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3   **Human perturbations reduce dung beetle diversity and dung removal**

4   **ecosystem function**

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32 **Abstract**

33 Biodiversity drives ecological functioning, ultimately providing ecosystem services. Ecosystem

34 processes are favored by greater functional diversity, particularly when groups of functionally

35 different species interact synergistically. Many of such functions are performed by insects,

36 among which dung beetles stand out for their important role in dung decomposition. However,

37 anthropogenic disturbances are negatively affecting their ecological dynamics and ecosystem

38 services. We conducted a manipulative field study, to evaluate the effect of human disturbance on

39 dung beetle diversity (abundance, species richness, and functional group richness) and dung

40 removal rates, comparing perturbed and conserved forests in three regions of Colombia

41 (Caribbean, Andes, and Amazon). We also assess the relationship between dung beetle diversity

42 and dung removal rates. Dung beetle diversity was assessed using pitfall traps, and specimens

43 were measured and assigned to functional groups according to body size and dung relocation

44 strategy. We used exclusion control units and experimental units to assess dung degradation with

45 and without dung beetle activity and evaluate differences in removal rates between two dung

46 removal strategies: paracoprids and telecoprids. Dung removal rates, abundance, and functional

47 group richness were lower in perturbed forests compared to conserved forests. Dung removal

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48   increased with abundance, species richness, and functional group richness. Moreover, dung

49   removal performed by telecoprids increased with species richness of telecoprids and paracoprids.

50   Our results evidence a negative effect of human perturbation on dung beetle richness, abundance,

51   and dung removal rates, and also that dung beetle diversity and functional group richness enhance

52   dung removal rates.

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59   **1   INTRODUCTION**

60   Biodiversity maintains ecological functioning and provides ecosystem services (Hooper *et al*.,

61   2005). Here, ecosystem functions are the result of the interactions between structures and

62   processes that contribute to the maintenance of the ecosystem (Turner *et al*., 2000), and

63   ecosystem services are the benefits that human populations obtain, directly and indirectly, from

64   ecosystems (Costanza *et al*., 1997; Millennium Ecosystem Assessment, 2005; Boyd & Banzhaf,

65   2007; Wallace, 2007; Lamarque *et al*., 2011; Costanza *et al*. 2017; Díaz *et al*. 2018). Usually,

66   ecosystem dynamics, functioning, and productivity are enhanced by diversity (Tilman *et al*.,

67   2014), which corresponds not only to the number of species, but also to the number of functional

68   groups that play different ecological roles (Slade *et al*., 2007; Manning *et al*., 2016; Menéndez *et*

69   *al*., 2016; Slade *et al*., 2019; Noriega *et al*., 2021). Indeed, increments in species richness and

70   functional diversity generate positive responses in ecosystem functionality (Pasari *et al*., 2013),

71   while some ecosystem functions and services disappear in areas with low diversity (Hooper *et al*.,

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72   2002; but see Slade *et al*., 2014). However, much of the information available on the relationship

73   between diversity and ecosystem functioning is based on correlational rather than experimental

74   approaches, and on the use of indirect measurements (Noriega *et al*., 2018), which limits our

75   understanding of the impact of global changes on ecosystem functioning. Therefore, field and/or

76   laboratory experiments are essential to obtain direct quantifications of both diversity and

77   ecological processes.

78   Human activities have generated a high level of perturbation in most, if not all,

79   ecosystems, promoting the radical changes in biogeochemical cycles that have turned the

80   Anthropocene into a new geological epoch (Waters *et al*., 2016). Human disturbances result in a

81   general transformation of the temporal and spatial dynamics of populations and communities

82   (Sousa, 1984). Indeed, anthropogenic drivers of global change (*e*.*g*., land-use change, logging,

83   fragmentation, agricultural and cattle expansion), typically exert negative effects on species

84   richness, abundance, and composition, thus affecting species interactions (Tylianakis *et al*., 2008),

85   community structure (Bregman *et al*., 2015; Kenyon *et al*., 2016; Noriega *et al*., 2020), and

86   aggregation patterns (Horgan, 2006), ultimately affecting ecosystem functioning (Larsen *et al*.,

87   2005; Braga *et al*., 2013). Indeed, altered community structure and local extinctions after habitat

88   loss can rapidly disrupt ecosystem functioning (Larsen *et al*., 2005). However, much of the

89   information available on the impact of human activities on ecosystem services is based on

90   correlational rather than experimental approaches, and on the use of indirect measurements

91   (Noriega *et al*., 2018), which limits our understanding of the impact of global changes on

92   ecosystem functioning. Therefore, field and/or laboratory experiments are essential to obtain

93   direct quantifications of both diversity and ecological processes.

94   In this study we evaluate the effects of land use perturbation on dung removal rates (*i*.*e*.,

95   the rate at which dung is cleared from the soil surface, by typically being buried into deeper soil

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96   layers; *e.g.*, Slade *et al.*, 2011). This key ecosystem function mainly performed by dung beetles

97   influences nutrient cycling and soil structure, affecting the levels of nitrogen that plants can

98   capture, improving soil hydrological properties and soil aeration, and reducing greenhouse gas

99   fluxes from cattle farming (Bang *et al.*, 2005; Yamada *et al.*, 2007; Johnson *et al.*, 2016; Santos-

100 Heredia *et al.*, 2016; Slade *et al.*, 2016; Nervo *et al.*, 2017). Dung beetles (Coleoptera:

101 Scarabaeidae) contribute to several ecosystem services, like nutrient cycling, bioturbation,

102 secondary seed dispersal, parasite suppression, among others (*e.g.*, Andresen & Feer, 2005;

103 Nichols *et al.*, 2008; Badenhorst *et al.*, 2018; DeCastro-Arrazola *et al.*, 2020). Dung beetles can

104 be grouped in three main functional groups according to their feeding and nesting strategies

105 (Doube, 1990): (1) paracoprids (or tunnelers) that dig tunnels in the soil underneath the dung and

106 relocate vertically part of the dung on the ground; (2) telecoprids (or rollers) that make a ball with

107 the food resource and relocate part of the dung horizontally and vertically; and (3) endocoprids

108 (or dwellers) that live inside the dung pile or in the dung-soil interface. Species from this latter

109 functional group almost do not relocate dung away from the original pile, so the first two groups

110 perform most of this function. In addition, the interaction between these functional groups could

111 affect the ecosystems services they provide (Slade *et al.*, 2007).

112   In addition, dung beetles are good bioindicators of anthropogenic disturbances due to their

113 close relationship with both vegetation cover and mammal richness and abundance (Davis *et al.*,

114 2001; McGeoch *et al.*, 2002; Nichols *et al.*, 2009; Nichols & Gardner, 2011; Otavo *et al.*, 2013).

