

1 **Biodiversity in tropical plantations is influenced by surrounding native vegetation**
2 **but not yield: a case study with dung beetles in Amazonia**

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10
11 **ABSTRACT**

12 Human-modified forests, including plantations and managed forest, will be a major
13 component of tropical landscapes in the near future. To conserve biodiversity across
14 modified tropical landscapes we must first understand what influences diversity in
15 planted areas. We studied dung beetle communities in *Eucalyptus* plantations to assess
16 the influence of local (canopy openness and soil texture) and landscape factors
17 (surrounding native forest cover) on taxonomic and functional diversity, and to determine
18 whether biodiversity in plantations is affected by timber production. Dung beetle
19 community composition in *Eucalyptus* plantations was largely explained by the
20 surrounding native forest cover, as Simpson's diversity and functional diversity (Rao's
21 quadratic entropy) increased with the extent of native forest in buffer areas. However, the
22 abundance of dung beetle species associated with undisturbed forest was not explained
23 by any of the explanatory variables. The coarse sand content of the soil explained much
24 of the functional similarity between plantations and native forests, as well as variation in
25 dung beetle community structure. The total abundance of dung beetles in plantations
26 increased with coarse sand content, whereas body mass declined, and dung beetle
27 abundance and functional originality decreased with canopy openness. Timber production
28 intensity did not explain the variation in any of the measured diversity parameters. If
29 enhancing biodiversity in plantations is a management goal, then these results highlight
30 the importance of restoring or retaining native forest areas in modified landscapes. They
31 also suggest that integrated management could improve biodiversity in *Eucalyptus*
32 plantations without reducing timber production.

33 **Keywords:** Scarabaeinae, silviculture, land-sharing, land-sparing, forestry

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36 INTRODUCTION

37 Planted forests are rapidly expanding at a rate of around 5 million ha⁻¹ yr⁻¹, with
38 much of that increase occurring in tropical landscapes as a result of the growing global
39 demand for timber, cellulose and oils (FAO 2010, Vijay et al. 2016). In Brazil,
40 *Eucalyptus* spp. plantations have rapidly become important sources of pulp, lumber,
41 charcoal, plywood and firewood. By 2016, Eucalyptus plantations covered an area of c.
42 7.5 million ha, which is c. 100,000 ha more than the previous year (IBGE 2017). The
43 expansion of these silvicultural systems over native habitat contribute to the worldwide
44 loss of biodiversity and can jeopardise many ecosystem functions and services (Green
45 2005, Newbold et al. 2014, Barlow et al. 2018). To minimise biodiversity losses, it is
46 important to assess how to maximise the biodiversity and functional value of the human-
47 modified landscapes that are increasingly prevalent in the tropics, and are likely to cover
48 most of the world in the near future (Ellis and Ramankutty 2008, DeClerck et al. 2010,
49 Barlow et al. 2018).

50 There is a growing interest in the value of forested production systems for
51 maintaining biodiversity (Barlow et al. 2007) and management alternatives targeting this
52 goal have become more common in the last decade. A growing number of studies have
53 shown how some taxa can persist in tropical crops that emulate structural aspects of native
54 forests and landscapes, including cocoa agroforestry (Schroth and Harvey 2007, Cassano
55 et al. 2012), oil palm (Koh and Wilcove 2008, Gray et al. 2014, Dislich et al. 2016), coffee
56 plantations (Tadesse et al. 2014), and timber monocultures including *Eucalyptus* (Bremer
57 and Farley 2010). Such studies suggest that both local conditions, such as structural
58 complexity or canopy cover, and landscape context, such as proximity to remnants of
59 native forests, can enhance the biodiversity in plantations. However, although native
60 species from forest remnants can improve ecosystem functioning within modified areas
61 (Blitzer et al. 2012), ecosystem processes can also change as a result of the distinct
62 functional structure of the biological community in the modified habitats (Hobbs et al.
63 2009, Tavares et al. 2019).

64 Despite advances in biodiversity conservation in the tropics, efforts to improve the
65 conservation value of plantations (e.g., certification by the Forest Stewardship Council)
66 are undermined by a lack of knowledge about the specific characteristics of managed
67 forests and plantations that can increase or maintain biodiversity. In part, this lack of
68 information has arisen because most studies assessing tropical diversity focus on the
69 remnants of native vegetation instead of the production matrix, which considers the

70 plantation as well as the surrounding landscape (Carnus et al. 2006, Franklin and
71 Lindenmayer 2009). Hence, although plantations are frequently established near or within
72 areas of native forest, the relative importance of local conditions for enhancing
73 biodiversity vs. the extent and proximity of nearby natural habitats is not always clear.
74 Furthermore, most studies of biodiversity in tropical plantations to date have focused on
75 species diversity, but we know very little about changes in functional diversity following
76 forest modification (but see Audino et al. 2014, Cisneros et al. 2014, Beiroz et al. 2018).

77 Studies of taxonomic diversity are of great value for conservation but studies of
78 functional diversity can also provide information about the mechanisms underlying
79 biodiversity loss (Cardinale et al. 2012, Mouillot et al. 2013). As plantations are
80 intensively managed, they represent strong environmental constraints for most species
81 and reduce functional diversity within sites (Bässler et al. 2014). Whereas forest habitats
82 have greater diversity and canopy structure, which enhances environmental heterogeneity
83 and provides habitats for species with different niches (Basset et al. 2001, Košulič et al.
84 2016). Thus, management strategies emulating environmental conditions of native forests
85 may help maintain functional diversity. In addition, the diversity of the surrounding
86 landscape can promote greater biodiversity within modified and degraded sites (Costa et
87 al. 2017). Consequently, it is conceivable that greater environmental heterogeneity within
88 plantations as well as greater native habitat cover in the surrounding landscape could
89 promote migration and persistence of diverse species in human-modified habitats (Mori
90 et al. 2018).

