond to ones listed in Table 1 (P: paracoprids, T: telecoprids, E: endocoprids and Small (S):  $< 10$  mm, Medium (M): 10-18 mm and Large (L):  $> 18$  mm)

**Fig. 4** Beta diversity components ( $\beta_{sim}$  [a,b] and  $\beta_{nes}$  [c,d]) of Palmari (Brazil – successional) and Monilla (Colombia - interannual) during the rainy season, between types of habitat (ChN: new abandoned “chagra”, ChA: old abandoned “chagra”, SF: secondary forest, PF: primary forest, SNF: secondary new forest and SOF: secondary old forest), and sampling years (2002, 2003, 2004) in the Amazon region. Different letters, above bars, indicate statistically significant differences (Wilcoxon’s test;  $p < 0.05$ ) among years/seasons/forests

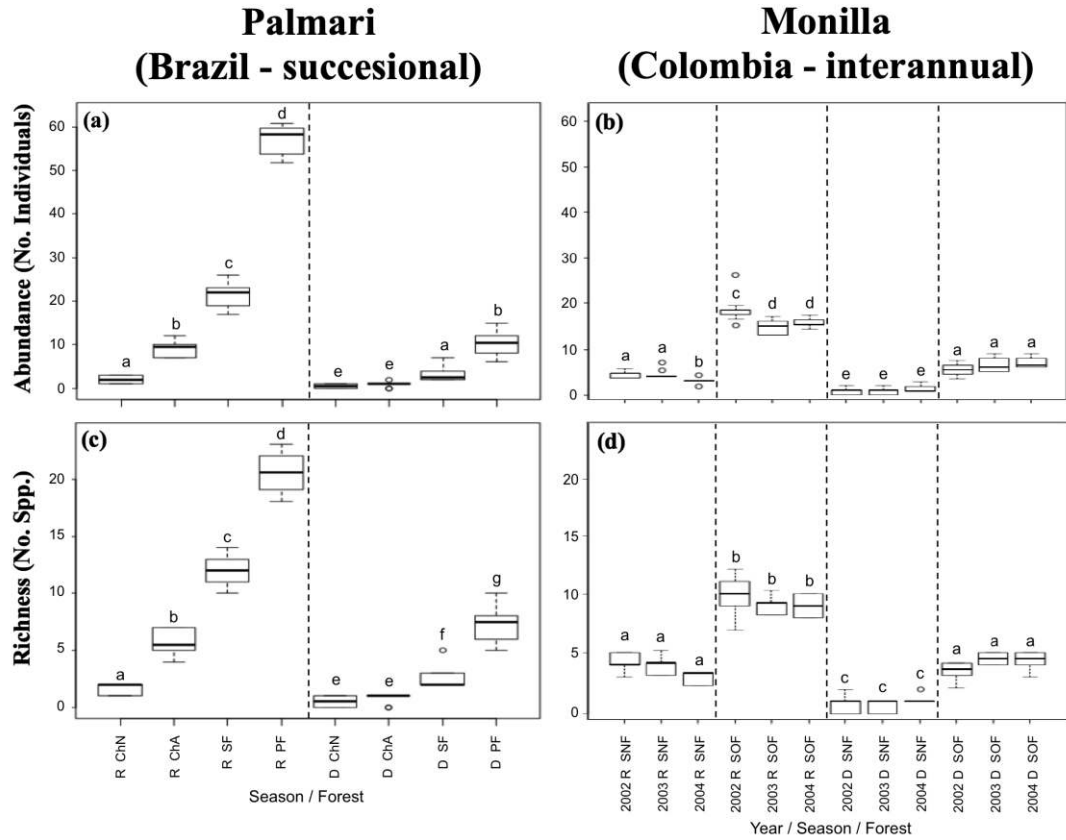
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**Fig. 6** Beta diversity components: a) nestedness pattern in successional habitats (Palmari – Brazil, ChN: new abandoned “chagra”, ChA: old abandoned “chagra”, SF: secondary forest, PF: primary forest); and b) turnover pattern in interannual comparisons (Monilla – Colombia) of dung beetles assemblage structure in the Amazon region. Numbers indicate the total number of species that were found only in each habitat or year