115 Dung beetles are negatively affected by anthropogenic disturbances. Indeed, in forested areas,

116 impacts like area reduction, fragmentation, selective cutting, hunting, etc., lead to changes in their

117 abundance, richness, and functional composition of the assemblages (Nichols *et al.*, 2007; Slade

118 *et al.*, 2011; Braga *et al.*, 2013; Tonelli *et al.*, 2018). Consequently, the ecosystem functions they

119 perform, like dung removal and seed burial, are also negatively affected by forest management

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120   (Slade *et al*., 2011). Here, we (a) characterize the relationship between dung removal rate and

121   dung beetle species richness, abundance and functional diversity in Neotropical forests, and (b)

122   assess whether the effects of anthropogenic disturbance on dung beetle diversity affect the

123   delivery of this key ecological process. Since dung beetle species belonging to different

124   functional groups use distinct dung removal strategies, we also (c) evaluate the relative effect of

125   the diversity of paracoprids and telecoprids on dung removal rates. These objectives allow us to

126   evaluate three specific predictions: (1) dung beetles from perturbed forests present lower

127   abundance, richness, functional group richness and dung removal rates, independently of the

128   geographical region considered; (2) total dung removal is positively associated with dung beetle

129   abundance, richness, and functional group richness; and (3) the dung removal performed by each

130   functional group (either paracoprids and telecoprids) increases with their respective abundance

131   and richness. We achieved these goals by conducting field experiments in tropical forests subject

132   to two different disturbance levels (conserved and perturbed) in three environmentally different

133   regions (Caribbean, Andes, and Amazon areas in Colombia).

134

135   **2   METHODS**

136   **2.1 Study areas**

137   We established three study areas, one in each of the three largest Colombian ecoregions:

138   Caribbean, Andes, and Amazon. The Caribbean region (151,118 km^2), is a flat region with warm

139   tropical climate that occupies 9% of the national territory, characterized by the presence of

140   swamps, lagoons near the coasts, and tropical rain and dry forests. The Andes (282,450 km^2)

141   occupy 33% of the territory, and are characterized by a diversity of ecosystems from valleys,

142   foothill and mountain tropical rain forests, and *paramos*, with steep climatic variations that

143   depend on the altitude. The Amazon is located in the south of the country (315.00 km^2), occupies

144 29% of its territory, and is characterized by warm climate, a high rainfall rate, and the presence of

145 tropical rain forests. For detailed descriptions of environmental conditions and vegetation cover

146 of all three ecoregions see Hernández *et al*. (1992). In each region, we selected a study area that

147 included both a conserved tropical rain forest –a primary forest or a secondary forest with more

148 than 50 years of recovery since disturbance– and a disturbed tropical rain forest –a secondary

149 forest affected in the last 5-10 years by an anthropogenic perturbation (typically intensive logging

150 of large trees; J.A. Noriega pers. obs.). These study areas were established at the following

151 locations: (1) Caribbean - in the private reserve Kalashe-Kalabria (11.269 N; 74.085 W; 180 m

152 a.s.l.), located near the Atlantic coast; (2) Andes - in a private farm near San Vicente de Chucuri

153 (6.845 N; 73.385 W; 1500 m a.s.l.), located in the Oriental mountain system; and (3) Amazon -

154 located near the indigenous reserve Mocagua (3.795 S; 70.217 W; 103 m a.s.l.). Each of these

155 regions has a different degree of sampling coverage of dung beetles (*i.e*., amount of sampling

156 sites and number of published studies) that was taken into account as a reference standard

157 (Noriega *et al*., 2015). In addition, there is a spatial gradient of decreasing disturbance from the

158 Caribbean (less conserved) to the Amazon (more conserved), caused by anthropogenic

159 disturbances (*i.e*., agricultural and cattle industries) in these regions (Etter *et al*., 2006;

160 Echeverría-Londoño *et al*., 2016). The size of the forest fragments included in the study varies

161 between 39 and 53 ha (Caribbean = 43 and 39 ha; Andes = 40 and 42 ha; and Amazon = 53 and

162 49 ha for primary and disturbed forest, respectively). Within each study area, conserved and

163 disturbed forest fragments were separated from each other by 3 to 5 km. Thus, a total of six

164 sampling sites were defined based on a combination between regions and forest types (see Figure

165 S1A for more details).

166

167 **2.2 Dung beetle surveys**

168   Sampling design consisted of a 1,000 m linear transect per site, placed at the center of each forest

169   (*i.e*., at least 100 m from the border of the forest to minimize any possible edge effect). Each

170   transect included 20 baited pitfall traps (hereafter referred as 'sampling units'; Figure S1B)

171   placed 50 m from each other (Larsen & Forsyth, 2005; Figure S1B). The distance between our

172   pitfall traps and experimental units is a potential caveat, taking into consideration that some dung

173   beetle individuals could fly up to 1.5-2 km per day (Paik 1976). Each pitfall trap consisted of a 1

174   L plastic bucket buried at ground level and filled with 500 ml of water mixed with kitchen salt

175   and scentless soap (following Noriega & Fagua, 2009). On top of the bucket, a metallic wire

176   sustained a surgical mesh filled with 300 g of a mixture of fresh pig and human dung

177   (homogenized and mixed in 4:1 proportion; Figure S1B). The amount of dung was chosen to be

178   similar to that produced by large terrestrial mammals in Colombia, and we used the mixture

179   because previous sampling campaigns showed that it is highly attractive to dung beetles in this

180   region (J.A. Noriega pers. obs.). Traps were left in the field for 48 hours. After this period, dung

181   beetle specimens were collected and labeled in individual containers filled with ethanol (70%), to

182   be later identified to species level using different taxonomic identification keys (Edmonds, 1994;

183   Génier, 1996; González *et al*., 2009; Camero, 2010; Edmonds & Zidek, 2010; Vaz-de-Mello *et

184   al*., 2011). Voucher specimens were deposited in the Entomological Collection of the Museum of

185   Natural History of Los Andes University (EANDES) and the reference collection of the first

186   author (CJAN). Ten individuals of each species and region (or less when there were not enough

187   available) were randomly selected to measure the total length of each individual (from the

188   external border of the clypeus to the external border of the pygidium) and calculate the average

189   species body size; these measurements were performed using an electronic digital caliper

190   (Powerfix – Z22855, ± 0.01 mm). Also, each species was assigned to one of the three main dung

191   beetle functional groups, defined according to their food relocation-nesting behavior (Doube,

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192   1990): paracoprids, telecoprids, and endocoprids. Then, nine different groups were defined by

193   combining each of these behaviors with the average body size of the species, in three categories

194   (large>18.0 mm, medium 17.9-10.0 mm, and small<10.0 mm, following Doube, 1990; see Figure

195   S2). This combination between food relocation and body size is used to classify dung beetles into

196   functional groups, as it informs on their functional redundancy, as well as on changes in dung

197   beetle community structure in response to anthropic disturbance (*e.g*., Slade *et al*., 2007;

198   Barragán *et al.*, 2011). Functional richness was defined as a simple metric for functional

199   diversity, calculated as the number of functional groups. Finally, we described variations in body

200   size per sampling unit through Community Weighted Mean (CWM; Lavorel *et al*., 2008). CWM

201   was calculated as the average body length (mm; Figure S2) of each species weighted by its

202   relative abundance in each sampling unit.