91 Information on the relationships between species' functional traits and the filters
92 driving community assembly (i.e. environment, biotic interaction, dispersal processes) in
93 human-modified habitats can provide valuable information for management strategies
94 that balance production and conservation (Cadotte et al. 2011). We therefore aimed to
95 assess the influence of local and landscape factors on biodiversity in *Eucalyptus*
96 plantations set within a matrix of primary Amazonian forest in Brazil, using dung beetles
97 as a focal organism. Dung beetles provide a useful indicator to assess the effects of habitat
98 modification, because most species show a high degree of habitat specificity and are
99 sensitive to environmental changes in tropical forests (Spector and Ayzama 2003, Larsen
100 et al. 2006, Nichols et al. 2007, 2009). Dung beetles can also be examined from both
101 taxonomic and functional perspectives, as their functional or behavioural traits can be
102 linked to ecological processes via their responses to habitat changes (i.e., environmental
103 filters, Barragán et al. 2011, Slade et al. 2011, Nichols et al. 2013). We evaluated the dung

104 beetle communities in *Eucalyptus* plantations to understand how local and landscape
105 conditions influence dung beetle species and functional diversity and shape their
106 community structure. We focussed on canopy openness as a key environmental condition
107 in plantations because open canopies are associated with higher temperatures and lower
108 levels of humidity in air and soil, which negatively affect many dung beetle species
109 (Gardner et al. 2008, Larsen 2012, Hosaka et al. 2014). We evaluated the extent of native
110 forest cover around each plantation as a key landscape condition, as dung beetle
111 communities in modified habitats may depend on native forest as a source of species
112 (Gray et al. 2016). Finally, we assessed the impact of timber production on dung beetle
113 diversity, as the economic viability is key to ensure the implementation of management
114 strategies to increase biodiversity (see Naumov et al. 2018). We used native forest areas
115 as a baseline representing highly diverse habitat to test the following hypotheses:

116 1) Plantations that have a similar degree of canopy openness to native forests will
117 also have comparable dung beetle communities. Plantations with a high level of canopy
118 openness will have lower taxonomic and functional diversity of dung beetle communities
119 compared to native forest. Canopy openness will also affect community composition and
120 structure in plantations, reducing the number of native forest-associated species and
121 increasing the functional β -diversity.

122 2) Plantations with a high proportion of surrounding native forest cover will have a
123 higher taxonomic or functional diversity of dung beetles. The extent of the surrounding
124 native vegetation will influence community composition and structure such that greater
125 cover of surrounding native forest will increase the number of forest-associated species
126 within plantations, resulting in a functional structure similar to primary forest.

127 3) Based on the premise that the intensification of production and the suppression
128 of native vegetation has negative impacts on biodiversity (Flohre et al. 2011), dung beetle
129 taxonomic and functional diversity metrics will decline with increasing timber production
130 and hence dung beetle communities in plantations and native forests will be more
131 dissimilar at sites with high timber production.

132

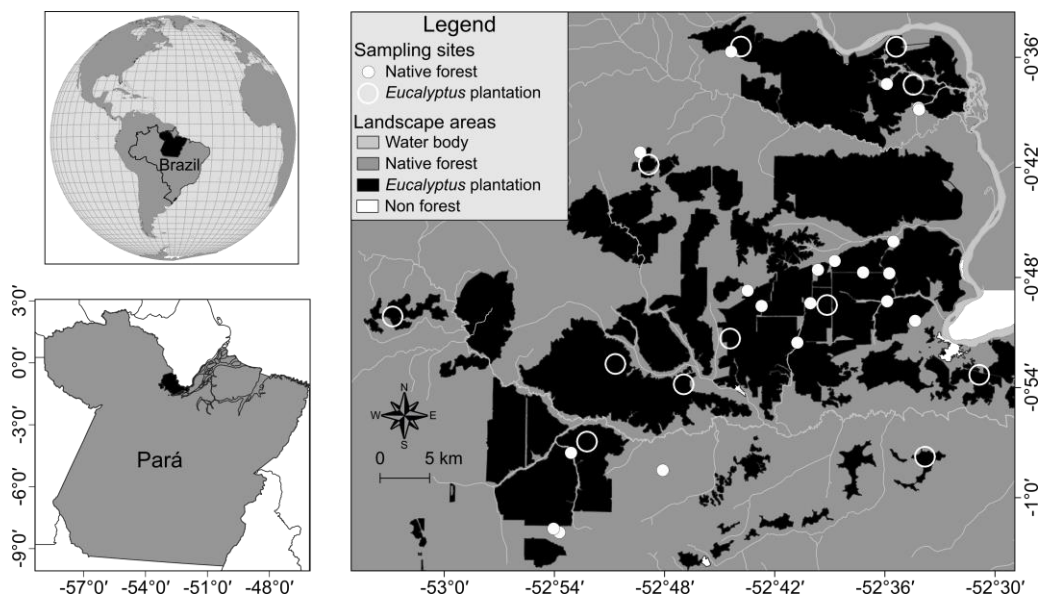
133 **MATERIAL AND METHODS**

134 *Study site*

135 Our data was collected in the Jari River basin in the north-eastern Brazilian
136 Amazon, on the border between Pará and Amapá States (00°27' - 01°30' S, 51°40' - 53°20'
137 W). The area has a mean annual temperature of $26.9 \pm 0.6^\circ\text{C}$, with mean maxima and

138 minima of $31.4 \pm 1.1^\circ\text{C}$ and $22.5 \pm 0.2^\circ\text{C}$, respectively (Climate-Data.org 2016). It has a
 139 tropical monsoon climate, with a marked wet season from January to June, a distinct dry
 140 season from September to November, and an average annual rainfall of 2115 mm (Amw
 141 in Köppen climate classification; Parry et al. 2007). The intensive replacement of native
 142 forest by exotic tree plantations started in 1967 and the area is now a continuous block of
 143 virtually undisturbed *terra firme* primary forest ($> 5000 \text{ km}^2$) connected by primary forest
 144 corridors (*ca.* 200 m wide) with large patches of exotic tree plantations, mainly
 145 *Eucalyptus* sp. (450 km^2 ; Figure 1; Parry et al. 2007).

146



147

148 Figure 1: Map of the Jari River basin in Pará State, Brazil, showing the location of *Eucalyptus* plantations
 149 in which dung beetle communities were sampled; white circles delineate 1-km buffers around the plantation
 150 sites, and white dots represent reference sites in native forest.

151

152 *Dung beetle sampling*

153 The annual rainfall in 2009 was considered high for the region, with 2081 mm
 154 during the wet season and 153 mm in the previous dry season (mean dry season rainfall
 155 from 2008 to 2013 was 113 mm). We sampled dung beetles during March and April 2009
 156 in 12 *Eucalyptus* plantations, varying in age from 2–5 years (stands are harvested after 5–
 157 7 years). The *Eucalyptus* sites have been cleared, burned and bulldozed since the early
 158 1970's to 1980's and all native vegetation colonizing the understorey is periodically
 159 cleared or suppressed by herbicidal treatment (Louzada et al. 2010). The distance between
 160 plantations and the nearest area of native forest ranged from 0.2 to 1.6 km. We also
 161 sampled in eight primary forest corridors and 12 areas of undisturbed primary forest; we
 162 considered these collectively as sites of 'native forest', as they could facilitate

163 colonisation into the plantations. Furthermore, although the community structure of dung
164 beetles differs between forest corridors and undisturbed forest sites (Barlow et al. 2007),
165 they are comparatively much more similar to undisturbed forest than plantations (Beiroz
166 et al. 2018).