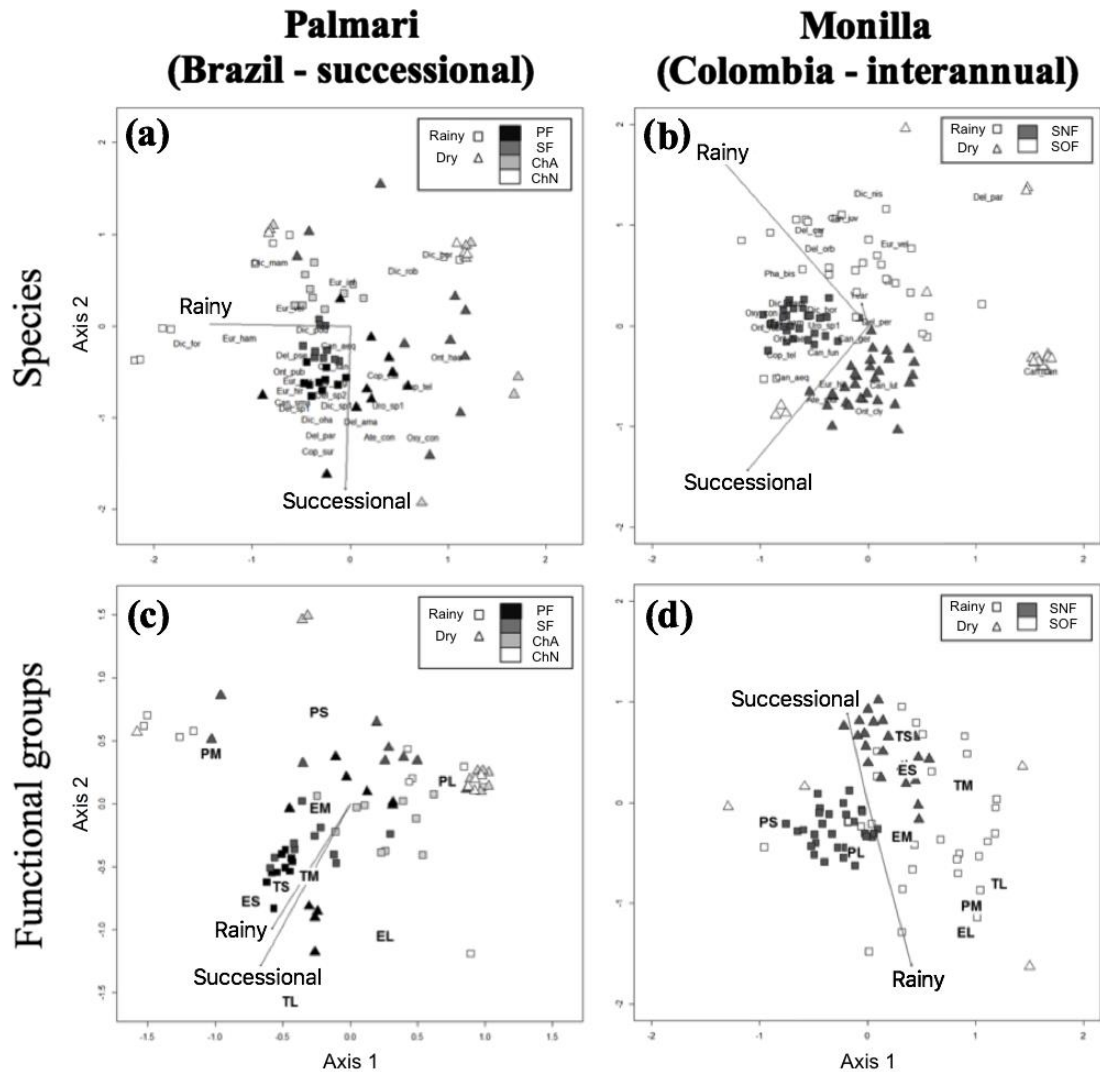


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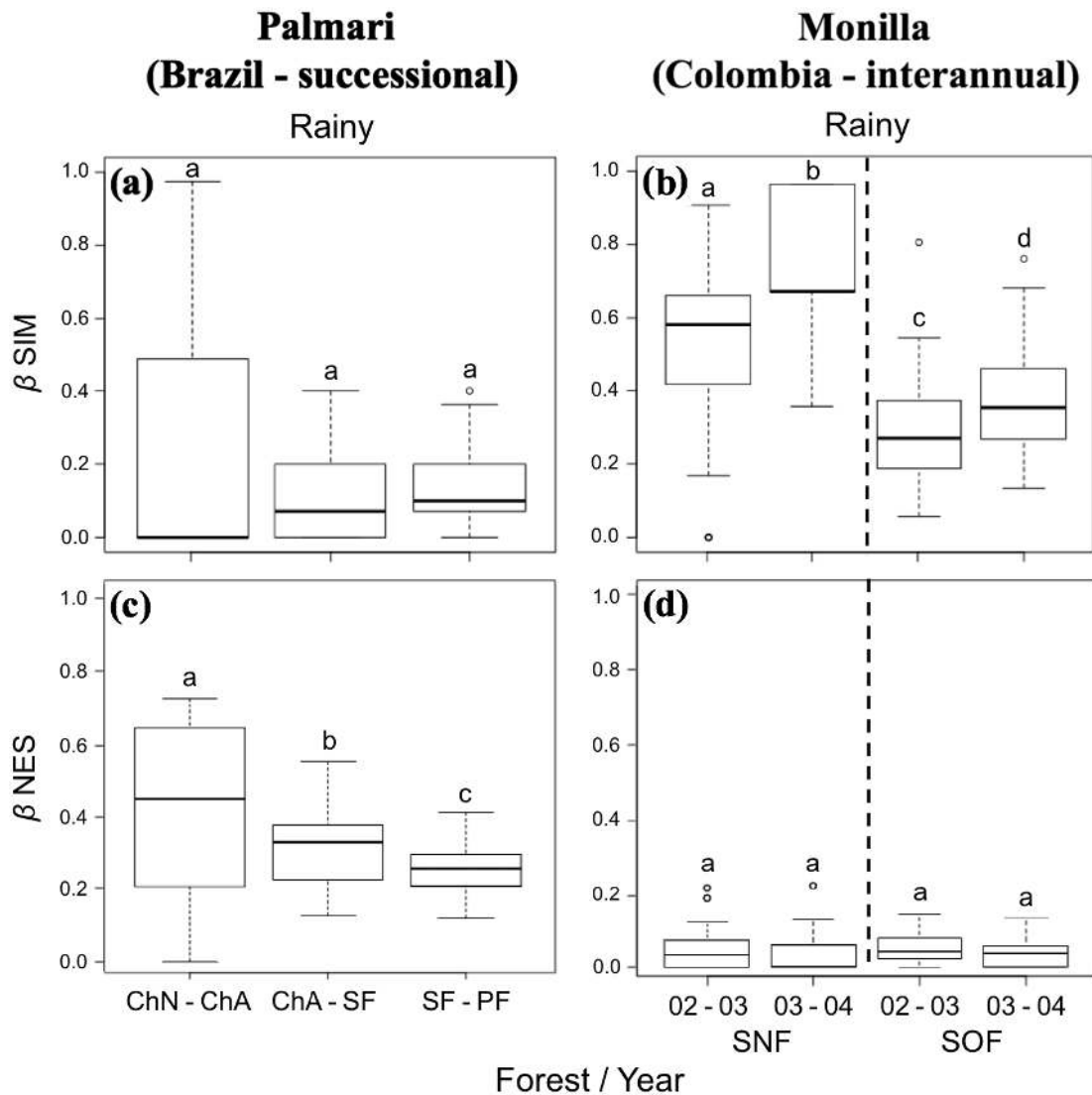