203

204   **2.3 Dung removal experiments**

205   Twenty experimental units were installed at each sampling site, separated by 50 m (Larsen &

206   Forsyth, 2005; Figure S1B). Each experimental unit consisted of a 5 L bucket (height: 30 cm;

207   diameter: 25 cm) buried in the soil, filled with the same soil of the area, and topped with 300 g of

208   the same dung mixture used in the pitfall traps (Figure S1B). The initial dung pads were weighed

209   directly in the field with a digital pocket scale ($\pm$ 0.01 g). In addition, five control units were

210   active at the same time as the experimental units, placed 150 m from each other, and 100 m from

211   the experimental transect (Figure S1B); these allow evaluating how much weight is lost by

212   evaporation (*i.e*., average evaporation rate). Each control unit consisted of 300 g of the same

213   fresh dung used in the traps and experimental units, placed directly on the ground surface with a

214   plastic dish (diameter: 30 cm) buried below it to avoid any dung loss by soil invertebrates, and

215   covered with a fine nylon green mesh (mosquito net – aperture diameter < 1 mm) to prevent

216   access by dung beetles (Figure S1B). Both the experimental and control units were covered with

217   a plastic dish to protect them from the rain, and were left simultaneously in the field for 48 hours.

218   After that period, the experimental units were removed, and the remaining dung left on the

219   surface (*i.e*., dung not removed) was cleaned in order to remove all the extra substrate attached to

220   it and any possible dung beetles inside of it. Afterwards, the remaining dung from each

221   experimental unit was placed separately inside a plastic bag and weighed. We repeated this same

222   process for the dung left in the control units after the end of the experiment. To quantify the dung

223   removed by paracoprids (DRP), we checked carefully inside each bucket, cleaning meticulously

224   the manure found there to separate the buried dung from the soil attached to it. Then this dung

225   was weighed directly in the field for each experimental unit. We calculated the excrement

226   removed by telecoprids as the portion of the original dung (300 g) remaining after the subtraction

227   of the dung removed by paracoprids, the dung not removed, and the evaporation of the total

228   initial weight of the experimental units. In the laboratory, each dung pad from the experimental

229   and control units was dried at 80 ℃ (176 ℉) for 72 hours and weighed again (dry weight). The

230   dung removal protocol was carried out first, and the sampling of dung beetle diversity started 24

231   hours after it. Dung beetles found in the dung while measuring dung removal were released back

232   to the wild, so this treatment had no significant effect on the assemblages present in each forest

233   fragment. Given the stability in weather conditions during the surveys, it can be assumed that the

234   short period of time that elapsed between measuring dung removal and dung beetle diversity had

235   no effect in our ability to sample the assemblage that performed the function. In each site, dung

236   removal protocols and species sampling were done in rainy season and during the abundance

237   peak of local dung beetle assemblages (Caribbean site: March 2013, Andean site: February 2014,

238   Amazonian site: March 2015; these peaks were determined from previous studies, J.A. Noriega

239   pers. obs.).

240   Dry weights of all measurements (*i.e.*, both experimental and control units) were used to

241   calculate the total dung removal rate (TDRR), using the following three equations:

242

243   DE = (DIC - DFC) (eq. 1)

244   DRT = DIE - (DRP + DNR + DE) (eq. 2)

245   TDRR = (DRP + DRT) (eq. 3)

246

247   where DE is average dung evaporation rate; DIC is the initial wet weight of the control

248   dung; DFC the final wet weight of the control dung after 48 hours; DRT is the weight of the dung

249   removed by telecoprids; DIE is the initial weight of the experimental dung; DRP is the weight of

250   the dung removed by paracoprids; DNR is the final weight of the experimental dung not removed

251   after 48 hours; TDRR is the total dung removal rate, that includes the dung removed by

252   paracoprids (that corresponds to the dung collected from inside the buckets) and the dung

253   removed by telecoprids (calculated using the second equation). As endocoprids do not reallocate

254   dung away from the dung pat, our sampling design does not allow isolating their contribution to

255   dung removal. Therefore, we did not take into account their independent contribution to dung

256   removal in the analyses; rather, we assume that their effect on dung removal rates will generate

257   some variability that will remain unexplained in the results. All weights were measured in grams.

258   It is important to mention that although other animal groups could also be removing portions of

259   the dung (*e.g.*, termites, ants, earthworms, etc.), they do so in much smaller quantity than dung

260   beetles, so their potential effects on dung removal in this study were negligible according to our

261   observations *in situ*. Given the short time of the experiment (48 hours), we included the potential

262   presence of eggs and larvae of flies as part of the total weight of the dung, assuming that it does

263   not have any significant influence on final weights.

264

2.4 Data analysis

Species accumulation curves were constructed to evaluate the completeness of the surveys

conducted in each sampling zone, using pitfall traps as sampling units. The order of entrance of

the sampling units in the curve was randomized 100 times in *EstimateS* v. 9.1.0 (Colwell, 2013),

and inventory completeness was assessed from the final slope of this smoothed curve (*i.e.*, the

difference in observed richness between the last two sampling units; Hortal & Lobo, 2005). We

measured the heterogeneity in species abundances (*i.e.*, species diversity) using the Shannon–

Wiener entropy index. The effects of anthropogenic disturbance on diversity and ecosystem

functioning (prediction 1) –both overall and in each region– were evaluated with linear regression

models. Here, we included abundance, diversity metrics (*i.e.*, richness, Shannon index, and

CWM), and dung removal rates (*i.e.*, TDRR, DRP, and DRT) as dependent variables, and study

area (with three levels: Caribbean, Andes, and Amazon), forest disturbance (with two levels:

conserved and perturbed), and their two-way interaction as factors. Such models were applied

separately to each dependent variable.

The relationships of abundance, species richness, and functional richness (*i.e.*, number of

functional groups, out of the nine defined above) with total dung removal (prediction 2) were

evaluated with mixed-effects models (Pinheiro & Bates, 2000). We evaluated both Linear and

Nonlinear Mixed-effect Models (LMM and nLMM, respectively) to account for potential non-

linearity in the relationship between biodiversity variables and total dung removal, using the *nlme*

R package (Pinheiro *et al.,* 2020). The relationships of abundance, species richness, and

functional richness with dung removal by paracoprids and telecoprids were also tested in

different models. In these models, we included sampling zone (with six levels obtained from the

intersection of the three study areas and the two forest types) as a single random factor to account

288   for the non-independence in environmental conditions of the experimental units (see Pinheiro &

289   Bates, 2000; Harrison *et al.*, 2018). In a visual inspection all these relationships were apparently

290   linear, and quadratic relationships obtained from nLMMs did not increase the explanatory power

291   of the models (not shown); therefore, we only present the results of the linear relationships

292   obtained from LMMs. Finally, we applied Linear Mixed-effect Models (LMM) using the *lme4*

293   package (Bates *et al*., 2015) to evaluate whether dung removal performed by either paracoprids

294   and telecoprids was affected by the diversity of each functional group (prediction 3). Here, we

295   developed two independent models, where dung removal by paracoprids and telecoprids were

296   used as response variables in each of these models, and where the abundance, richness, and

297   Shannon diversity index of either paracoprids or telecoprids were considered to be the

298   independent variables of both models; in both cases, sampling zone was included as a random

299   factor. We selected variables through stepwise backward elimination of variables, excluding

300   predictors from the models when either parameters or interactions were not significant. We

301   calculated Pearson correlation coefficients (r) for the relationships between variables of the

302   reduced models from predictions 2 and 3, and we used the *piecewiseSEM* package (Lefcheck,

303   2015) to calculate the coefficient of determination (R^2) for each reduced model and for the

304   regression analyses.

