

1 **Title:** Selective logging effects on ‘brown world’ faecal-detritus pathway in tropical forests: a
2 case study from Amazonia using dung beetles

3

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11 **Abstract:**

12 While a significant effort has been made to understand how human activities influence
13 biodiversity, less attention has been given to the consequences of tropical forest disturbance on
14 belowground functional processes and its linkages with environmental drivers. Here, we
15 demonstrate how selective logging influenced dung beetle communities and two associated
16 ecological processes – namely, dung consumption and incidental soil bioturbation – in the
17 eastern Brazilian Amazon, using a robust before-and-after control-impact design. We tested
18 hypotheses about logging-induced changes on environmental condition (canopy cover, leaf
19 litter and soil texture), community metrics (e.g. dung beetle species richness and biomass) and
20 beetle-mediated faecal-detritus processing; and on the importance of the environment for beetle
21 communities and functional processes. We show that post-logging changes in canopy openness
22 do not necessarily mediate logging impacts on dung beetle diversity and biomass, which were
23 directly influenced by reduced impact logging (RIL) operations. Although neither
24 environmental condition (leaf litter or soil sand content) nor faecal consumption and incidental
25 soil bioturbation were directly affected by RIL, the relationships between environmental
26 condition and biological components were. By showing that selective logging alters the
27 linkages among belowground ecological processes and environmental drivers, we provide
28 support that logged forests can retain some important functioning processes, in particular faecal
29 consumption, even when the dung beetle diversity and biomass are impoverished. These results
30 provide support for the resistance of functional processes to logging-induced changes in
31 biodiversity.

32 **Keywords:** Amazon forest; brown world; dung beetle; dung removal; faecal-detritus pathway;
33 reduced-impact logging.

34

35 **Abbreviations:**

36 BACI: Before-and-After Control-Impact experimental design

37 DBH: Diameter at breast height

38 FSC: Forest Stewardship Council

39 FAO: Food and Agriculture Organization of the United Nations

40 GLM: Generalised Linear Model

41 RIL: Reduced-Impact Logging

42

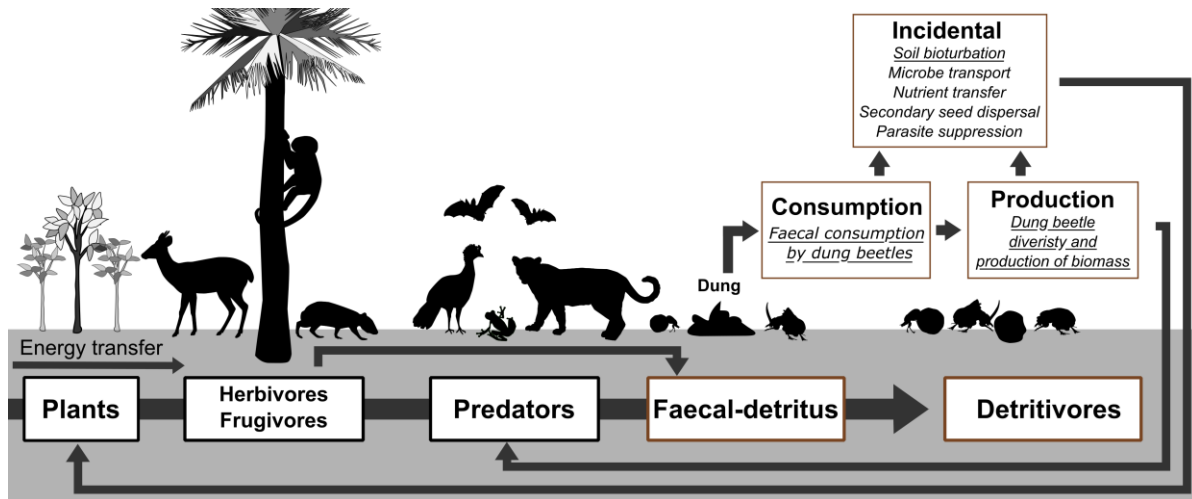
43 1. Introduction

44 Forest degradation poses a major threat to natural forests and, because it takes place over much
45 larger spatial scales, can result in just as much biodiversity loss as deforestation (Barlow et al.,
46 2016). Millions of hectares of tropical forests have been allocated for timber production
47 (Guariguata et al., 2010) and selective logging is considered a primary driver of tropical forest
48 degradation (Gatti et al., 2015; Pearson et al., 2017). Given the increased global demand for
49 low-cost timber (Blaser et al., 2011), understanding the ecological consequences from logging
50 operations is a key challenge for reconciling timber production and tropical forest
51 conservation.