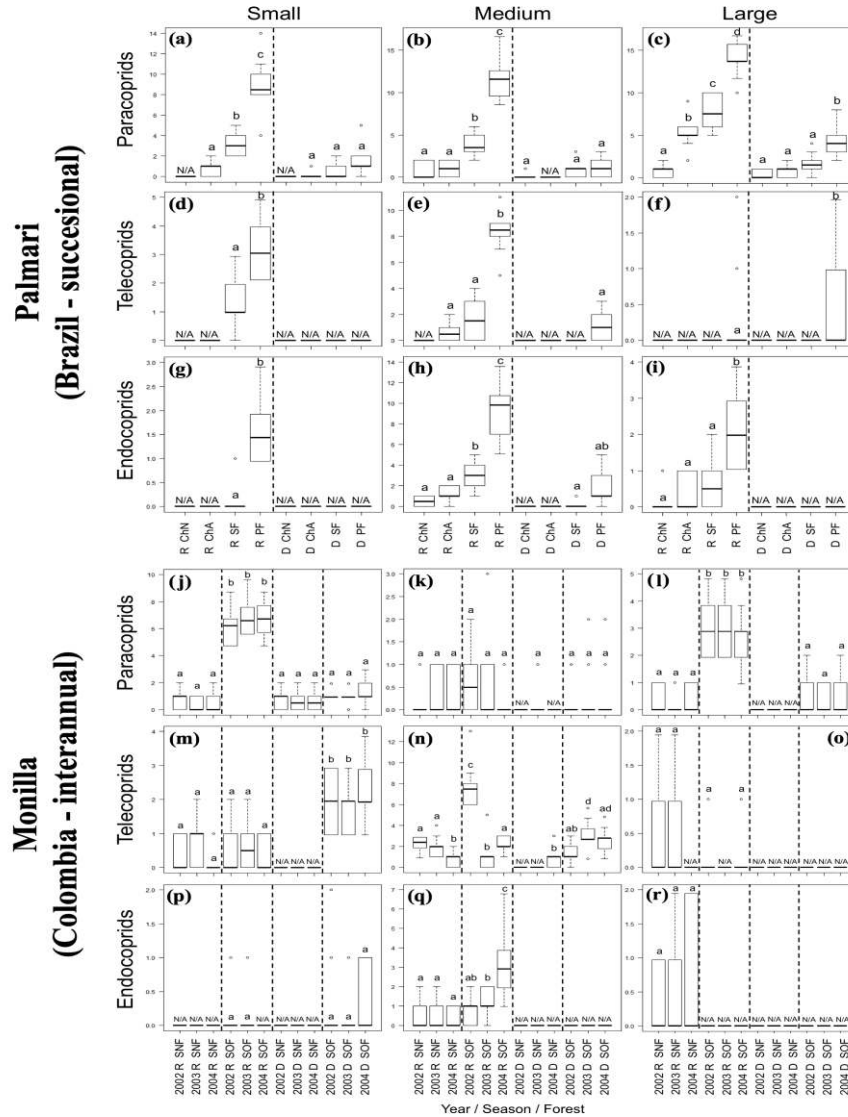
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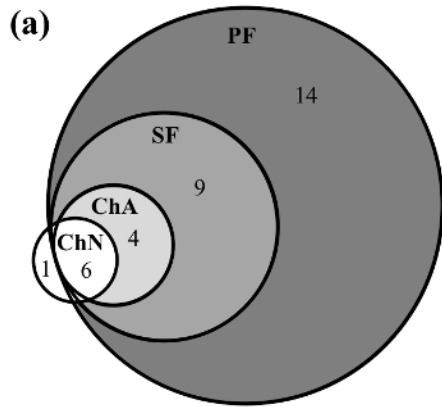