305   The assumptions of normality and homogeneity of variance of the residuals were tested in

306   all models using the Shapiro-Wilk normality test and the Bartlett homogeneity of variances test,

307   respectively. We transformed the Shannon's diversity index using a power transformation (x^2) in

308   order to meet the assumption of normality. In presence of heteroscedasticity in the residuals of

309   several models, we applied weighted least square regression (Strutz, 2016) by including weights

310   (1/variance) into the model using the Extract Model Weights function. Post-hoc tests for multiple

311   testing were applied using the *lsmeans* package (Lenth, 2016) with Bonferroni adjustments (to

312 account for type I errors), whenever there were significant (p<0.05) main effects or interactions

313 of factors with more than two levels. All analyses were performed in *R* version 3.3.1 (R Core

314 Team, 2015), except when indicated otherwise.

315

316 **3   RESULTS**

317 A total of 6,793 individuals belonging to 62 species were collected during the surveys (Table 1,

318 Figure 1). Species accumulation curves in each sampling zone demonstrate a good sampling

319 coverage (ranging from 83.5 to 98% total species sampled; Figure S3). *Canthon aequinoctialis*

320 was the most abundant species overall (n=1,301, 19.2%). Only *Eurysternus caribaeus* was

321 common to all three study areas (n=244, 3.6%), whereas 12 species were present in two of them,

322 and 49 only in one (Table 1). Paracoprids were the most abundant functional group (n=3,319; 37

323 spp.), followed by telecoprids (n=2,474; 16 spp.), and the least abundant were endocoprids

324 (*Eurysternus* spp., n=1,000; 9 spp.; Table 1, Figure 1). No large endocoprids were found in any

325 of the sites, whereas large paracoprids were absent from the Caribbean site, small endocoprids

326 from the Andean site, and large telecoprids from the Amazonian site (Table 1, Figure S2).

327

328 **3.1 Effects of anthropogenic perturbation on dung removal and diversity**

329 Total dung removal rate was affected by a significant study area $\times$ forest two-way interaction

330 (Table 2). It increased from the more disturbed study area (Caribbean), to the more conserved one

331 (Amazon). Conserved forests presented significantly higher removal rates compared to perturbed

332 forests in all three localities (Figure 2A). Both study area and forest type have significant effects

333 on dung removal by paracoprids and telecoprids, while their two-way interaction was not

334 significant (Table 2). Further, there was a significant two-way interaction between type of forest

335 and functional group richness ($F_{1,236}$=21.32; p<0.001; Figure 2B). Post-hoc contrasts revealed no

336   significant differences between removal rates by paracoprids and telecoprids in conserved forests

337   (post-hoc contrast: estimate=0.86; p=0.90), while they do differ significantly in perturbed forests

338   (post-hoc contrast: estimate=-7.35; p<0.001), where removal rate by telecoprids was higher

339   (Figure 2B). Study area and forest type have significant effects on the abundance of dung beetles,

340   following the same trend as dung removal rates (*i.e*., abundance decreases in perturbed forests;

341   Table 2; Figure S4). However, the two-way interaction between these two factors was not

342   significant (Table 2). Species richness, Shannon's diversity index and CWM were significantly

343   affected by the area × forest two-way interactions (Table 2). Contrasts also revealed higher

344   diversity values in conserved than in perturbed forests, and the same gradient of increasing values

345   from the Caribbean to Amazonian forests (see Figure S4).

346

347   **3.2 Effects of diversity and assemblage structure on dung removal**

348   Overall, there were positive and significant relationships of total dung removal rate, dung

349   removal by paracoprids, and dung removal by telecoprids with abundance, species richness,

350   Shannon's diversity index, and CWM (Figure 3; Table 3). There were significant slightly convex

351   relationships of total dung removal rate with species richness (t-value=3.679; p<0.001) and

352   Shannon's diversity index (t-value=3.157; p=0.002; Figure 3), while the relationships of total

353   dung removal rate with abundance and CWM were mainly linear. Dung removal by paracoprids

354   also increased with abundance, species richness, Shannon's diversity index, and CWM of

355   paracoprids, and significant slightly convex relationships existed between dung removal by

356   paracoprids and species richness (t-value=2.938; p=0.004) and Shannon's diversity index (t-

357   value=2.365; p=0.020; Figure 3), while the relationships of total dung removal rate with

358   abundance and CWM were mainly linear in most of its range. Besides, the same holds true for

359   dung removal by telecoprids (DRT), which presents linear relationships with higher values with

15

360 increasing abundance, species richness, Shannon's diversity index, and CWM of telecoprids

361 (Figure 3, Table 3), but no significant non-linear effects existed ($F_{1,117} \leq 3.28$; $p \geq 0.07$). LMMs

362 indicate that dung removal by paracoprids (DRP) was significantly affected by paracoprids

363 richness (t-value=-1.999; p=0.048) and marginally significant for both abundance (t-value=1.789;

364 p=0.076) and Shannon's diversity index of telecoprids (t-value=-1.777; p=0.078) (Table S1). On

365 the other hand, dung removal by telecoprids was positively affected by telecoprids richness (t-

366 value=2.255; p=0.027) and remarkably, by paracoprids richness (t-value=2.112; p=0.037),

367 suggesting a potential existence of a positive effect of the diversity of paracoprids on the function

368 performed by telecoprids. However, we also found a weak negative relationship between dung

369 removal by telecoprids and paracoprids abundance (t-value=-2.411; p=0.018; Table S1),

370 suggesting a potential negative interaction between these two functional groups.

371

372 **4 DISCUSSION**

373 Human disturbances produce generalized ecological changes that alter the natural dynamics of

374 communities at different levels and spatial and temporal scales, producing a complex gradient of

375 effects that range from small changes in populations to massive transformations of the landscape

376 (Sousa, 1984). As a result, these perturbations are responsible for changes in the diversity and

377 structure of communities, also affecting ecosystem functioning and service provisioning (Slade *et*

378 *al*., 2011). Indeed, our results evidence that dung removal is affected by anthropogenic actions

379 through biodiversity loss. The lower removal rates of perturbed forests are clearly associated with

380 lower dung beetle richness, abundance, and functional diversity. Overall, these results were

381 similar in the three study areas, located in environmentally contrasting regions. Species richness,

382 abundance, and functional diversity were positively associated with total and specific dung

383 removal rates, corroborating the existence of a relationship between biodiversity and ecosystem

384 functioning.