167 At each site, we set up one transect of five pitfalls traps, located 150 m apart and at
168 least 500 m from the edge. The traps consisted of plastic containers (19 cm diameter and
169 11 cm deep), which were part-filled with water, salt, and detergent, baited with 30 g of
170 human dung, and protected from rain with a plastic lid suspended 20 cm above the
171 surface. Sampling took place over a period of 48 hours at each site. Dung beetle
172 specimens were transported from the field in 90% alcohol, and then sorted and stored in
173 paper envelopes in the laboratory. We identified the dung beetles using the New World
174 Scarabaeinae key to genera and subgenera (Vaz-De-Mello et al. 2011), a field guide for
175 dung beetles in the Jari River basin (Louzada et al. *in prep.*), and the reference collection
176 ‘Coleção de Referência de Escarabeíneos Neotropicais’ at the Universidade Federal de
177 Lavras (CREN – UFLA) in Minas Gerais State, Brazil. Identifications were made to
178 species level where possible; where there was uncertainty, beetles were identified to
179 genus level and assigned a morphospecies number. All specimens were deposited at
180 CREN – UFLA.

181 We obtained information on dung beetle functional groups with two independent
182 surveys, in January and February 2012, and in November and December 2013 (see Beiroz
183 et al. 2017 for details). The beetles were grouped by activity period, dietary preference,
184 and nesting behaviour. To determine the diurnal or nocturnal activity period we sampled
185 beetles from 7:00 to 18:00 and from 19:00 to 6:00, respectively. To assess dietary
186 preference (coprophagous, necrophagous, or generalists) we baited the pitfall traps with
187 dung and carrion and assigned the dung beetle species as necrophagous or coprophagous
188 based on the statistical significance ($p < 0.05$) of IndVal analysis for carcass or dung
189 baited pitfalls, respectively; or as generalist when there was no significant association
190 with any bait ($p > 0.05$; Beiroz et al. 2018). Finally, beetles were assigned as rollers
191 (telecoprids), tunnelers (paracoprids), or dwellers (endocoprids), based on their genus
192 (Halfpter and Matthew, 1966; Beiroz et al. 2017). We obtained average species body mass
193 calculated from the mean dry mass of 15 individuals (or the maximum number available)
194 of each species using a precision balance (0.001 g) after oven-drying for 48 h in 40 °C;
195 for species with few sampled individuals we used additional specimens previously
196 deposited at CREN – UFLA.

197

198 ***Predictors of taxonomic and functional metrics***

199 We used canopy openness as a key environmental variable that was likely to
200 influence the response of dung beetles within the range of the age of our plantation sites
201 (2-5 years), as new sites are rapidly colonized and more open canopies are associated with
202 higher temperatures and lower levels of humidity in air and soil, which negatively affect
203 many dung beetle species (Gardner et al. 2008, Larsen 2012, Hosaka et al. 2014). To
204 estimate canopy openness, we took semi-hemispheric photographs of forest canopy at
205 1.5-m above ground level at each pitfall trap location in 2009 and analysed the images in
206 gap light analyser (GLA) software to obtain the percentage openness (Frazer et al. 1999).
207 Canopy openness was not correlated to *Eucalyptus* tree age (Figure S1) and could
208 therefore be assessed independently of timber production.

209 We estimated the percentage of native forest cover within a 1-km buffer
210 surrounding each sampling point in *Eucalyptus* plantations using GIS data provided by
211 the landowner. The size of the buffer was determined based on previous studies of dung
212 beetles movement (da Silva and Hernández 2015) to give a realistic distance for
213 recolonisation of disturbed areas within 1-2 years.

214 Timber production was calculated from data provided by the landowner in tons of
215 timber produced per hectare and corrected for the age of the trees at harvest ($\text{t ha}^{-1} \text{age}^{-1}$).
216 The landowner provided data on timber biomass obtained from each plantation site from
217 2007 up to 2013, and we used the mean value of all these years as the timber production
218 variable. However, due to the confidentiality of commercial data we only give the
219 standardized value. Finally, to account for the potential confounding influence of soil
220 structure on some dung beetle functional groups and community metrics (Beiroz et al.
221 2017), we also determined the average coarse sand content (g kg^{-1}) of each site. Soil
222 samples were taken from 0-10 cm depth at four points near each pitfall trap at each site
223 in 2013, we then calculated the average value for each site. The company informed their
224 density of timber biomass obtained from each plantation site from 2007 up to 2013, and
225 we used the mean value of all these years as the timber production variable. However,
226 due to agreement reasons we show the standardized value.

227

228 ***Data analysis***

229 All analyses were conducted in R version 3.4.4 (R Core Team 2018) and all
230 environmental variables were standardised to zero mean and unit standard deviation prior

231 to analysis. We analysed data from *Eucalyptus* plantation plots using the native forest
232 data as a baseline reference, but we did not make direct statistical comparisons between
233 plantations and native forest sites.

234 To assess the composition and structure of dung beetle communities at each site,
235 we calculated Jaccard's dissimilarity based on presence-absence data, and Bray-Curtis'
236 dissimilarity based on number of individuals per species, using the *vegdist* function in the
237 *vegan* package (Oksanen et al. 2017). Total dung beetle abundance and species richness
238 were determined from the number of individuals and (morpho-) species at each
239 *Eucalyptus* site. The community-weighted mean of dung beetle body mass (CWM body
240 mass) at each site was calculated as the mean species body mass, weighted by the relative
241 abundance of the species (for more details Lavorel et al. 2008). We calculated the
242 Simpson's diversity index (1-D) for each sampling site using the *diversity* function in the
243 *vegan* package and the conceptually similar Rao's quadratic entropy index (FDq) using
244 the function *mpd* in the *picante* package (Kembel et al. 2010). FDq was calculated using
245 beetle functional groups as categorical traits and the log-transformed data of mean species
246 body mass as a continuous trait. These indices give a combined measure of taxonomic
247 (Simpson's diversity) and functional (FDq) diversity and evenness. To provide a measure
248 of functional redundancy or singularity, we also calculated functional originality (FOri;
249 Mouillot et al. 2013). FOri estimates the isolation of species in functional space by
250 dividing the minimum functional distance (higher than zero) of each species by the
251 maximum of overall distance in the PCoA generated by the *dbFD* function in the *FD*
252 package (Laliberté et al. 2014).

253 The capacity of plantations to harbour species from native forest areas was
254 determined by the number of individuals of dung beetle species associated with native
255 forest. We assigned the species into groups associated with native forest or plantations
256 using the 'simple majority' from the CLAM statistical approach (*clamtest* function) in the
257 *vegan* package and we applied the sample coverage correction for rare species based on
258 species with less than 10 individuals (Chazdon et al. 2011). To obtain a metric of
259 functional similarity between *Eucalyptus* plantations and native forest, we calculated the
260 mean and standard deviation of functional β -diversity for each pair of *Eucalyptus* and
261 native forest sites based on the partitioning of FDq using the *RAO* function in R (De Bello
262 et al. 2010, Ricotta et al. 2011).