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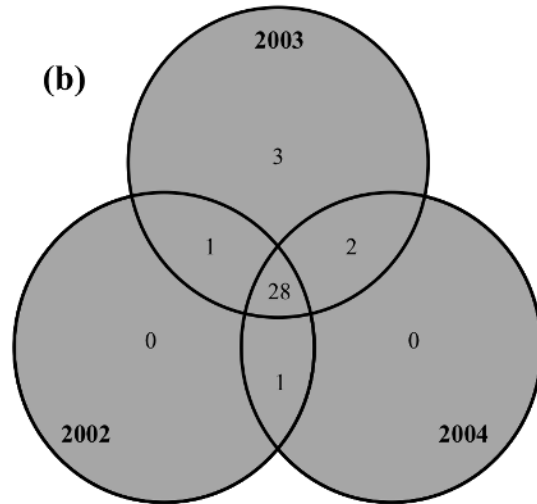


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**Palmari  
(Brazil - sucesional)**



**Monilla  
(Colombia - interannual)**



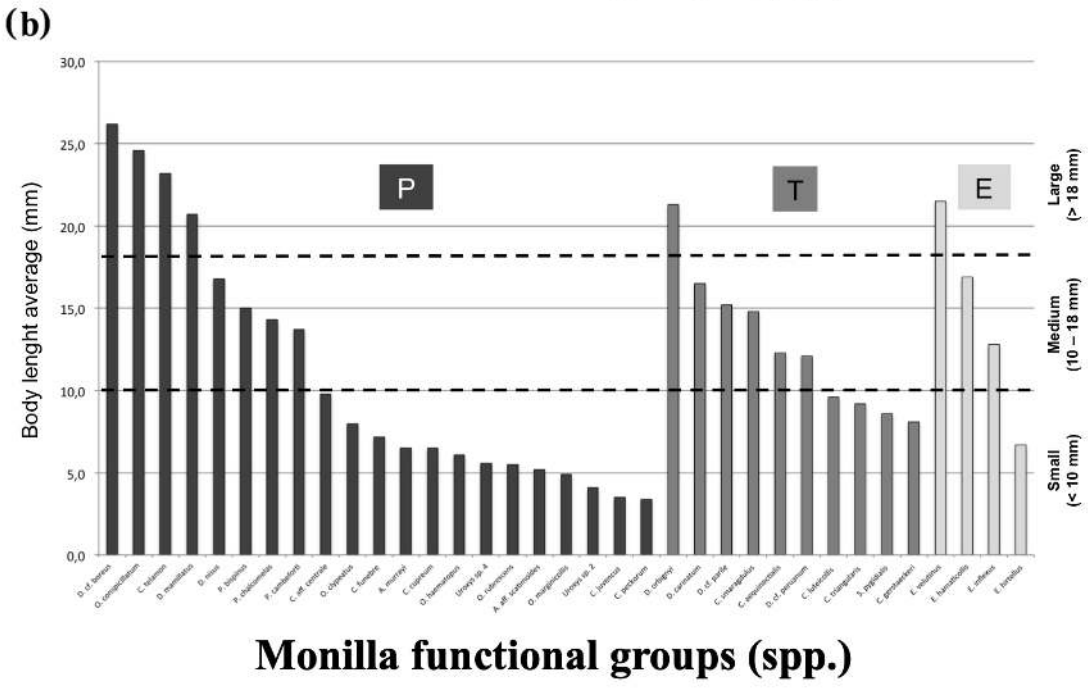
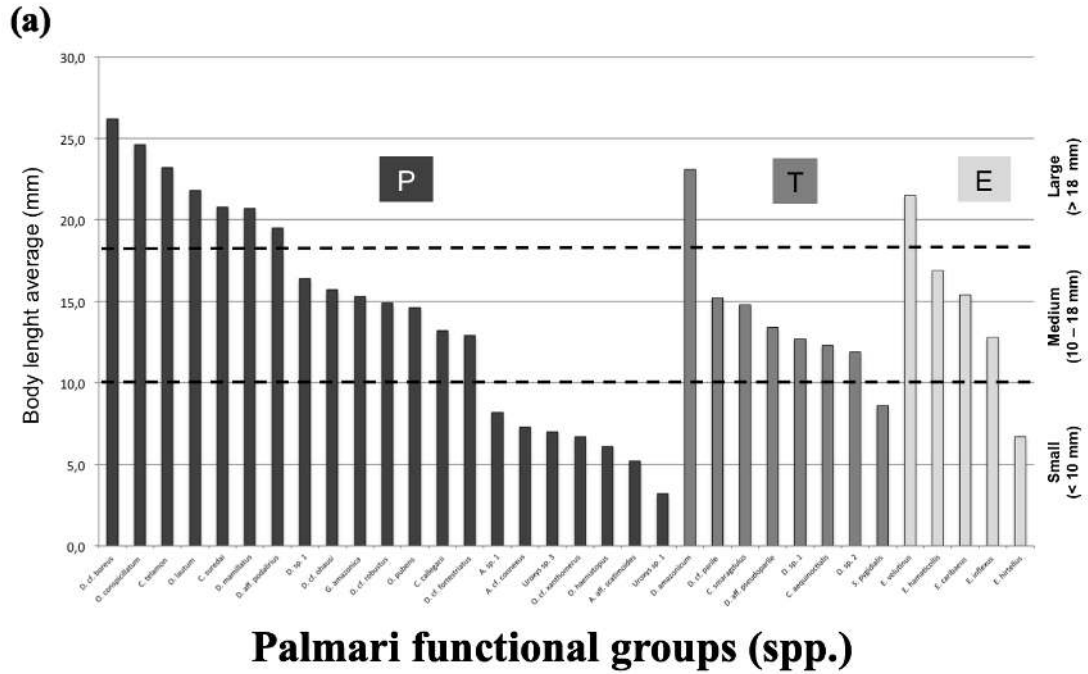
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**Table 1** Species list and abundance in Palmari (Brazil - successional) and Monilla (Colombia - interannual) in each type of habitat sampled (ChN: new abandoned “chagra”, ChA: old abandoned “chagra”, SF: secondary forest, PF: primary forest) and year (2002, 2003, 2004) in the Amazon region. FG corresponds to functional groups built based on relocation food behavior and body size (P: paracoprids, T: telecoprids, E: endocoprids and Small (S): < 10 mm, Medium (M): 10-18 mm and Large (L): > 18 mm; Appendix S1); AS is the average individual length in mm; and Code is the species code (used in Fig. 5)