52 Despite progress made to comprehend the logging consequences on forest structure and
53 canopy (Asner et al., 2006, 2004b; Gatti et al., 2015), biodiversity (David P. Edwards et al.,
54 2014; Richardson and Peres, 2016), ecosystem values such as carbon stocks (Berenguer et al.,
55 2014; Griscom et al., 2017), soil characteristics (Negrete-Yankelevich et al., 2007) and other
56 environmental aspects of tropical forests (Osazuwa-Peters et al., 2015), the impact of logging
57 on important ecosystem processes remains underrepresented in the literature. This is important,
58 as the sustainability of selective logging could be strongly linked to the extent to which
59 affected forests can maintain the ecosystem processes found in pristine forests (D. P. Edwards
60 et al., 2014; Ewers et al., 2015). Moreover, where effort has been given to understand the
61 impacts of selective logging on biodiversity and ecosystem functioning, studies normally focus
62 on aboveground components and comparatively little is known about logging consequences on
63 belowground biodiversity and brown world ecological processes (but see Slade et al., 2011). In
64 particular, faecal-detritus interactions and decomposition processes are critically important in
65 terrestrial environments and form intricate connections between below and aboveground sub-
66 systems (Moore et al., 2004). Although these interactions do not necessarily involve direct
67 trophic interactions, their decline or loss are expected to instigate a downstream cascade of

68 impacts on ecosystem processes, with dramatic implications for both ‘green’ and ‘brown’
69 worlds (Wu et al., 2011).

70 Dung beetles (Coleoptera: Scarabaeinae) are a focal group of detritivores that are
71 frequently used in ecological research linking biodiversity to ecosystem functioning under
72 changing environmental conditions (e.g. Braga et al., 2013; Slade et al., 2011). Through dung
73 manipulation for feeding and nesting purposes (Hanski and Cambefort, 1991), dung beetles
74 play a vital role in facilitating the transfer of energy and matter through dung-based pathways
75 (Nichols and Gardner, 2011). They influence a range of specific detritus processes (Fig. 1),
76 such as faecal consumption and soil bioturbation (Nichols et al., 2007), dung beetle biomass
77 production for predators (Young, 2015), secondary seed dispersal (Griffiths et al., 2016, 2015)
78 and microbial transport across the soil-surface (Slade et al., 2016). Although previous
79 investigation has shown that impacts of human activities in tropical forests on dung beetles are
80 mediated by habitat type and via body-size-dependent responses (Nichols et al., 2013b),
81 conclusions were based on a space-for-time design which may underestimate the impacts from
82 human disturbance (França et al. 2016a). Moreover, despite evidence highlighting the
83 importance of environmental context to predict dung beetle-mediated ecological processes
84 within undisturbed forests (Griffiths et al., 2015), we are not aware of any empirical study
85 exploring the extent to which an anthropogenic forest disturbance, such as selective logging,
86 alters the importance of environmental drivers for dung beetle-mediated faecal-detritus
87 processes.



88
 89 **Figure 1.** Dung beetle-mediated faecal detritus-pathway. The energy flow comes from Sun and
 90 other key soil elements (e.g. N and P), being assimilated by plants. Plants are consumed by
 91 herbivores and frugivorous, which in turn are consumed by predators. These animals, through
 92 defecating, produce the resources for the faecal-detritus pathway. Dung beetles mediate many
 93 incidental detritus-processing such as soil bioturbation, seed dispersal and nutrient transfer
 94 from detritus to the soil, therefore providing a positive feedback for plants. They also consume
 95 faeces directly, leading to secondary beetle biomass production, and are consumed by their
 96 own predators. Processes investigated in this study are underlined.

97 In this paper, we address these gaps by using a BACI experimental design to explore the
 98 impacts from selective logging in the eastern Brazilian Amazonia. Specifically, we examine (1)
 99 how environmental conditions, dung beetle communities and associated ecological processes at
 100 different stages of the dung-detrital pathway are affected by logging operations, and (2) how
 101 potential logging-induced changes in environmental drivers are reflected in ecosystem
 102 functional processes provided by dung beetles. We predict that forest disturbance induced by
 103 selective logging (1) has negative consequences on forest structure (Asner et al., 2004a), dung
 104 beetle communities and associated detrital processes (Slade et al., 2011); and (2) alters the
 105 relative importance of the environmental context for dung beetle communities and associated
 106 functional processes. We expect that, first because disturbance tends to alter both
 107 environmental heterogeneity and diversity/productivity relationships (Cardinale et al., 2000).
 108 Second, because previous research has shown that forest disturbance alters the importance of
 109 habitat variables for arthropod communities (Oliver et al., 2000), and dung beetles and
 110 associated ecological functions are greatly influenced by environmental context (Davis et al.,
 111 2001; Griffiths et al., 2015). Our findings are not only important for understanding how forest

112 disturbance shapes environmental drivers and belowground ecosystem functioning in tropical
113 forests, but also provide new insights into the ecological value of selectively logged tropical
114 forests and how environmental context mediates the biological consequences of human
115 activities.