263 To evaluate the influence of environmental variables and timber production on
264 biodiversity metrics, we built a distance-based linear model (DistLM) for dung beetle

265 community composition and structure, using the *dblm* function on the *dbstats* package
266 (Boj et al. 2017); we used generalised linear models (GLM) with a negative binomial
267 error distribution for species abundance (*glm.nb* function in the *MASS* package; Venables
268 and Ripley 2002), a quasi-Poisson distribution for species richness, a Gamma distribution
269 for CWM body mass, and linear models (LM) with Gaussian distribution for Simpson's
270 diversity, FDq and FOr. We first checked for collinearity among explanatory variables
271 using the variance inflation factor (*vif* function in the *car* package; Fox and Weisberg
272 2011), which was equal to or lower than 2.16 in all cases. All full models therefore
273 included canopy openness, forest cover, timber production and coarse sand content as
274 explanatory variables - the last variable was included because it has strong influence on
275 dung beetles (Beiroz et al. 2017), even it is not modified in plantations and we did not
276 aim to evaluate its significance. We selected the best models for each response variable
277 based on their AICc values using the *dredge* function in the *MuMIn* package (Bartoń
278 2016) to rank our models, or manually for DistLMs. As models for species richness were
279 fitted using a quasi-Poisson error distribution, they were evaluated using quasi-AICc
280 values (QAICc).

281 To test whether the environmental variables predicted the abundance of dung beetle
282 species associated with native forest or the functional β -diversity shared between native
283 forest and plantations, we built a GLM with a negative binomial distribution for native
284 forest species and Gaussian distribution for functional β -diversity. We used the same
285 explanatory variables (albeit excluding timber production) and model selection process
286 as described above.

287 Finally, we evaluated the influence of timber production by assessing its importance
288 based on the change in AICc values compared to the best-fitted models for each
289 biodiversity metric, whereby a decrease in the AICc value indicate an effect of timber
290 production on diversity metrics.

291

292 **RESULTS**

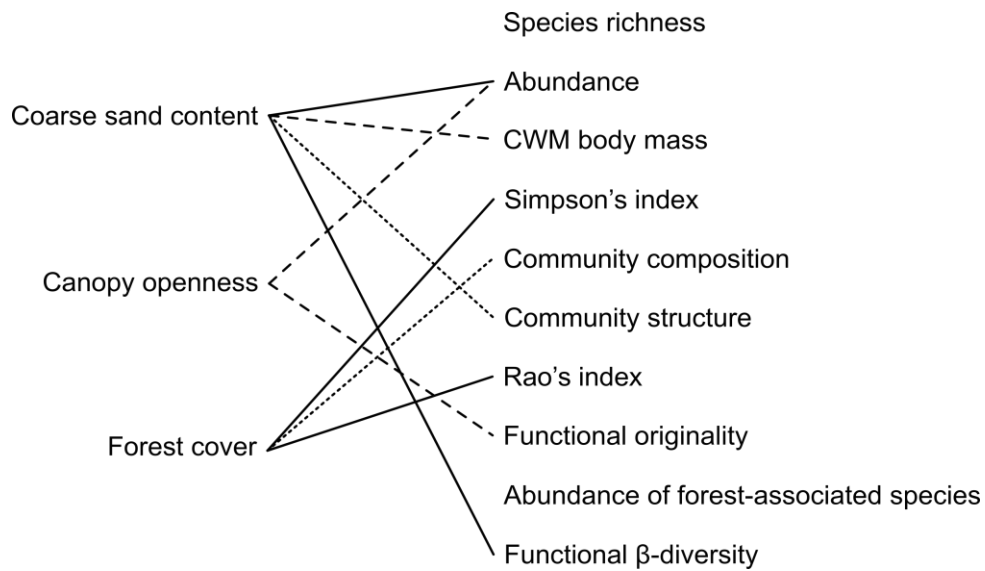
293 We sampled 8324 individuals of dung beetles from 89 species, 43 of which were
294 labelled as morphospecies. In *Eucalyptus* plantations, we recorded 1995 individuals of 50
295 species, and in native forests we sampled 6329 individuals of 78 species. *Eucalyptus*
296 plantations and native forest shared 39 species. Most of species exclusive to plantations
297 were singletons (*Ateuchus* sp. C, *Canthon mutabilis*, *Eurysternus cyclops*, *Onthophagus*
298 *onthochromus*) or doubletons (*Canthon* aff. *acutus*, *Canthon lituratus*, *Trichillidium* sp.

299 A). Four species were found frequently in plantations *Canthon* aff. *heyrovskyi* (5
300 individuals), *Onthophagus* aff. *marginicollis* (8 individuals), *Ontherus sulcator* (15
301 individuals) and *Canthon simulans* (78 individuals) and the most abundant species in
302 *Eucalyptus* plantations was *Ontherus carinifrons* (587 individuals).

303 We obtained information to assign 8218 individuals from 69 (morpho-) species to
304 functional groups (99% of the total individuals and 78% of all morphospecies). When
305 dung beetles were grouped by dietary preference, 72% were coprophagous (5219
306 individuals of 50 species), 12% were necrophagous (467 individuals of 11 species) and
307 16% were generalists (2532 individuals of 8 species). For nesting behaviour, 58% were
308 tunnelers (6099 individuals of 40 species), 26% were rollers (1056 individuals of 18
309 species) and 16% were dwellers (1063 individuals of 11 species). We were able to assign
310 activity period to 7884 individuals of 60 species (95% of the total individuals and 67% of
311 all morphospecies), of which 55% (3971 individuals of 33 species) were diurnal and the
312 remaining 45% (3913 individuals of 27 species) were nocturnal.