Tribe	Genus	Species	FG	AS	Code	Palmari				Monilla			Total	
						ChN	ChA	SF	PF	2002	2003	2004		
Ateuchini	<i>Ateuchus</i>	<i>A. murrayi</i> (Harold, 1868)	PS	6.5	<i>Ate_mur</i>	0	0	0	0	2	3	1	6	
		<i>A. cf. connexus</i> (Harold, 1868)	PS	7.3	<i>Ate_con</i>	0	0	0	7	0	0	0	7	
		<i>A. aff. scatimoides</i> (Balthasar, 1939)	PS	5.2	<i>Ate_sca</i>	0	0	0	3	0	1	1	5	
		<i>A. sp. 1</i>	PS	8.2	<i>Ate_sp1</i>	0	0	0	4	0	0	0	4	
	<i>Uroxys</i>	<i>Uroxys sp. 1</i>	PS	3.2	<i>Uro_sp1</i>	0	0	0	11	0	0	0	11	
		<i>Uroxys sp. 2</i>	PS	4.1	<i>Uro_sp2</i>	0	0	0	0	12	13	15	40	
		<i>Uroxys sp. 3</i>	PS	7.0	<i>Uro_sp3</i>	0	0	0	5	0	0	0	5	
		<i>Uroxys sp. 4</i>	PS	5.6	<i>Uro_sp4</i>	0	0	0	0	0	2	0	2	
Coprini	<i>Canthidium</i>	<i>C. cupreum</i> (Blanchard, 1843)	PS	6.5	<i>Can_cup</i>	0	0	0	0	1	1	2	4	
		<i>C. funebre</i> Balthasar, 1939	PS	7.2	<i>Can_fun</i>	0	0	0	0	8	9	5	22	
		<i>C. gerstaeckeri</i> Harold, 1867	PS	8.1	<i>Can_ger</i>	0	0	0	0	5	2	4	11	
		<i>C. aff. centrale</i> Boucomont, 1928	PS	9.8	<i>Can_cen</i>	0	0	0	0	9	6	9	24	
	<i>Dichotomius</i>	<i>D. mamillatus</i> (Felsche, 1901)	PL	20.7	<i>Dic_mam</i>	5	29	29	18	11	9	8	109	
		<i>D. nisus</i> (Olivier, 1789)	PM	16.8	<i>Dic_nis</i>	0	0	0	0	1	3	3	7	
		<i>D. cf. boreus</i> (Olivier, 1789)	PL	26.2	<i>Dic_bor</i>	7	20	29	81	14	12	16	179	
		<i>D. cf. fortistriatus</i> (Luederwaldt, 1923)	PM	12.9	<i>Dic_for</i>	7	10	23	73	0	0	0	113	
		<i>D. cf. ohausi</i> (Luederwaldt, 1923)	PM	15.7	<i>Dic_oha</i>	0	0	0	9	0	0	0	9	
			<i>D. cf. robustus</i> (Luederwaldt, 1935)	PM	14.9	<i>Dic_rob</i>	0	0	7	12	0	0	0	19
			<i>D. aff. podalirius</i> (Felsche, 1901)	PL	19.5	<i>Dic_pod</i>	0	8	21	37	0	0	0	66
			<i>D. sp. 1</i>	PM	16.4	<i>Dic_sp1</i>	0	0	0	9	0	0	0	9
		<i>Ontherus</i>	<i>O. pubens</i> Génier, 1996	PM	14.6	<i>Ont_pub</i>	0	0	6	12	0	0	0	18
Deltochilini	<i>Canthon</i>	<i>C. aequinoctialis</i> (Harold, 1868)	TM	12.3	<i>Can_aeq</i>	0	6	10	58	81	35	48	238	