116 2. Material and methods

117 2.1 Study site

118 The study was carried out within a logging concession area of 1.7 Mha located in the state of
119 Pará in north-eastern Brazilian Amazonia (0°53S, 52°W; Appendix A, Fig. A1). This area
120 comprises a mosaic of *Eucalyptus* plantations and regenerating secondary forests embedded
121 within a large matrix of evergreen dense tropical rainforest (Souza, 2009) subjected to low
122 levels of disturbance (Barlow et al., 2010; Parry et al., 2009). This region is within the
123 equatorial/tropical rainforest climate (Af, Köppen's classification), with annual rainfall and
124 average temperature of 2,115 mm and 26°C, respectively (Souza, 2009).

125 This logging concession is certified by the Forest Stewardship Council (FSC) and
126 follows the FAO model code with reduced-impact logging (RIL) on a 30-year rotation (FSC,
127 2014). Main activities under RIL include pre-harvest mapping, measurement and identification
128 of all commercially viable trees with DBH \geq 45cm within 10 ha (250 x 400 m) logging
129 management units planned to be logged with a specific logging intensity ($\text{m}^3 \text{ha}^{-1}$). Moreover,
130 harvest incorporates methods that aim to minimize residual stand damage, such as vine cutting,
131 directional felling, and planning of roads, skid trails and log decks (Dykstra and Heinrich,
132 1996).

133 2.2 Experimental design

134 We used the company's pre-harvest inventory to select 34 management units (hereafter sample
135 units). These included 29 'logging' units destined to be logged along a gradient of planned

136 logging intensities and five ‘control’ units that would not be logged during the course of the
137 study. The five unlogged control units were the same size as the logging units (Appendix A,
138 Fig. A1), and were located approximately 6.5 km from the closest logging units to ensure
139 sampling independence and to avoid any spillover effects from harvesting operations (Block et
140 al., 2001). Importantly, control units held a dung beetle community representative of
141 undisturbed primary forests in our study region (França et al. 2016a).

142 We sampled environmental variables, dung beetles and their associated detritus
143 processes twice within each sample unit: the pre-logging survey occurred between June and
144 July 2012, a few weeks before logging operations began. The post-logging dung beetle survey
145 took place in 2013, approximately 10 months after logging activities ended. It also occurred in
146 June and July, to minimize possible seasonal effects. RIL operations started in July and ended
147 in September 2012; logging intensity ranged from 0 to 50.3 m³ ha⁻¹ of timber (or 0 to 7.9 trees
148 ha⁻¹) that was eventually extracted within our sample units (see França et al. 2016b for logging
149 intensity details). All data were sampled at exactly the same locations and following the same
150 methods in both surveys. Sampling locations were relocated based on marking tape, or by GPS
151 when disturbance from logging activities meant this could not be found.

152 2.3 Environmental drivers of ecosystem processes

153 To evaluate whether selective logging would lead to changes in forest structure and the relative
154 importance of environmental variables for dung beetle-mediated processes (first and second
155 questions, respectively) we assessed the canopy openness, leaf litter weight and soil texture at
156 the same locations the dung beetles were sampled at each of the pre- and post-logging surveys
157 (Appendix A, Fig. A2).

158 Canopy openness was quantified by taking hemispherical photographs with a *Nikon*
159 FC-E8 fisheye lens attached to a *Nikon D40* camera levelled ~1.20 meter from the ground.
160 Photographs were taken when the sky was overcast or in the early morning and late afternoon

161 using optimum exposure for each site (Zhang et al., 2005). The Gap Light Analyser software
162 (GLA version 2.0; Frazer et al., 1999) was used to estimate the ‘canopy openness %’ factor,
163 which represents the ratio of the total amount of open space to the total area of the
164 hemispherical photograph (Frazer et al., 1999). This approach has been widely used to account
165 for the canopy openness (Medjibe et al., 2014; Niemczyk et al., 2015; Silveira et al., 2010). In
166 addition, leaf litter was collected from the forest floor within a 25×25 cm square randomly
167 placed ~1 m from each pitfall trap (Appendix B, Fig. B1). We used a *Shimatzu* AY220 balance
168 scale (*Shimadzu Corporation, Kyoto, Japan*) accurate to within ±0.001g to obtain the leaf litter
169 weight after drying it at 60 °C for 96-h. For analysis purpose and to get an aggregate value,
170 canopy openness and leaf litter metrics were the averages among the six samples taken within
171 each of the sample units. Lastly, we also took a soil sample (~10 cm depth) at the six trap
172 locations, forming a composite soil sample to represent the soil texture (clay, silt and coarse
173 sand fractions) within the sample units at each survey. Granulometric analyses were conducted
174 in the soil laboratory of *Jari Celulose S.A.* In the same way as previous dung beetle-research,
175 we also considered the sand proportion as our soil texture measure (Gries et al., 2012; Griffiths
176 et al., 2015).