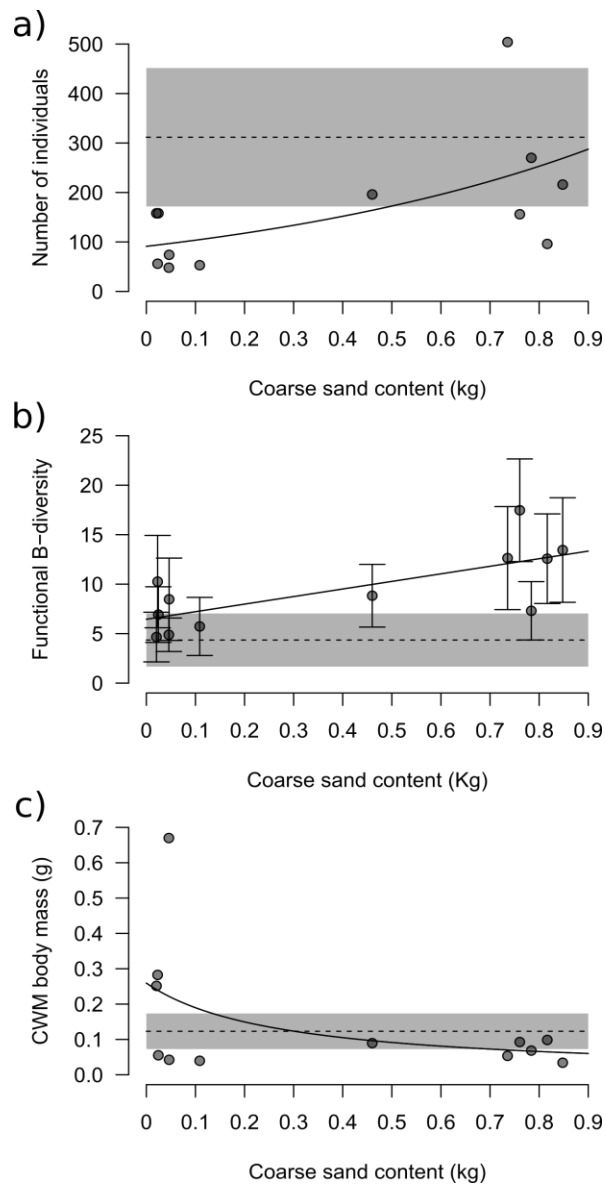
313 Most dung beetle metrics were lower in the plantations compared to reference forest
314 sites (dashed lines in Figure 3 and Figure S2). Among plantation sites, the coarse sand
315 content of the soil largely explained the variation in dung beetle community structure
316 (Table S3, Figure 2), whereby abundance and functional β -diversity increased with coarse
317 sand content (Table S3, Figures 2 and 3a-b), whereas CWM body mass decreased slightly
318 (Table S3, Figures 2 and 3c-d). The canopy openness in *Eucalyptus* plantations was
319 negatively related to dung beetle abundance, although the relationship was weak, and
320 FOr_i (Table S3, Figures 2 and 4a and d). None of the other community metrics were
321 explained by canopy openness in plantations (Table S3, Figure 2).

322 The percentage cover of surrounding forest explained much of the variation in dung
323 beetle community composition in *Eucalyptus* plantations (Figure 2, Table S3) and was
324 positively related to Simpson's diversity and FD_q (Table S3, Figures 2 and 4b). Indeed,
325 the two dung beetle communities sampled from plantations with >23% native forest cover
326 within the 1-km buffer zone were as functionally diverse as native forest communities
327 (Figure 4c). None of the explanatory variables predicted variation in the total species
328 richness or abundance of forest-associated species within plantations (Table S3, Figure
329 2).



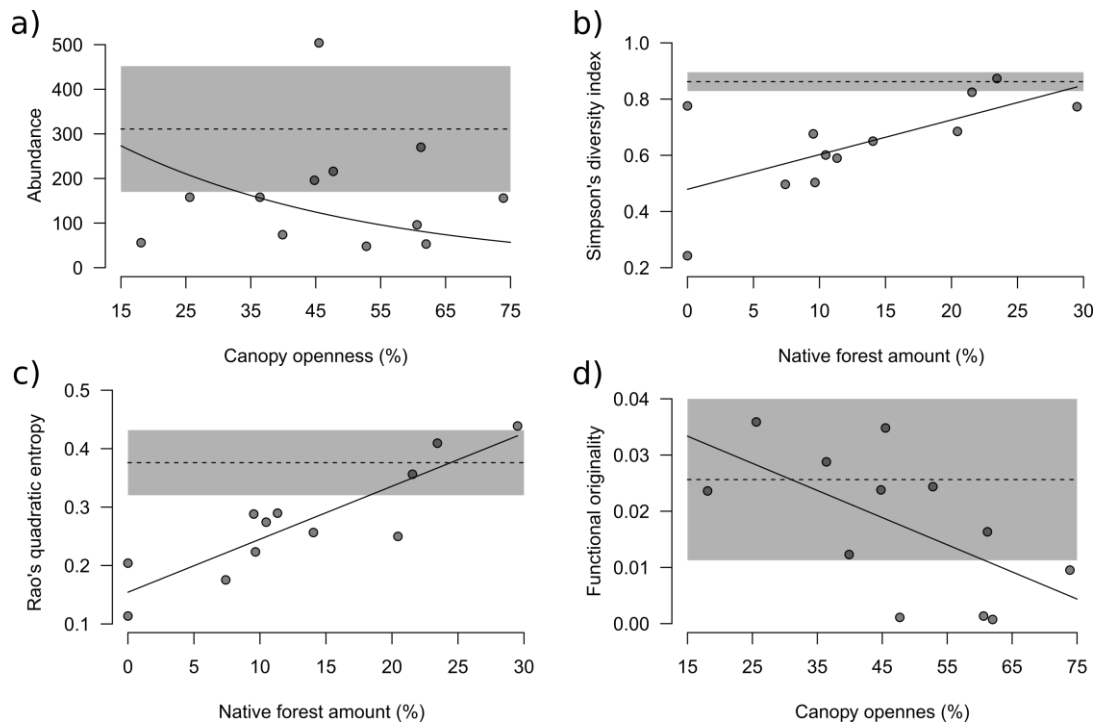
330

331 Figure 2: Environmental variables explaining variation in dung beetle community diversity metrics in
 332 *Eucalyptus* plantations in the Brazilian Amazon; showing explanatory variables (left) and response
 333 variables (right) of final models with $\Delta AICc > 2$; the lines indicate explanatory variables that were retained
 334 in the final models, and the absence of connecting line indicates no relationship between explanatory and
 335 response variables. Solid lines indicate positive effects, dashed lines indicate negative effects and we used
 336 dotted lines for community composition and structure, as it is not possible to determine the direction of the
 337 effect.



338

339 Figure 3: The influence of coarse sand content on (a) dung beetle abundance, (b) functional β -diversity
 340 compared to native forest (the bars represent the standard deviations for *Eucalyptus* plantation) and (c)
 341 community-weighted mean (CWM) body mass of dung beetle communities in *Eucalyptus* plantations. The
 342 solid lines represent the predictive model, the dashed lines and the grey area are the mean and standard
 343 deviation values for the native forest (baseline).



344

345 Figure 4: The influence of environmental variables affected by land management on diversity metrics of
 346 dung beetle communities in *Eucalyptus* plantations, showing the relationship between canopy openness and
 347 (a) dung beetle abundance, and the influence of the surrounding native forest cover on (b) Simpson's
 348 diversity index, (c) Rao's quadratic entropy, and (d) functional originality. The solid lines represent the
 349 predictive model, the dashed lines and the grey area are the mean and standard deviation values for the
 350 native forest (baseline).

351

352 There was no clear effect of timber yield on dung beetle diversity, as including
 353 timber production in the models inflated AICc and QAICc by more than two unit values
 354 for all response variables (Table S3).