		<i>C. juvenus</i> (Harold, 1868)	TS	3.5	<i>Can_juv</i>	0	0	0	0	3	7	1	11	
		<i>C. luteicollis</i> Erichson, 1847	TS	9.6	<i>Can_lut</i>	0	0	0	0	23	19	24	66	
		<i>C. smaragdulus</i> (Fabricius, 1781)	TM	14.8	<i>Can_sma</i>	0	0	0	4	1	0	1	6	
		<i>C. triangularis</i> (Drury, 1770)	TS	9.2	<i>Can_tri</i>	0	0	0	0	0	1	0	1	
	<i>Cryptocanthon</i>	<i>C. peckorum</i> Howden, 1973	TS	3.4	<i>Cry_pec</i>	0	0	0	0	0	2	1	3	
	<i>Deltochilum</i>	<i>D. amazonicum</i> Bates, 1887	TL	23.1	<i>Del_ama</i>	0	0	0	8	0	0	0	8	
		<i>D. carinatum</i> (Westwood, 1837)	TM	16.5	<i>Del_car</i>	0	0	0	0	9	9	1	19	
		<i>D. orbignyi</i> (Blanchard, 1846)	TL	21.3	<i>Del_orb</i>	0	0	0	0	7	5	1	13	
		<i>D. cf. parile</i> Bates, 1887	TM	15.2	<i>Del_par</i>	0	0	5	9	2	1	5	22	
		<i>D. cf. peruanum</i> Paulian, 1938	TM	12.1	<i>Del_per</i>	0	0	0	0	15	14	9	38	
		<i>D. aff. pseudoparile</i> Paulian, 1938	TM	13.4	<i>Del_pse</i>	0	0	0	14	0	0	0	14	
		<i>D. sp. 1</i>	TM	12.7	<i>Del_sp1</i>	0	0	0	6	0	0	0	6	
		<i>D. sp. 2</i>	TM	11.9	<i>Del_sp2</i>	0	0	0	6	0	0	0	6	
	<i>Scybalocanthon</i>	<i>S. pygidialis</i> (Schmidt, 1922)	TS	8.6	<i>Scy_pyg</i>	0	0	13	30	2	1	2	48	
Oniticellini	<i>Eurystemus</i>	<i>E. caribaeus</i> Herbst, 1789	EM	15.4	<i>Eur_car</i>	0	0	6	19	0	0	0	25	
		<i>E. hamaticollis</i> Balthasar, 1939	EM	16.9	<i>Eur_ham</i>	3	3	7	34	14	13	35	109	
		<i>E. hirtellus</i> Dalman, 1824	ES	6.7	<i>Eur_hir</i>	0	0	2	16	5	4	3	30	
		<i>E. inflexus</i> (Germar, 1824)	EM	12.8	<i>Eur_inf</i>	2	8	20	57	0	3	0	90	
		<i>E. velutinus</i> Bates, 1887	EL	21.5	<i>Eur_vel</i>	1	3	7	20	3	4	7	45	
Onthophagini	<i>Onthophagus</i>	<i>O. clypeatus</i> Blanchard, 1846	PS	8.0	<i>Ont_cly</i>	0	0	0	0	4	2	2	8	
		<i>O. haematopus</i> Harold, 1875	PS	6.1	<i>Ont_hae</i>	0	9	32	60	37	37	39	214	
		<i>O. marginicollis</i> Harold, 1880	PS	4.9	<i>Ont_mar</i>	0	0	0	0	2	1	2	5	
		<i>O. rubescens</i> Blanchard, 1843	PS	5.5	<i>Ont_rub</i>	0	0	0	0	12	16	12	40	
		<i>O. cf. xanthomerus</i> Bates, 1887	PS	6.7	<i>Ont_xan</i>	0	0	4	13	0	0	0	17	
Phanaeini	<i>Coprophanaeus</i>	<i>C. callegarii</i> Arnaud, 2002	PM	13.2	<i>Cop_cal</i>	0	0	10	16	0	0	0	26	
		<i>C. suredai</i> Arnaud, 1996	PL	20.8	<i>Cop_sur</i>	0	0	0	8	0	0	0	8	
		<i>C. telamon</i> (Erichson, 1847)	PL	23.2	<i>Cop_tel</i>	0	0	11	15	6	6	8	46	
	<i>Gromphas</i>	<i>G. amazonica</i> Bates, 1870	PM	15.3	<i>Gro_ama</i>	1	0	0	0	0	0	0	1	
	<i>Oxystemon</i>	<i>O. conspicillatum</i> (Weber, 1801)	PL	24.6	<i>Oxy_con</i>	0	3	7	21	2	3	1	37	
		<i>O. lautum</i> (Macleay, 1819)	PL	21.8	<i>Oxy_lau</i>	0	0	0	4	0	0	0	4	
	<i>Phanaeus</i>	<i>P. bispinus</i> Bates, 1868	PM	15.0	<i>Pha_bis</i>	0	0	0	0	5	3	1	9	
		<i>P. cambeforti</i> Arnaud, 1982	PM	13.7	<i>Pha_cam</i>	0	0	0	0	1	3	3	7	
		<i>P. chalconelas</i> (Perty, 1830)	PM	14.3	<i>Pha_cha</i>	0	0	0	0	2	3	0	5	
						Abundance	26	99	249	699	299	253	270	1895
						Richness	7	10	19	33	30	34	31	55