385   Forest perturbation alters the diversity, structure and functioning of dung beetle

386 assemblages due to the combined effects of the reduction of both forest cover and mammal

387 populations, and the drastic changes in microclimatic conditions (Braga *et al*., 2013; França *et al*.,

388 2018; Raids & Slade, 2019). As a consequence, this may cause a reduction of the ecosystem

389 services provided by dung beetles, which in turn can interrupt nutrient cycles, leading to an

390 impoverishment of soil quality (Stokstad, 2004). In this context, our results show that

391 anthropogenic perturbations in primary forests reduce the abundance of individuals and the

392 richness of both species and functional groups. This, in turn, reduces dung removal, potentially

393 hampering the ecological processes related to this ecosystem service (*e.g*., nutrient cycling, soil

394 aeration, and water porosity). Our results are in accordance with previous evidence suggesting

395 that different types and levels of perturbation have a negative effect on dung removal rates

396 (Horgan, 2006; Braga *et al*., 2013; Kenyon *et al*., 2016; Manning *et al*., 2017). However, a few

397 studies show no direct relationship between dung removal and other functions (Carvalho *et al*.,

398 2020), and in some cases dung removal was not affected by direct logging impacts (França *et al*.,

399 2018). Further, our study also reveals that these results hold constant throughout different

400 localities, representing the spatial gradient of decreasing disturbance from the Caribbean to the

401 Amazon caused by different development of the agricultural and cattle industries in these regions

402 during the last five decades (Etter *et al*., 2006). The effects of diversity on functioning remain

403 similar from the more conserved and diverse Amazon region to the more disturbed and poorer

404 Caribbean region (see, *e.g*., Echeverría-Londoño *et al*., 2016), which supports the idea that some

405 general impacts of human perturbations on diversity and ecosystem functioning may be

406 consistent rather than context dependent. Besides, it is essential to point out the potential

407   influence of the heterogeneity of the surrounding landscape in each locality, which is a probable

408   source of species that may be moving using the dominant vegetation matrix and affecting local

409   diversity (see, *e.g.*, Gilroy *et al*., 2014; Beiroz *et al*., 2018).

410   The positive effect of dung beetle diversity on several ecosystem services is already well

411   documented in the literature (Slade *et al*., 2007; Menéndez *et al*., 2016; Meyer *et al*., 2016), and

412   can be placed within the Biodiversity–Ecosystem Functioning (BEF) relationship (Tilman *et al*.,

413   2014). Particularly, dung removal is strongly influenced by changes in dung beetle species

414   richness and functional diversity in conserved and perturbed areas alike (*e.g*., Beynon *et al*.,

415   2012; Braga *et al*., 2013; Tixier *et al*., 2015; our results). This effect may arise from both the

416   complementarity in the functionality of the species present in an assemblage (Hoehn *et al*., 2008),

417   and the positive effects of the interactions between species (Cardinale *et al*., 2007), that would

418   enhance ecosystem service provision through a wider variety of different strategies for

419   performing the same function. Therefore, species loss in perturbed habitats causes a reduction in

420   such variety of functions, promoting a functional impoverishment that leads to diminished

421   ecological performance of local assemblages (Braga *et al*., 2013). In this context, it is important

422   to point out that in perturbed forests dung removal was significantly higher by telecoprids

423   compared to paracoprids, showing that some paracoprid species (especially large species) are

424   more sensitive to anthropic perturbations, and especially by the reduction of mammal presence on

425   those forests (Raine & Slade 2019). Although we do not have information on the mammal

426   species present in the study sites, it is expected that when a habitat is altered, its mammal

427   community will be affected too, which leads to a lower dung production, and therefore a lower

428   demand of dung removal (Nichols *et al*. 2009; Raine & Slade 2019).

429   Nonetheless, functional redundancy in the assemblages may help maintaining ecosystem

430   functionality despite species loss (Oliver *et al*., 2015). In the case of dung beetles, the higher

431   abundance of small and medium-sized species –in particular paracoprids– can compensate the

432   potential loss of functionality associated with the absence of large species (Amézquita & Favila,

433   2010; Slade *et al*., 2017). However, this may not be the case for other ecosystem functions; for

434   example, small beetles cannot compensate the relocation of large seeds that large species provide.

435   In this sense, paracoprids are highly effective decomposers, providing an enormous contribution

436   to dung removal (Slade *et al*., 2011; Braga *et al*., 2013; Nervo *et al*., 2014). Nevertheless, it is

437   important to note that in our study, dung removal also increases with increasing richness of

438   individual functional groups. Besides, it is possible that reductions in abundance, or even the

439   occurrence of local extinctions, of some key species, and especially large paracoprids (*e*.*g*.,

440   *Coprophanaeus telamon*, *C. suredai*, *Phanaeus chalcomelas*, or *P. hermes*), had negative effects

441   on dung removal rates (see Slade *et al*., 2007). Interspecific competition for food resources has

442   been traditionally assumed to be the main mechanism regulating the interaction between dung

443   beetles and the structure of their assemblages (Hanski & Cambefort, 1991). However, the overall

444   positive relationship between removal rates and species richness suggests that the effect of

445   interspecific competition on this ecosystem service may be relatively small.

446   Beyond species richness, high functional group diversity enhances ecosystem functioning

447   (Larsen *et al*., 2005). Dung beetle multi-functionality is associated to high diversity levels and the

448   combination of different functional groups (Manning *et al*., 2016; 2017; Slade *et al*., 2019). Our

449   results indicate that a diverse assemblage combined with functional group complementarity are

450   important to maintain the ecological process of dung removal performed by dung beetles, and

451   support the ecosystem services they provide. Complementarity between different dung beetle

452   functional groups also enhances the outcome of different ecosystem services related to

453   decomposition beyond the complementarity at the species level, with positive effects not only on

454   dung removal (see Slade *et al*., 2007; Slade & Roslin, 2016; Milotić *et al*., 2019; note that these

455 studies have been conducted mainly in pastures and outside tropical areas), but also on soil

456 microbial respiration (Menéndez et al., 2016). Our results show an apparent enhancement of

457 telecoprids' dung removal activity associated with the diversity of paracoprids species, as well as

458 an apparent negative association between paracoprids abundance and telecoprids dung removal.

459 However, these results must be evaluated with caution, as the protocol used in this study was not

460 specifically designed for evaluating interactions between guilds. Also, the experimental set up

461 could have led us to overestimate the dung removed by telecoprids, as dung removal could have

462 been performed by other species other than dung beetles; still, we believe this effect is almost

463 negligible and does not compromise our results.

464

465 **5   CONCLUSIONS**

466 Our results reveal that ecological processes, and particularly dung removal, are positively

467 affected and maintained by high levels of richness, abundance and functional diversity. Moreover,

468 this study strengthens the evidence for the generalized negative impacts of human activities on

469 the diversity and structure of dung beetle assemblages, consequently leading to reduced dung

470 removal rates, and also possibly to a generalized decay on the ecosystem functioning of very

471 different regions. We found preliminary evidence for the existence of a potential positive

472 interaction between dung beetle functional groups that possibly enhances the ecosystem services

473 they provide. Further experimental manipulative studies are necessary to elucidate the nature (*i.e.*,

474 competition or facilitation) and importance of interactions between paracoprids and telecoprids,

475 and their potential impacts on multiple ecosystem functions and services. In any case, future

476 management and conservation strategies should consider how human-induced changes in

477 biodiversity affect ecosystem functioning and service provisioning, including a multifunctional

478 approach that measures several ecosystem functions.

479 **TABLE 1** Information on the species sampled in this study, together with the species abundance,

480 richness, Shannon's diversity index, and average dung removal found in two types of forests

481 (primary forests – PF and disturbed forests - DF) of the three study areas (Caribbean, Andes, and

482 Amazon). FG: functional groups (defined by the combination of food relocation behavior - P:

483 paracoprids, T: telecoprids, and E: endocoprids, and average body size – L: large >18.0 mm, M:

484 medium from 17.9 mm to 10.0 mm, and S: small < 10.0 mm). BS: average body size of the

485 individuals of each species (total length in mm).