177 2.4 Detritivore communities and faecal-detritus processes

178 We addressed our research questions by exploring the logging impacts on dung beetle
179 communities, assessed by using the relative dung beetle species richness and biomass, which
180 were considered as a proxy of the production available for dung beetle predators (Young,
181 2015); and two processes associated with the faecal-detritus pathway (Fig. 1): (1) faecal
182 consumption and (2) incidental detrital processes, evaluated by sampling the dung beetle-
183 mediated faecal removal and soil bioturbation, respectively.

184 2.4.1 Faecal consumption and incidental soil bioturbation

185 The day before dung beetles were sampled, we established two circular, 1-m diameter
186 mesocosm arenas (Braga et al., 2013), spaced 100 m apart, and located at least 75 m from the
187 edge of the sample units (Appendix A, Fig. A2). Each mesocosm was delimited by a nylon-
188 mesh fence (~15 cm tall) held by bamboo sticks (Appendix A, Fig. A3). To facilitate the
189 evaluation of these processes, we cleared the soil surface of any leaf litter and vegetation
190 before placing a single 200-g experimental faecal deposit (4:1 pig to human ratio following
191 Marsh et al., 2013) at the centre of each mesocosm (Braga et al., 2013, 2012).

192 This mesocosm design allows dung beetles to freely enter the arena, and perform their
193 feeding and nesting activities that result in further underground relocation of faecal resources
194 while limiting the horizontal dung removal of brood balls by roller species to the contained
195 area (~0.785 m²). After 24-h exposure period to the dung beetle communities, we weighed the
196 remaining dung (when present) and calculated the faecal consumptions rates. This 24-h period
197 of exposition was the same as previous studies following this protocol (Braga et al., 2013,
198 2012; Nichols et al., 2013b) and was chosen based on known movements of dung beetles
199 (Silva and Hernández, 2015) to avoid the risk of beetles from outside the unit perform the
200 faecal-detritus processes measured within the mesocosm. A parallel humidity control
201 experiment was set aside each arena (Appendix A, Fig. A3). Thus, changes in humidity of each
202 experimental faecal deposit were considered to calculate the faecal consumption rates (see
203 Appendix B for details). To quantify the incidental soil bioturbation rates as consequence of
204 excavations by dung beetles, we collected the loose soil clearly found above the soil surface
205 and weighed it after drying it at 60 °C for a week (Braga et al., 2013, 2012). We pooled the
206 data from the two arenas to get an aggregate value of dung beetle-mediated functional
207 processes for each sample unit.

208 *2.4.2 Detritivore biomass and richness*

209 We sampled dung beetles by using six standardized baited pitfall traps (19 cm diameter and 11
210 cm deep) spaced 100 meters apart in a 2x3 rectangular grid within each sample unit (Appendix
211 A, Fig. A2B). This trap spacing helped ensure independence between them (Silva & Hernández
212 2015) as well as an even spatial coverage of each sample unit. Traps were buried with their
213 opening at ground level, containing approximately 250 ml of a saline solution and a small bait-
214 container with ~35 g of fresh dung (4:1 pig to human ratio, Marsh *et al.* 2013). Data from the
215 six pitfall traps in each sample unit were pooled to get an aggregate value and improve
216 representation.

217 We restricted our sample window to 24 hours in each collection period, as short sample
218 periods are known to be efficient at attracting a representative sample of the local beetle
219 community (Braga *et al.*, 2013; Estrada and Coates-Estrada, 2002). Moreover, longer sample
220 periods would have increased the probability of attracting dung beetles from outside of the
221 sample units (Silva and Hernández, 2015), and therefore from units with different
222 environmental conditions. In addition, evidence from data collected in the same region
223 suggests 24-h sampling periods as good predictor of community metrics from longer sampling
224 durations (França *et al.* 2016a).

225 All trapped dung beetles were dried and transported to the laboratory where they were
226 identified to species, or morphospecies where the former was not possible. We assessed the dry
227 mean body mass for each species by weighing up to 15 individuals using a *Shimadzu AY220*
228 balance (*Shimadzu Corporation, Kyoto, Japan*) accurate to within ± 0.001 g. Beetle biomass
229 was estimated by summing all inferred body masses from each sample. Voucher specimens
230 were added to the collection of Neotropical Scarabaeinae in the Insect Ecology and
231 Conservation Laboratory, Universidade Federal de Lavras, Lavras, Brazil; and in the
232 Entomological Section of the Zoology collection of Universidade Federal de Mato Grosso,
233 Cuiabá, Brazil.