355

356 DISCUSSION

357 We evaluated how local forest structure (canopy openness), landscape context
 358 (surrounding native forest cover) and timber production influence the taxonomic and
 359 functional diversity of dung beetles in *Eucalyptus* plantations. Our hypothesis that canopy
 360 openness would have a substantial influence on dung beetle diversity was not fully
 361 supported, as only dung beetle abundance and functional originality were negatively
 362 related to canopy openness. We also found no evidence to support our hypothesis that
 363 timber production intensity would have a negative impact on dung beetle diversity.
 364 However, we found strong support for our hypothesis on the important role of landscape
 365 context, as the proportion of native forest cover surrounding *Eucalyptus* plantations
 366 influenced dung beetle community composition, taxonomic and functional diversity.

367

368 ***Influence of local and landscape variables on dung beetle biodiversity in plantations***

369 All measured environmental variables (coarse sand content, canopy openness and
370 forest cover) explained some variation in dung beetle community metrics (Figure 2).
371 Although the coarse sand content of the soil is not affected by plantation management, it
372 is nonetheless relevant in this context because it influences soil texture and soil fertility
373 (Stadler et al. 2015), which are both important factors for determining the suitability of
374 plantation areas, as well as the extent of the required management (Zinn et al. 2002, Touré
375 et al. 2013). Dung beetle community structure and abundance in plantations were strongly
376 related to the coarse sand content in the soil (Figures 2 and 3), a pattern that has also been
377 observed in undisturbed forest sites in the same region (Beiroz et al. 2017). This
378 relationship is conceivably a result of nesting requirements, because increased sand
379 content is likely to negatively influence the survival rate of the offspring of roller dung
380 beetles, which nest in shallow galleries and are sensitive to upper humid zone of soils
381 with low sand content (Hanski and Cambefort 1991, Osberg et al. 1993, Davis et al.
382 2010). On the other hand, tunnellers dig deeper galleries, allowing them to nest in sandy
383 soils with a deeper humid zone. Accordingly, the functional structure of dung beetles in
384 plantations was more similar to forest communities in soils with lower coarse sand content
385 (Figure 3c), probably due to the higher capacity of these soils to support roller species.
386 Our results indicate that soil texture could also be an important filter for functional β -
387 diversity of dung beetles by altering the ratio of rollers to tunnelers, and should therefore
388 be considered on conservation strategies focusing in dung beetle communities.

389 Our results provide strong support for the important role of landscape context in
390 contributing to the biodiversity of plantations, as the extent of native forests in the area
391 surrounding the *Eucalyptus* plantations was associated with higher taxonomic and
392 functional diversity of dung beetles in the plantations (Figures 4b and c). A greater
393 coverage of native forests may enhance spillover (Gray et al. 2014, Marsh et al. 2018)
394 and increased movement of forest species through the plantation. It is possible that some
395 of the sampled individuals of native forest species are only foraging in managed sites,
396 which may not necessarily indicate suitable plantation conditions if these individuals
397 cannot sustain populations or perform key functions within the plantations. These
398 functional considerations merit further investigation, especially as the effect of native
399 forest amount was stronger in functional aspects of the community than in taxonomic
400 diversity. We demonstrate that some plantations had higher functional metrics values than

401 the baseline, despite only ~20% native forest cover in the buffer area, which is below the
402 previously reported fragmentation threshold for taxonomic diversity (~30% native forest
403 cover; Andr en 1994, Pardini et al. 2010).

404 Although the functional diversity in plantations increased with the surrounding
405 forest cover (Figures 4c), the extent of forest cover was not related to functional similarity
406 between native forest and plantations. Instead, functional β -diversity was more strongly
407 related to coarse sand content (Figure 3b), and functional originality declined with canopy
408 openness (Figure 4d). These results suggest that there is high functional redundancy in
409 dung beetle communities in plantations, and support a niche-based community assembly
410 in which dung beetle species are selected by both landscape and local filters (Audino et
411 al. 2017). It is conceivable that greater native forest cover around plantations reduces the
412 harshness of dispersal filters, increasing the possibility of colonisation by species that
413 would not otherwise tolerate the environmental conditions in the plantations, which is
414 indicated by the positive relationship between native forest cover and Simpson's diversity
415 and FDq (Figure 4b and c). Greater native forest cover would therefore facilitate the
416 dispersal of forest-associated dung beetle species into plantations, but coarse sand content
417 and canopy openness would influence their ability to establish viable populations.

418 Our findings indicate that plantations surrounded by a matrix of native forests can
419 support more diverse dung beetle communities than those in landscapes dominated by
420 human-modified habitats (Gray et al. 2014, Filgueiras et al. 2016). Yet it is not clear if
421 this is a positive or negative outcome for conservation. On the one hand, increasing native
422 forest cover could facilitate the movement of forest species into and through non-native
423 habitats (Arellano et al. 2013). On the other hand, plantations could function as 'sink'
424 habitats for populations of native species; this would occur if mortality exceeded birth
425 rates and plantations were unable to sustain viable populations without repeated
426 colonisation from native forests (Hansen and DeFries 2007). In this case, high levels of
427 biodiversity within plantations could have negative consequences, as plantations would
428 represent ecological traps for native forest species (Kokko and Sutherland 2001,
429 Schlaepfer et al. 2002).

430 Besides environmental and landscape conditions, it is important to conduct further
431 investigation into the availability and quality of resources for dung beetles in plantations
432 (i.e. mammal dung). Monocultures tend to promote the hyper-abundance of a few species
433 (Senior et al. 2013), which might reduce dung beetle functional diversity by altering the
434 composition and availability of dung resources (Nichols et al. 2009). Thus, further studies

435 are necessary to evaluate the roles of landscape context and local conditions on dispersal
436 and establishment. We also urgently need to assess the stability and resilience of dung
437 beetle communities in modified habitats, focussing on both the short- and long-term
438 potential for plantations to sustain diverse dung beetle communities and the ecosystem
439 functions they underpin. The proximity of viable source populations in native forest, and
440 the inclusion of forest species in plantations could increase dung beetle functional
441 diversity and enhance or restore ecosystem processes affected by land-use change (Rand
442 et al. 2006, Blitzer et al. 2012, Hobbs et al. 2014), as the loss of forest-associated species
443 reduces the functional activity of dung beetle communities in human-modified habitats
444 near native areas (Gray et al. 2016). In our study, the structure of the dung beetle
445 communities in plantations differed from that of forest communities, but the functional
446 metrics we evaluated suggest that they nonetheless have the potential to sustain their role
447 in ecosystem functioning (Ricotta et al. 2016, Leitão et al. 2016), especially when they
448 are supported by dispersal from adjacent native forest.