Supplementary material



**Appendix S1** Definition of the functional groups based on guilds (P: paracoprids, T: telecoprids and E: endocoprids) and body size (Small (S): < 10 mm, Medium (M): 10-18 mm and Large (L): > 18 mm) for each locality: a) Palmari (Brazil - successional) and b) Monilla (Colombia - interannual) in the Amazon region



**Appendix S2** Observed (Sobs) and estimated percentage of species richness

completeness calculated by four estimators (ACE, ICE, Chao 1 and Jack 1) for each locality (Palmari: Brazil and Monilla: Colombia), season (Rainy and Dry), habitat type (80, 30, 5 and 0 years and SOF: secondary old forest and SNF: secondary new forest), and years (2002, 2003, 2004)

Site	Season	Habitat	Year	$S_{obs}$	Estimator			
					ACE	ICE	Chao 1	Jack 1
Palmari (Brazil)	Dry	80 years		16	86.1	91.9	88.3	94.7
		30 years		8	87.6	93.5	89.5	95.0
		5 years		4	89.2	94.7	90.2	98.7
		0 years		3	91.3	96.0	93.1	100
	Rainy	80 years		33	85.2	90.0	87.5	91.7
		30 years		19	85.7	90.6	87.9	92.4
		5 years		10	86.3	91.3	88.4	95.6
		0 years		6	88.9	93.4	89.1	99.2
Monilla (Colombia)	Dry		2002	11	78.3	92.1	87.5	95.6
		SOF	2003	13	77.5	91.7	86.5	97.5
			2004	14	79.2	92.5	88.3	98.1
			2002	2	78.5	92.7	88.4	98.3
		SNF	2003	3	78.3	92.5	88.1	98.0
	Rainy		2004	4	79.0	93.9	89.3	98.6
			2002	23	73.6	91.8	85.4	94.5
		SOF	2003	21	74.0	91.9	85.7	95.7
			2004	21	73.9	91.4	85.5	94.4
			2002	17	74.5	90.3	86.3	97.5
	SNF	2003	14	75.1	91.9	87.2	98.1	
		2004	10	76.2	92.1	88.1	98.9	

**Appendix S3** Richness and abundance models (Poisson) and AICc values for Palmari (Brazil - successional) and Monilla (Colombia - interannual). The explained deviance of the best model in terms of AICc is also provided