234 2.5 Statistical analyses

235 All statistical analyses were performed within the R computing environment (R Core Team,
236 2017). We addressed our first question by using generalised linear models (GLMs) with a
237 logarithmic link function (Zuur et al., 2009) in the *glm()* routine (*stats* package, R Core Team,
238 2017). We ran an independent GLM followed by a two-way ANOVA to assess the influence of
239 the explanatory variables “survey” (two levels: pre- and post-logging), “treatment” (two levels:
240 control and logging sites), and the interaction “survey \times treatment” on the environmental
241 metrics (canopy openness, leaf litter weight, and soil sand proportion) and dung beetle-
242 mediated detritus processes (species richness, biomass, and rates of faecal consumption and
243 soil bioturbation). Post hoc pairwise t-tests with non-pooled standard deviations were used
244 when both “survey” and “treatment” significantly affected the response variables. A quasi-
245 binomial error structure was used for proportion data (canopy openness and soil sand
246 proportion); and quasi-Poisson error structure was used for overdispersed count data (leaf litter
247 weight, beetle biomass, and rates of dung removal and soil bioturbation) (Crawley, 2002).
248 Spatial autocorrelation within our dataset was assessed by performing Pearson-based Mantel
249 tests (Legendre and Legendre, 1998) with 1000 permutations (*mantel* routine, *vegan* package,
250 Oksanen et al. 2015). Mantel tests were made separately for dung beetle species richness and
251 biomass from each survey, allowing us to examine whether spatial correlation existed on both
252 sets of analysis (Appendix B).

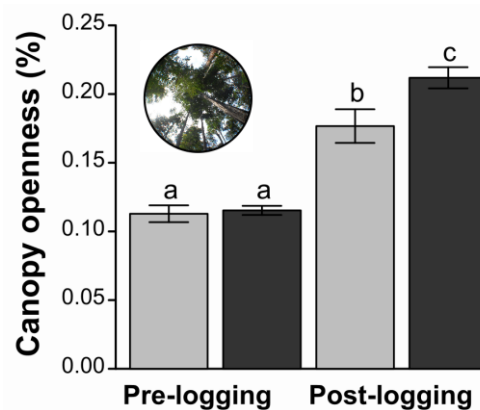
253 Because we also sought to examine how potential logging-induced changes on
254 environmental drivers influence those on beetle-mediated detrital processes (second question),
255 we used a hierarchical partitioning (HP) analysis (Chevan and Sutherland, 1991) to compare
256 the relative and independent importance of our three environmental variables on the dung
257 beetle richness, biomass, and rates of faecal consumption and incidental soil bioturbation. HP
258 is a multi-regression technique in which all possible linear models are jointly considered to

259 identify the most likely predictors while minimizing the influence of multicollinearity and
260 providing the independent contribution of each predictor (Chevan and Sutherland, 1991).
261 Competing models were evaluated based on R^2 goodness of fit statistic, which allowed us to
262 interpret the independent effects as proportion of explained variance. Significance ($\alpha = 0.05$) of
263 independent effects of each predictor was calculated using a randomization test with 1000
264 iterations (Mac Nally, 2002; Walsh and Nally, 2013).

265 We analysed each response variable separately at each survey (pre and post-logging) to
266 evaluate whether these faecal-detritus processes are influenced by similar drivers after logging
267 operations. Gaussian distributions were tested using the Shapiro-Wilk normality test through
268 the *Shapiro.test()* function (*stats* package, Patrick Royston 1995). Hierarchical partitioning and
269 further randomization-significance tests were executed using the *hier.part* package (Walsh and
270 Nally, 2013). Table C1 (Appendix C) demonstrates the data used for GLM's and HP analyses.

271 3. Results

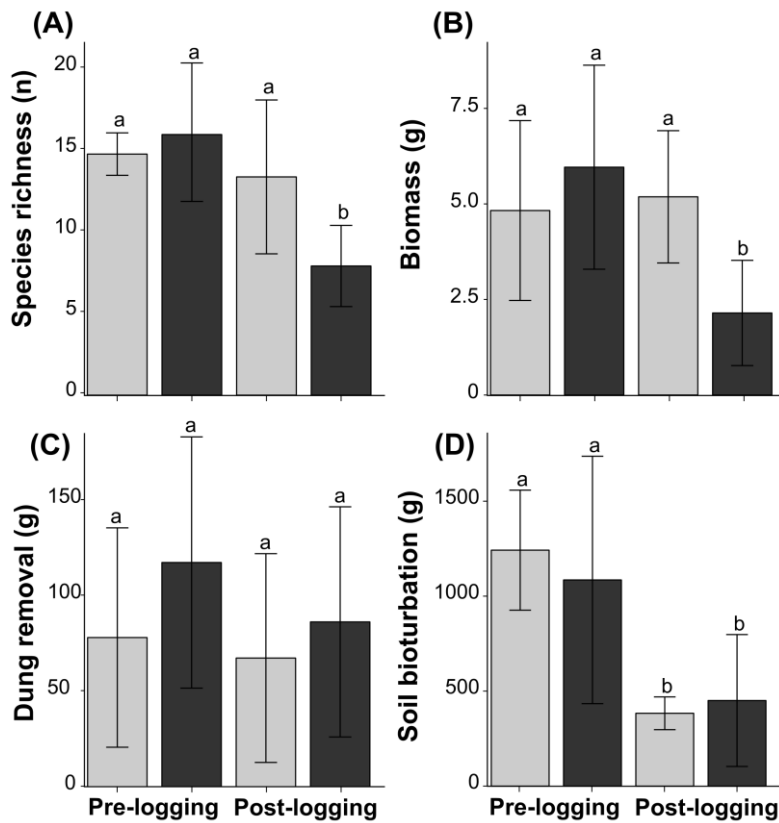
272 The canopy openness was the only environmental aspect changing between surveys (two-way
273 ANOVA: *survey* \times *treatment* $F_{1, 64} = 1.4$, $p = 0.230$; *treatment* $F_{1, 65} = 3.7$, $p = 0.058$; *survey* $F_{1, 66} = 174.2$, $p < 0.001$), and increased significantly in logged forests (t-test, P-values ≤ 0.02 ; Fig.
274 2).
275