486

Tribe	Species	FG	BS	Caribbean		Andes		Amazon	
				PF	DF	PF	DF	PF	DF
Ateuchini	*Ateuchus murrayi*	PS	6.5	0	0	0	0	1	0
	Ateuchus pygidialis	PS	7.3	0	0	0	0	97	48
	Ateuchus sp. 1	PS	8.0	0	0	0	0	1	0
	Ateuchus sp. 2	PS	8.2	0	0	111	62	0	0
	Ateuchus sp. 3	PS	7.9	7	0	0	0	0	0
	Uroxys sp. 1	PS	4.2	0	0	0	0	5	2
	Uroxys sp. 2	PS	3.8	0	0	0	0	3	1
	Uroxys sp. 3	PS	5.5	0	0	65	16	0	0
	Uroxys sp. 4	PS	4.6	0	0	1	0	0	0
	Uroxys sp. 5	PS	3.3	60	73	0	0	0	0
	Uroxys sp. 6	PS	4.0	22	26	0	0	0	0
Coprini	*Canthidium atomarium*	PS	5.0	0	0	0	0	0	5
	Canthidium aurifex	PS	7.5	0	0	33	13	0	0
	Canthidium cupreum	PS	6.4	0	0	0	1	31	0
	Canthidium euchalceum	PS	7.1	271	139	0	0	0	0
	Canthidium funebre	PS	7.2	0	0	0	0	10	0
	Canthidium haroldi	PS	8.3	0	0	3	0	0	0
	Canthidium moestum	PS	6.8	14	0	0	0	0	0
	Canthidium sp. 1	PS	7.2	0	0	23	9	0	0
	Dichotomius belus	PM	14.5	0	18	0	0	0	0
	Dichotomius gamboensis	PM	13.2	2	9	0	0	121	67
	Dichotomius mamillatus	PL	20.7	0	0	0	0	7	13
	Dichotomius ohausi	PM	15.6	0	0	0	0	0	1
	Dichotomius podalirius	PL	19.2	0	0	0	0	63	46
	Dichotomius protectus	PL	19.6	0	0	97	31	0	0
	Dichotomius satanas	PM	16.5	0	0	29	13	0	0
	Ontherus appendiculatus	PM	14.0	0	0	3	0	1	0
Deltochilini	*Canthon acutus*	TS	7.0	20	7	0	0	0	0

	Species			1	2	3	4	5	6
	Canthon aequinoctialis	TM	12.1	0	0	396	185	408	312
	Canthon lituratus	TS	6.2	5	2	0	0	0	0
	Canthon luteicollis	TS	9.6	0	0	0	0	42	6
	Canthon mutabilis	TS	6.9	0	2	0	0	0	0
	Canthon politus	TS	7.4	0	0	47	15	5	0
	Canthon septemmaculatus	TM	10.0	5	0	11	0	0	0
	Canthon subhyalinus	TS	9.0	0	0	76	34	0	0
	Canthon variabilis	TS	5.8	556	159	0	0	0	0
	Deltochilum carinatum	TM	16.5	0	0	0	0	18	7
	Deltochilum crenulipes	TM	15.2	0	0	0	0	63	24
	Deltochilum orbignyi	TL	21.0	7	3	18	9	0	0
	Deltochilum tesselatum	TL	18.8	0	0	17	0	0	0
	Malagoniella astyanax	TM	17.2	4	0	0	0	0	0
	Scybalocanthon pygidialis	TS	8.6	0	0	0	0	6	0
Oniticellini	*Eurysternus caribaeus*	EM	15.2	3	10	14	69	85	63
	Eurysternus cayennensis	EM	10.2	0	0	0	0	104	98
	Eurysternus foedus	EM	14.3	0	0	84	22	6	0
	Eurysternus hamaticollis	EM	16.9	0	0	0	0	38	5
	Eurysternus hypocrite	EM	17.5	0	0	0	0	117	86
	Eurysternus impresicollis	ES	7.4	15	16	0	0	0	0
	Eurysternus marmoreus	EM	13.6	0	0	15	18	0	0
	Eurysternus mexicanus	EM	10.7	8	3	64	39	0	0
	Eurysternus wittmerorum	ES	9.3	0	0	0	0	11	7
Onthophagini	*Onthophagus acuminatus*	PS	6.2	0	0	264	127	201	160
	Onthophagus buculus	PS	6.8	92	125	0	0	0	0
	Onthophagus clypeatus	PS	8.0	0	0	0	0	23	11
	Onthophagus curvicornis	PS	6.7	0	0	8	3	0	0
	Onthophagus lebasi	PS	6.4	0	0	15	5	0	0
	Onthophagus marginicollis	PS	4.9	190	242	0	103	0	0
Phanaeini	*Coprophanaeus suredai*	PL	20.8	0	0	0	0	6	0
	Coprophanaeus telamon	PL	23.0	0	0	7	0	28	10
	Phanaeus chalcomelas	PM	14.3	0	0	0	0	14	0
	Phanaeus hermes	PM	14.4	6	0	5	0	0	0
	Phanaeus prasinus	PM	15.2	4	1	0	0	0	0
	Species richness			19	16	24	19	28	20
	Abundance			1291	835	1406	774	1515	972
	Shannon's diversity index *H'*			1.237	1.22	1.570	1.516	1.718	1.59
	Total dung removal (g)			39.4	19.0	47.8	25.0	52.4	35.4
	Dung removal by paracoprids (g)			21.3	7.0	24.2	9.2	25.6	12.5
	Dung removal by telecoprids (g)			18.1	12.0	23.6	15.8	26.8	22.9

487

488

489 **TABLE 2** Linear regression models assessing the effects of study area (Caribbean, Andes, and

490 Amazon) and type of forest disturbance (conserved and perturbed forests) on the abundance,

491 species richness, Shannon's index, community weighted mean (CWM), total dung removal rate

492 (TDRR), dung removed by paracoprids (DRP), and dung removed by telecoprids (DRT).

493

Response	Parameter	df	F value	$p -$	sig.	R^2
Abundance	Study area	2	8.30	< 0.001	***	
	Forest type	1	242.09	< 0.001	***	0.810
	Area×Forest ✦	2	1.41	0.248	-	
Species richness	Study area	2	163.89	< 0.001	***	
	Forest type	1	110.53	< 0.001	***	0.809
	Area×Forest	2	22.81	< 0.001	***	
Shannon	Study area	2	129.13	< 0.001	***	
	Forest type	1	21.56	< 0.001	***	0.726
	Area×Forest	2	3.13	0.047	*	
CWM	Study area	2	2105.32	< 0.001	***	
	Forest type	1	6.80	0.010	*	0.737
	Area×Forest	2	4.97	0.009	**	
TDRR	Study area	2	91.60	< 0.001	***	
	Forest type	1	608.60	< 0.001	***	0.882
	Area×Forest	2	5.84	0.003	**	
DRP	Study area	2	5.96	0.003	**	
	Forest type	1	151.49	< 0.001	***	0.585
	Area×Forest ✦	2	0.23	0.794	-	
DRT	Study area	2	40.59	< 0.001	***	
	Forest type	1	31.81	< 0.001	***	0.427
	Area×Forest ✦	2	1.36	0.261	-	

494

495 ✦ Two-way interactions between Forest and Region that were not significant in these models,

496 were thus removed from the initial model by stepwise backward elimination. Sample size (N)

497 was 120, and residuals have 116 degree of freedom (df) for reduced models and 114 df for non-

498 reduced models. Significance values (sig.) are indicated by asterisks: * (0.05>p≥0.01), **

499 (0.01>p≥0.001), and *** (p<0.001). R^2 values are reported for all reduced models.