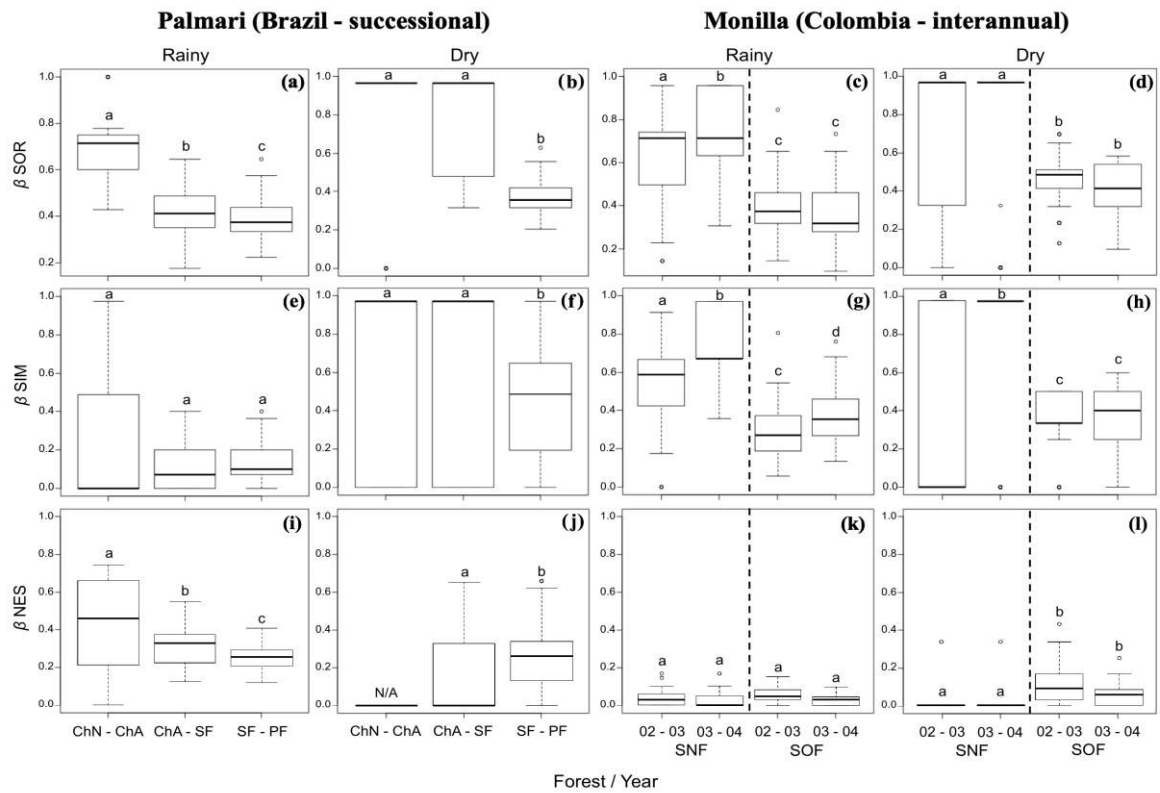
		Models		AICc
Palmari (Brazil)	Richness models	Mod 1	Season:ForestType	281.85*
		Mod 2	Season+ForestType	283.52
	Explained deviance: 94.53%			
	Abundance models	Mod 1	Season:ForestType	322.11
		Mod 2	Season+ForestType	320.78*
		Mod 3	Season	1300.24
		Mod 4	ForestType	939.72
	Explained deviance: 97.41%			
Monilla (Colombia)	Richness models	Mod 1	Year:Season:ForestType	411.51
		Mod 2	Year+Season:ForestType	405.73
		Mod 3	Year:Season+ForestType	410.28
		Mod 4	Year+Season+ForestType	409.73
		Mod 5	Season:ForestType	401.75*
		Mod 6	Year	652.13
	Explained deviance: 88.68%			
	Abundance models	Mod 1	Year:Season:ForestType	456.28
		Mod 2	Year+Season:ForestType	458.59
		Mod 3	Year:Season+ForestType	453.94*
		Mod 4	Year+Season+ForestType	461.24
		Mod 5	Year:Season	807.10
Mod 6		ForestType	653.51	
Explained deviance: 92.83%				

\* = lower AICc value

**Appendix S4** Spearman correlation ( $r$ ) between non-metric multidimensional scaling ordination (NMDS) axes based on Palmari (Brazil - successional) and Monilla (Colombia - interannual) species and functional group records and explanatory variables. Squared correlation coefficient ( $R^2$ ) between the NMDS ordinations and explanatory variables are also presented for additional confirmation

	<b>Palmari</b>	<b>Rainy</b>	<b>Successional</b>	<b>Monilla</b>	<b>Rainy</b>	<b>Successional</b>	<b>Year</b>
<b>NMDS based</b>	r (Axis 1)	-0.49***	ns	r (Axis 1)	-0.53***	-0.38***	ns
<b>on species</b>	r (Axis 2)	ns	-0.65***	r (Axis 2)	0.69***	-0.40***	ns
	$R^2$ (NMDS)	0.27***	0.34***	$R^2$ (NMDS)	0.55***	0.42***	ns
<b>NMDS based</b>	r (Axis 1)	-0.31**	-0.40***	r (Axis 1)	ns	ns	ns
<b>on functional</b>	r (Axis 2)	-0.43***	-0.51***	r (Axis 2)	-0.63***	0.22*	ns
<b>groups</b>	$R^2$ (NMDS)	0.20***	0.38***	$R^2$ (NMDS)	0.33***	0.10**	ns

ns = non significant, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$



**Appendix S5** Beta ( $\beta_{sor}$ ,  $\beta_{sim}$ ,  $\beta_{nes}$ ) analysis for Palmari (Brazil – successional) and Monilla (Colombia - interannual) between types of habitat (ChN: new abandoned “chagra”, ChA: old abandoned “chagra”, SF: secondary forest, PF: primary forest, SNF: secondary new forest and SOF: secondary old forest), years (2002, 2003, 2004), and seasons (Rainy and Dry) in the Amazon region. N/A: no species available for comparisons. Different letters, above bars, indicate statistically significant differences (Wilcoxon’s test;  $p < 0.05$ ) among years/seasons/forest