449

450 *Is there a trade-off between timber production and biodiversity conservation within* 451 *plantations?*

452 We found no relationship between the intensity of timber production and any of the
453 studied dung beetle community metrics (Figure 4). This suggests that plantations could
454 potentially be managed to deliver both high yields and biodiversity conservation.
455 However, there are many caveats to this: first, dung beetles are a small component of total
456 biodiversity, and many native forests species are not found in plantations (Louzada et al.
457 2010). Second, the mechanisms underpinning the high diversity in plantations require
458 testing to assess whether the populations are self-sustaining and performing useful
459 ecological functions. Finally, our measure of timber production was a snapshot at one
460 point in time, and more work is needed to assess whether both biodiversity and production
461 can be maintained over multiple rotations, and to determine the effects of fertilizer and
462 pesticide use on dung beetle communities in plantations.

463

464 *Final considerations*

465 Even though the plantations supported communities with a distinct functional
466 structure, as little as 20% of native forest cover in the surrounding landscape increased
467 the measured functional diversity to values approaching those measured in primary forest
468 areas (Figure 3g). However, the 1-km buffer considered in our study did not account for

469 the fact that all sites were set within a much larger continuous area of native forest, which
470 in turn is likely to maintain diversity across the landscape (Numa et al. 2012, Ochoa-
471 Quintero et al. 2014). It is therefore crucial that we maintain the extent of forest cover
472 required by the current Brazilian ‘forest code’, which mandates the conservation of up to
473 80% of forest on properties across most of the Legal Amazon region (Brasil 2012). Our
474 findings suggest that the surrounding cover of native habitat is likely to improve
475 taxonomic and functional diversity by facilitating the movement of forest species into
476 plantations. However, further studies are required to understand the viability and
477 persistence of dung beetle populations within plantations, and to determine whether the
478 functional diversity of dung beetle communities enhances ecosystem functioning.

479 Previous studies have showed that *Eucalyptus* plantations have a great potential
480 conservation value if considered as complementary habitat for species from native forest,
481 and managed as a hybrid ecosystem (i.e. by conserving historical and novel features,
482 Hobbs et al. 2009, Tavares et al. 2019). Although we still need more information on
483 ecosystem processes and population persistence in plantations, our results suggest that
484 plantation management considering both landscape aspects and stand structure could
485 increase the conservation value of plantations (Tavares et al. 2019) if the presence of
486 functionally diverse dung beetle communities is deemed an important management goal.
487

488 **ACKNOWLEDGEMENT**

489 We thank *Grupo Jari*, especially Davi for logistic support, GIS, soil and rainfall
490 and timber production data, Irmão, Edvar and Maria for their support during the
491 fieldwork. Conselho Nacional de Pesquisa e Desenvolvimento (CNPQ) and Fundação de
492 Amparo à Pesquisa do estado de Minas Gerais (FAPEMIG) for funding the project (Site
493 Peld 23 – 403811/2012-0). WB thanks Coordenação de Aperfeiçoamento de Pessoal de
494 Nível Superior (CAPES) for the PhD scholarship (BEX 3711-14-15).

495

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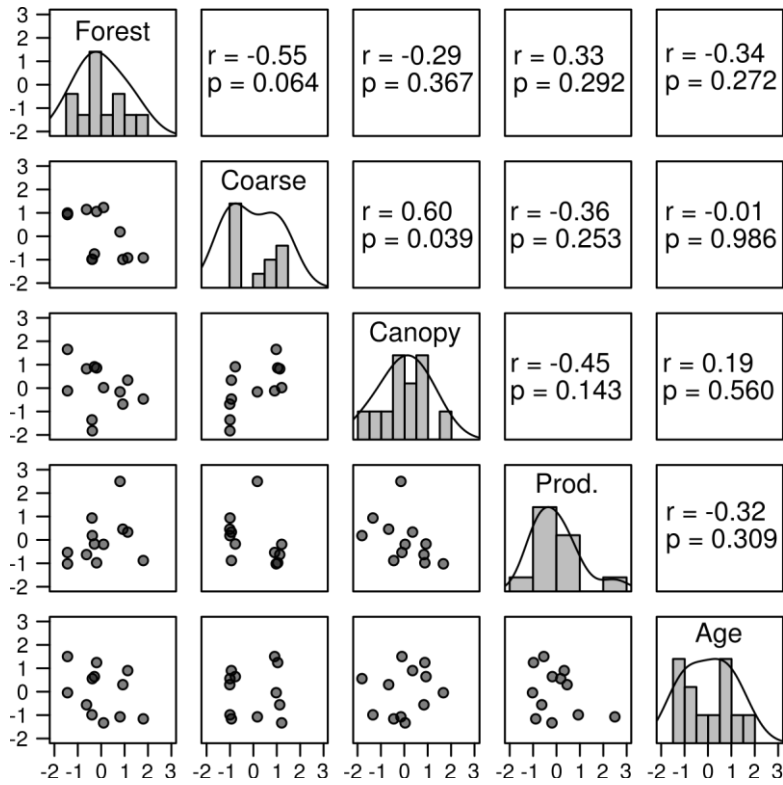
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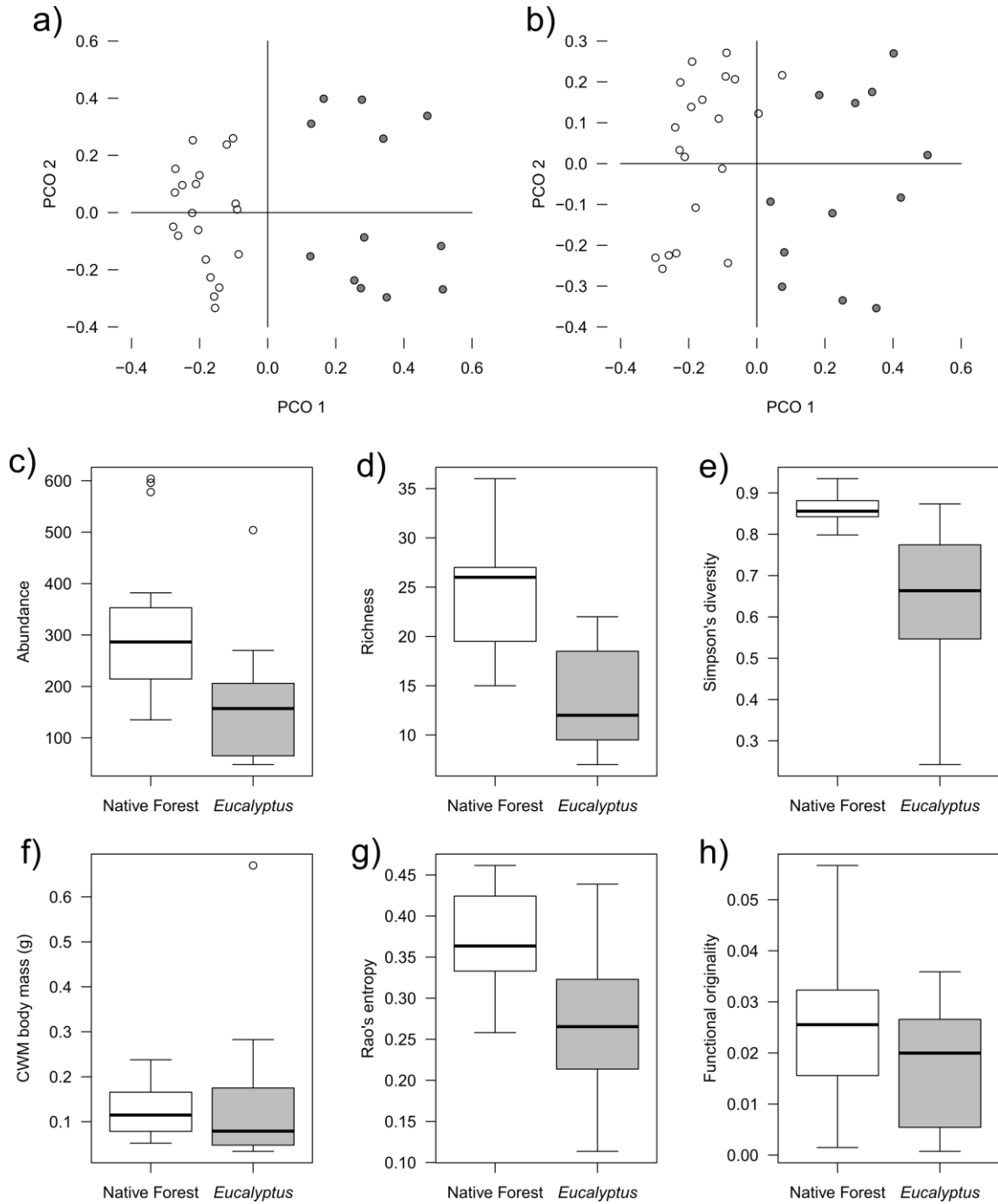
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755 SUPPLEMENTARY MATERIAL