276
277 **Figure 2.** Canopy openness changes between control (light grey bars) and logging sites (dark
278 grey bars) at surveys performed before (left bars in the panels) and after selective-logging

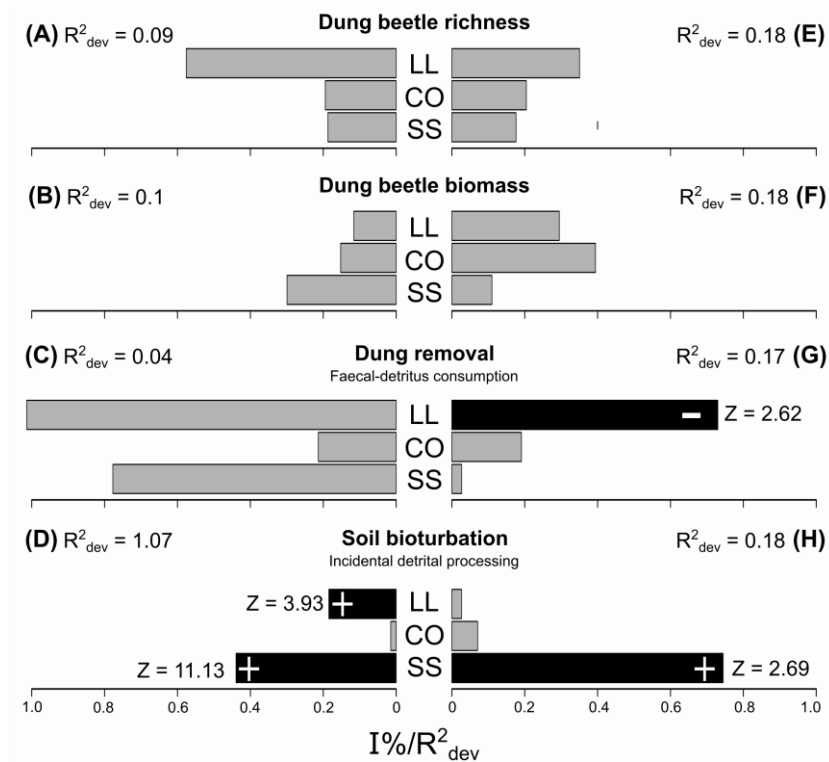
279 (right bars in the panels). Means \pm standard deviation (SD) followed by the same letter indicate
280 post hoc zero difference at 5%.

281 We also found negative logging impacts on dung beetle richness (two-way ANOVA:
282 *survey* \times *treatment* $F_{1, 64} = 7.8$, $p = 0.006$; *treatment* $F_{1, 65} = 3.2$, $p = 0.078$; *survey* $F_{1, 66} = 70.4$,
283 $p < 0.001$; Fig. 3A) and biomass (two-way ANOVA: *survey* \times *treatment* $F_{1, 64} = 11.4$, $p =$
284 0.001 ; *treatment* $F_{1, 65} = 1.7$, $p = 0.19$; *survey* $F_{1, 66} = 41.8$, $p < 0.001$; Fig. 3B), which reduced
285 up to 50% at logged forests (Fig 3A-B). However, while soil bioturbation decreased at both
286 control and logged sites in the second survey (two-way ANOVA: *survey* \times *treatment* $F_{1, 64} =$
287 0.3 , $p = 0.53$; *treatment* $F_{1, 65} = 0.07$, $p = 0.78$; *survey* $F_{1, 66} = 35.23$, $p < 0.001$; Fig. 3D), no
288 significant direct logging impacts were found on dung beetle-mediated faecal consumption
289 (two-way ANOVA: *survey* \times *treatment* $F_{1, 64} = 0.1$, $p = 0.750$; *treatment* $F_{1, 65} = 1.8$, $p = 0.173$;
290 *survey* $F_{1, 66} = 3.4$, $p = 0.069$; Fig. 3C). Importantly, although a very weak spatial
291 autocorrelation was found in the pre-logging dung beetle richness and biomass ($r = 0.18$ and r
292 $= 0.12$, respectively; all P-values ≤ 0.03), these metrics were not spatially structured in the
293 post-logging survey ($r = -0.41$ and $r = -0.42$, respectively; all P-values = 0.999), even when the
294 control units were excluded from analysis (Appendix B).