500

501   **TABLE 3** Results of the linear mixed models (LMM) assessing, in three separate models (A, B,

502   and C), the relationships between total dung removal, dung removal by paracoprids and

503   telecoprids dung removal (dependent variables), with the overall abundance, the overall richness,

504   the overall Shannon's index, and the overall CWM of local dung beetle assemblages

505   (independent variables). The proportion of variance (R^2) explained by each parameter and their

506   respective levels of significance are reported.

507

	Parameters	R^2	$F_{1.118}$	P
A. Total dung removal	Overall abundance	0.434	90.35	<0.001
	Overall Richness	0.383	73.41	<0.001
	Overall Shannon	0.229	35.19	<0.001
	Overall CWM	0.252	39.73	<0.001
B. Dung removal by paracoprids	Overall Abundance	0.362	23.84	<0.001
	Overall Richness	0.168	67.03	<0.001
	Overall Shannon	0.073	9.31	0.03
	Overall CWM	0.067	8.46	0.04
C. Dung removal by telecoprids	Overall Abundance	0.110	14.59	<0.001
	Overall Richness	0.256	40.52	<0.001
	Overall Shannon	0.202	20.58	<0.001
	Overall CWM	0.251	39.55	<0.001

508

509

510

Figure legends

FIGURE 1 Number of dung beetle species (rhombuses) and individuals (bars) from each functional group (P: paracoprids; T: telecoprids; E: endocoprids) collected in each study area (Caribbean, Andes, and Amazon).

FIGURE 2 Dung removal rates by: (a) all species (total dung removal rates) in each study area (Caribbean, Andes, and Amazon) and type of forest disturbance (conserved and perturbed), and (b) functional group (paracoprids and telecoprids) in each type of forest disturbance (conserved and perturbed). Different letters above and below boxes represent post-hoc contrast differences within each functional group among study areas when considering the same type of forest. Asterisks indicate significant differences (*** $p<0.001$) between conserved and perturbed forests within the same study area.

FIGURE 3 Relationships between dung removal rates (total dung removal rate: a-d; removal rate by paracoprids: e-h; and by telecoprids: i-l) and abundance, species richness, Shannon's index, and Community Weighted Mean (CWM) of all species (a-d), and paracoprids (e-h) and telecoprids (i-l) separately. R^2 values were obtained from regression analysis. Study areas are represented by different symbols (Amazon: circles, Andes: squares, Caribbean: triangles) and types of forest by colors (conserved: white, perturbed: black). Significant relationships between variables are indicated by asterisks: * ($0.05>p\geq0.01$), ** ($0.01>p\geq0.001$), *** ($p<0.001$).

530

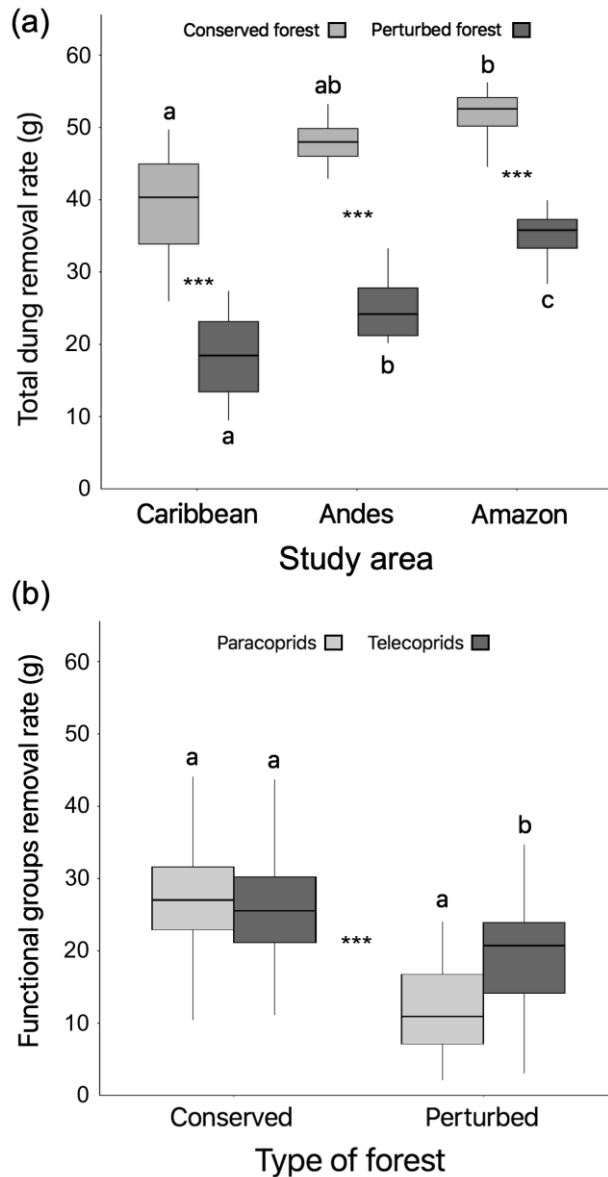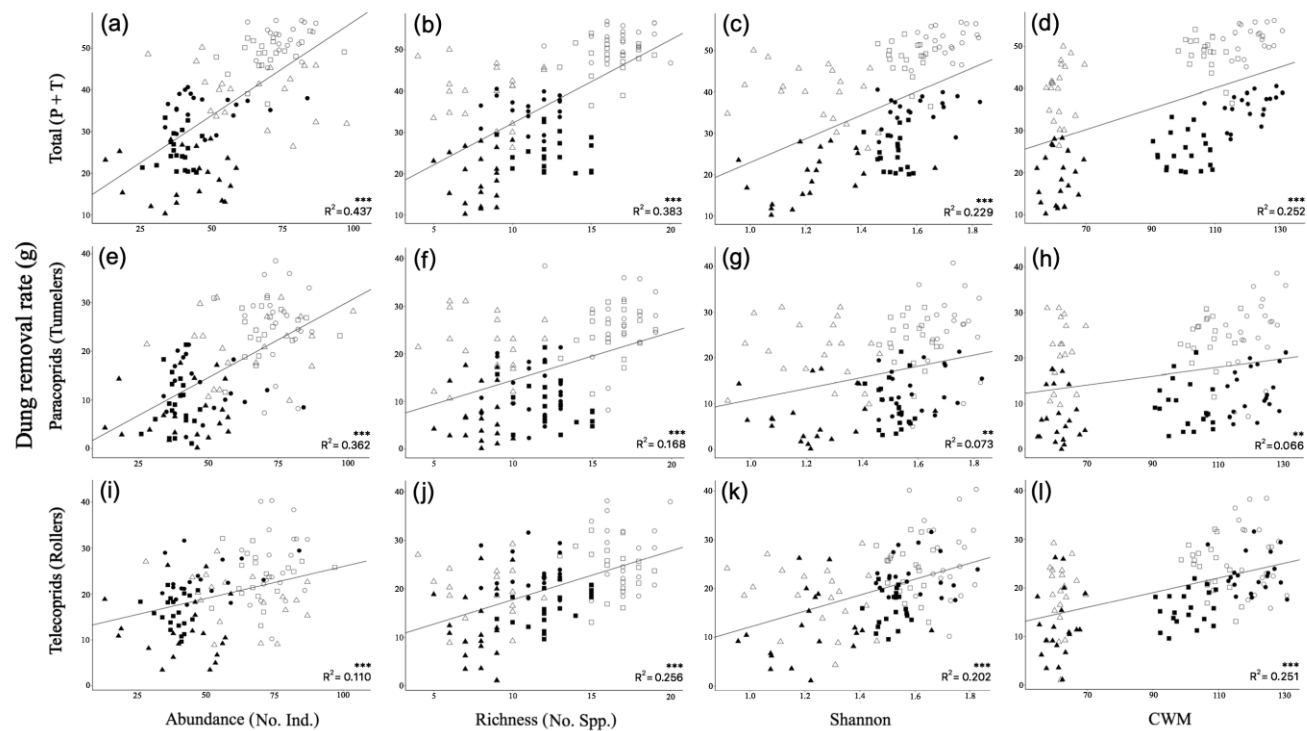**FIGURE 1** Number of dung beetle species (rhombuses) and individuals (bars) from each