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Figure S1: Pearson's correlations (r) and its 95% statistic significance (p) among standardized values of explanatory variables and age of *Eucalyptus* trees. 'Forest' is forest cover, 'Coarse' is coarse sand content, 'Canopy' is canopy openness, 'Prod.' is timber production and 'Age' is for trees' age.



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763 Figure S2: Comparisons between native forest (white) and *Eucalyptus* plantation (grey) areas, regarding
 764 community (a) structure and (b) composition, as well as the metrics of (c) abundance, (d) species richness,
 765 (e) Simpson's diversity index, (f) community-weighted mean body mass, (g) Rao's quadratic entropy, and
 766 (h) functional originality.

767 **SUPPLEMENTARY MATERIAL**

768 Table S3: Models based on AICc for each response variable with explanatory variables. ‘CO’ = Canopy
 769 openness, ‘CS’ = Coarse sand content, ‘FC’ = Forest cover, ‘TP’ = Timber production, and ‘w’ = Akaike
 770 weight for each model. Bold font highlights the models with $\Delta AICc \leq 2$ and italic font for the models fitted
 771 with TP. *Quasi-AICc for species richness.
 772

Community parameters	Model variables	AICc*	$\Delta AICc$	w	cumulative w
Species richness	NULL	31.11	0.00	0.556	0.556
	CO	34.40	3.29	0.107	0.664
	<i>TP</i>	<i>34.63</i>	<i>3.52</i>	<i>0.096</i>	<i>0.760</i>
	FC	34.73	3.62	0.091	0.851
	CS	34.77	3.67	0.089	0.940
Total abundance	CS	145.54	0.00	0.365	0.365
	CO+CS	145.94	0.40	0.300	0.665
	NULL	148.48	2.93	0.084	0.749
	FC	148.73	3.18	0.074	0.823
	<i>CS+TP</i>	<i>149.31</i>	<i>3.76</i>	<i>0.056</i>	<i>0.879</i>
CWM body mass	CS	-18.87	0.00	0.559	0.559
	NULL	-16.69	2.18	0.188	0.747
	CO+CS	-15.07	3.80	0.084	0.831
	FC+CS	-14.64	4.23	0.067	0.898
	<i>CS+TP</i>	<i>-14.33</i>	<i>4.54</i>	<i>0.058</i>	<i>0.956</i>
Simpson's' diversity index	FC	-6.69	0.00	0.492	0.492
	NULL	-3.76	2.92	0.114	0.606
	FO+CO	-3.20	3.49	0.085	0.692
	CS	-2.82	3.87	0.071	0.763
	CO	-2.34	4.34	0.056	0.819
	<i>FC+TP</i>	<i>-2.33</i>	<i>4.36</i>	<i>0.056</i>	<i>0.875</i>
	<i>CS+TP</i>	<i>-2.23</i>	<i>4.46</i>	<i>0.053</i>	<i>0.928</i>
Community composition	FC	-28.80	0.00	0.998	0.998
	<i>FC+TP</i>	<i>0.39</i>	<i>29.19</i>	<i>~0</i>	<i>0.998</i>
Community structure	CS	-64.05	0.00	~1.000	~1.000
	<i>CS+TP</i>	<i>-29.32</i>	<i>34.73</i>	<i>~0</i>	<i>~1.000</i>
Rao's quadratic entropy	FC	-32.90	0.00	0.566	0.566
	FC+CS	-30.48	2.43	0.169	0.735
	<i>FC+TP</i>	<i>-29.96</i>	<i>2.95</i>	<i>0.130</i>	<i>0.864</i>
	CO+FC	-28.50	4.40	0.063	0.927
Functional originality	CO	-68.18	0.00	0.431	0.431
	NULL	-66.33	1.85	0.171	0.602
	<i>TP</i>	<i>-65.28</i>	<i>2.90</i>	<i>0.101</i>	<i>0.703</i>
	CS	-64.63	3.55	0.073	0.777
	CO+TP	-64.18	4.00	0.058	0.835
	CO+FC	-63.89	4.29	0.051	0.885
	CO+CS	-63.48	4.70	0.041	0.926

773

774 Table S3: Cont.

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Community parameters	Model variables	AICc*	Δ AICc	w	cumulative w
	NULL	105.06	0.00	0.460	0.460
Abundance of forest-associated species	CO	107.18	2.12	0.159	0.619
	CS	108.39	3.33	0.087	0.706
	<i>TP</i>	<i>108.40</i>	<i>3.33</i>	<i>0.087</i>	<i>0.792</i>
	FC	108.44	3.37	0.085	0.878
	CO+CS	109.59	4.53	0.048	0.925
		CS	66.02	0.00	0.504
Functional β -diversity	FC+CS	68.60	2.58	0.139	0.643
	FC	68.83	2.81	0.124	0.767
	<i>CS+TP</i>	<i>70.30</i>	<i>4.28</i>	<i>0.059</i>	<i>0.826</i>
	CO+CS	70.33	4.31	0.058	0.884
	NULL	71.26	5.24	0.037	0.921

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