295
 296 **Figure 3.** Dung beetle species richness (A), biomass (B), and rates of dung removal (C) and
 297 incidental soil bioturbation (D) sampled in control (light grey bars) and logging sites (dark grey
 298 bars) at surveys performed before (left bars in the panels) and after selective-logging (right
 299 bars). Means \pm standard deviation (SD) followed by the same letter indicate post hoc zero
 300 difference at 5%.

301 Relating faecal-detritus pathways to environmental conditions before and after logging
 302 Hierarchical partitioning and randomization tests revealed no environmental influence on the
 303 variation of dung beetle species richness or biomass in either the pre- or post-logging
 304 assessment (Fig. 4). However, faecal consumption was negatively associated with leaf litter
 305 volume after logging operations (Fig. 4G). Leaf litter also had a positive association with pre-
 306 logging soil bioturbation rates, and this incidental detrital processing was positively related to
 307 the sand proportion in both pre- and post-logging surveys (Fig. 4D-H). Table C2 (Appendix C)
 308 show results of independent and joint effects of predictor variables for each faecal-detritus
 309 process performed by dung beetles.



310
 311 **Figure 4.** Distribution of the percentage of the independent effects of different predictors on
 312 dung beetle-mediated faecal detritus-processes. Left panels show pre-logging results (A-D) and
 313 right panels the post-logging ones (E-H). The x-axis shows the percentage of the independent
 314 effects (I %) divided by the total explained variance of the complete model (R^2_{dev}). LL = leaf
 315 litter weight (g), CO = canopy openness (%) and SS = Soil sandy (%). Black bars represent
 316 significant effects ($\alpha = 0.05$) as determined by the randomization test. Z-scores for the
 317 generated distribution of randomized I's (I value = the independent contribution towards
 318 explained variance in a multivariate dataset) and an indication of statistical significance are
 319 calculated as $(\text{observed} - \text{mean}(\text{randomizations}))/\text{SD}(\text{randomizations})$, and statistical
 320 significance is based on the upper 0.95 confident limit ($Z \geq 1.65$). Pearson's (ρ) positive or
 321 negative relationships are shown by + or -, respectively. R^2_{dev} (displayed in parenthesis beside
 322 each capital letter) is the total deviance explained by a generalized linear model including all
 323 the predictors considered for each faecal-detritus pathway response.

324 4. DISCUSSION

325 Understanding how anthropogenic disturbances alter natural environments – and thereby
 326 biodiversity and ecological functioning – is a question at the core of the current biodiversity
 327 crisis (Laurance, 2007). In this research, we used observations on natural dung beetle
 328 communities and associated ecological processes to explore the selective logging consequences
 329 on beetle-mediated detritus processes in tropical forests. While we demonstrate that RIL
 330 operations in the eastern Amazon negatively impacted dung beetle richness and biomass, we

331 also found support about the resistance of functional processes to logging-induced changes in
332 biodiversity (Ewers et al., 2015). Lastly, logging-induced forest canopy changes were not the
333 major drivers of beetle richness and biomass in either pre- or post-logging forests, although the
334 importance of leaf litter and soil texture for other beetle-mediated processes was altered after
335 RIL operations. Below, we discuss each finding in turn, before turning to the general
336 implications for reconciling timber trade and tropical forest conservation.

337 4.1 Selectively logged forests can retain belowground functional 338 processes

339 Our findings give support to previous research suggesting that functional processes operating
340 in tropical forests remain substantially resistant to forest degradation caused by logging (Ewers
341 et al., 2015). The maintenance of faecal consumption rates at logged forests occurred despite
342 the large losses in dung beetle richness and biomass, considered as key drivers for the dung
343 beetle-mediated ecological processes (Gregory et al., 2015; Nichols et al., 2013a). While
344 providing support that spatial autocorrelation in species diversity may change with disturbance
345 (Biswas et al., 2017), such logging-induced beetle and biomass losses were supported by
346 Mantel test results demonstrating that these post-logging patterns were driven by RIL
347 operations and not by spatial autocorrelation. Although faecal consumption did not change
348 among treatments, we surprisingly found soil bioturbation rates decreasing at both control and
349 logged sites in the post-logging survey (Fig. 3D). Such decoupled responses, both between
350 distinct dung beetle detrital processes and with their community metrics (e.g. species richness
351 and biomass), to forest degradation have been shown in tropical regions (Braga et al., 2013;
352 Nichols et al., 2013b), and might result from the fact that other taxa are able to perform faecal
353 consumption without removing as much soil to the surface as dung beetles. For example, ants,
354 termites, earthworms and micro-decomposers have been previously recorded participating in
355 faecal consumption (Dangles et al., 2012; Slade et al., 2016; Wu et al., 2011), and are likely to

356 buffer the functional consequences of dung beetle species and biomass losses in detritus food-
357 webs present within logged forests. Regardless of the factors giving rise to it, our research
358 provides empirical evidence that logged forests managed through RIL techniques can retain
359 part of the belowground ecological processes operating in pristine forests (D. P. Edwards et al.,
360 2014), even when invertebrate communities are largely affected (Ewers et al., 2015). Although
361 dung beetles are good predictors of responses of many other taxa (Barlow et al., 2016; F. A.
362 Edwards et al., 2014; Gardner et al., 2008a), we stress that using ecological processes mediated
363 by one taxa is not enough to argue that the patterns found here will occur everywhere and for
364 all taxa. Further logging research should be targeted across a broader sample of regions, taxa
365 and functional processes.

366 4.2 Selective logging alters linkages between environmental and 367 functional components in tropical forests

368 Evidence that forest degradation can change the environmental importance for decomposition
369 processes are underexplored in the literature. In particular, our study shows that logging
370 operations in the Brazilian eastern Amazon altered the occurrence, direction and strength of
371 linkages between environmental condition (leaf litter and soil texture) and the dung beetle-
372 mediated faecal consumption and soil bioturbation (Fig. 4). The positive influence that leaf
373 litter has on soil chemistry and quality (Nyeko, 2009; Uriarte et al., 2015) may explain its
374 interaction with pre-logging soil bioturbation rates; whereas, in the post-logging survey, leaf
375 litter effects on roller dung beetles (as suggested by Nichols et al., 2013a) is a likely reason for
376 its negative association with faecal consumption. These roller species usually roll their brood
377 balls away from the faecal deposit before burial beneath the soil (Hanski and Cambefort,
378 1991), a behaviour that may be hampered by the excess of leaf litter resulting from logged
379 trees. Lastly, it is very likely that sandy soil properties, such as pore space and reduced
380 cohesion, facilitate dung beetles to move larger amounts of earth to the soil surface when

381 building nesting tunnels (Griffiths et al., 2015; Marshall et al., 1996); which is a potential
382 explanation for its positive effects on pre- and post-logging soil bioturbation rates.

383 Two intriguing results we found in this research are (1) the increased canopy openness
384 at both control and logged sites in the second survey, and (2) the post-logging changes in dung
385 beetle richness and biomass occurring apart from the significant logging effects on canopy
386 openness (Fig. 2 and 3A-B). First, while the increased canopy opening within our control sites
387 is likely related to the natural heterogeneity and variation in canopy dynamics of Amazonian
388 forests, mainly responding to seasonal changes in water availability and solar radiation (Jones
389 et al., 2014), the significantly greater canopy openness found in logged sites reflects well-
390 known logging impacts on tropical forest canopies (Asner et al., 2006; Yamada et al., 2014).
391 Secondly, our results contrast markedly with the consensus reported by previous research
392 showing dung beetle responses to more severe forms of forest disturbance being majorly driven
393 by changes in forest structure (Hosaka et al., 2014; Nyeko, 2009). As selective logging is
394 known to cause sublethal and direct impacts on dung beetle communities (Slade et al. 2011,
395 Bicknell et al. 2014, França et al. 2016a, 2016b), we presume these findings reflect the
396 limitations of canopy openness as a measure of changes in forest structure, and the lower
397 intensity of RIL assessed in our research. Hemispherical photos taken 10 months after
398 disturbance inevitably capture both the state of the upper canopy and the regeneration in the
399 understorey, with the latter often obscuring the former. Moreover, the absence of
400 environmental influence on dung beetle communities within logged forests have also been
401 previously reported (Slade et al., 2011), which further outlines the difficulty of measuring
402 appropriate environmental metrics to assess the impacts of human activities on tropical
403 biodiversity (Gardner et al., 2008b; Oliveira et al., 2017).

404 4.4 Conclusions

405 This investigation addressed to better understand the role that environmental conditions have in
406 mediating the logging impacts on belowground functional processes. We found no support that
407 our measures of canopy openness mediated dung beetle responses to logging, but we provide
408 evidence that forest disturbances may alter the environmental importance for ecosystem
409 functioning in tropical forests. While the dung beetle patterns reported here highlight the
410 importance of within-forest disturbance (Barlow et al., 2016) and the irreplaceable role that
411 pristine forests have to retain tropical biodiversity (Gibson et al., 2011), we demonstrate that
412 carefully managed and certified selectively logged forests nevertheless can retain ecosystem
413 processes such as detrital consumption and soil bioturbation (D. P. Edwards et al., 2014; Ewers
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422 **Supplementary material:**

423 Additional supplementary material may be found in the online version of this article:

424 **Appendix A.** Supplementary figures.

425 **Appendix B.** Supplementary experimental procedures.

426 **Appendix C.** Supplementary tables.

427

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