functional group (P: paracoprids; T: telecoprids; E: endocoprids) collected in each study area

(Caribbean, Andes, and Amazon).

534

FIGURE 2 Dung removal rates by: (a) all species (total dung removal rates) in each study area (Caribbean, Andes, and Amazon) and type of forest disturbance (conserved and perturbed), and (b) functional group (paracoprids and telecoprids) in each type of forest disturbance (conserved and perturbed). Different letters above and below boxes represent post-hoc contrast differences within each functional group among study areas when considering the same type of forest. Asterisks indicate significant differences (*** $p < 0.001$) between conserved and perturbed forests within the same study area.

543

FIGURE 3 Relationships between dung removal rates (total dung removal rate: a-d; removal rate by paracoprids: e-h; and by telecoprids: i-l)

and abundance, species richness, Shannon's index, and Community Weighted Mean (CWM) of all species (a-d), and paracoprids (e-h) and

telecoprids (i-l) separately. R^2 values were obtained from regression analysis. Study areas are represented by different symbols (Amazon: circles,

Andes: squares, Caribbean: triangles) and types of forest by colors (conserved: white, perturbed: black). Significant relationships between

variables are indicated by asterisks: * ($0.05 > p \geq 0.01$), ** ($0.01 > p \geq 0.001$), *** ($p < 0.001$).

561

562 **AUTHOR CONTRIBUTIONS**

563 JAN conceived the idea and designed the research; JAN, SC, and HG gathered the data;

564 JAN, MMS, JH, and AMCS designed the analyses and structured the manuscript; JAN

565 and MMS analyzed the data; JAN, MMS, JH, and AMCS wrote the paper, and all

566 authors discussed results and approved the last version of the paper.

567

568 **CONFLICT OF INTEREST**

569 No potential conflict of interest was reported by the authors.

570

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576

577   **DATA AVAILABILITY STATEMENT**

578   The data that support the findings of this study are openly available in the Dryad Digital

579   Repository: https://doi.org/10.5061/dryad.pg4f4qrp2 (Noriega, March-Salas, et al.,

580   2021).

581   **SUPPORTING INFORMATION**

582   The following supporting information can be found online:

583   **Table S1.** Results of the Linear Mixed-effect Models on the relationships between the

584   dung removed by paracoprids and telecoprids with abundance, species richness, and

585   Shannon's diversity index of both groups.

586   **Figure S1.** Study areas and experimental procedures.

587   **Figure S2.** Species assignment to different functional groups.

588   **Figure S3.** Species accumulation curves for each type of forest and study area.

589   **Figure S4.** Dung beetle assemblage diversity and structure per study area and type of

590   forest.

591

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860

861 **SUPPLEMENTARY INFORMATION**

862

863 **TABLE S1** Results of the Linear Mixed-effect Models on the relationships between the

864 dung removed by paracoprids (DRP) and telecoprids (DRT) with abundance, species

865 richness, and Shannon's diversity index of both paracoprids and telecoprids. Only

866 significant, and nearly significant, parameters are shown.

867

Response	Parameter	Estimate	Df	t-value	p - value	sig.	R^2
DRP	Intercept	24.493	23.15	4.184	< 0.001	***	
	Richness – paracoprids	-0.932	115.47	-1.999	0.048	*	
	Abundance – paracoprids	0.132	113.98	1.789	0.076	•	0.701
	Shannon – telecoprids	-11.435	115.51	-1.777	0.078	•	
DRT	Intercept	14.429	27.48	4.234	< 0.001	***	
	Richness – paracoprids	0.889	110.50	2.112	0.037	*	
	Abundance – paracoprids	-0.165	112.60	-2.411	0.018	*	0.414
	Richness – telecoprids	1.462	76.68	2.255	0.027	*	

868

869 Some parameters were not significant ($p \geq 0.1$), and therefore, they were removed from

870 the final model by stepwise backward elimination. Sample size (N) was 120.

871 Significance values (sig.) is indicated by asterisks: • ($0.1 > p \geq 0.05$; marginally

872 significant), * ($0.05 > p \geq 0.01$), ** ($0.01 > p \geq 0.001$), and *** ($p < 0.001$). Conditional R^2

873 values are reported for each reduced model.

874
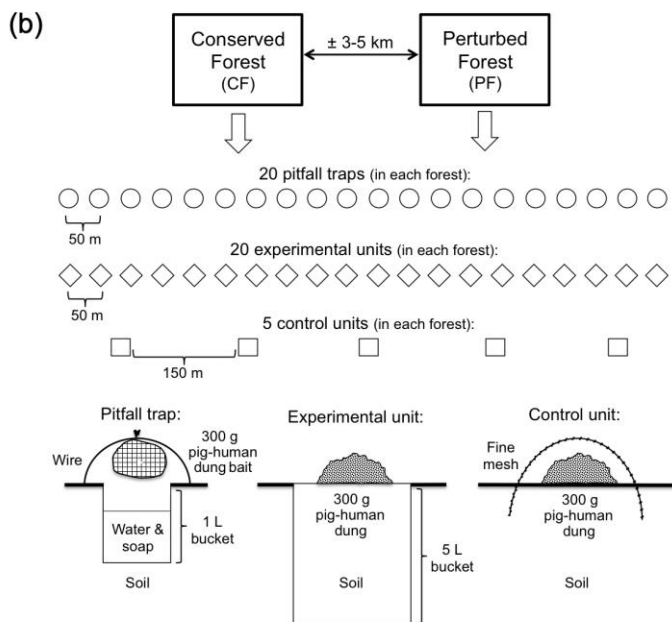
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876

877 **FIGURE S1** Study areas and experimental procedures. (a) Map of Colombia with its

878 five main ecoregions and location of the areas where experiments were conducted: (1)

879 Caribbean, (2) Andes, and (3) Amazon. (b) Sampling and experimental design with

880 experimental and control units, and pitfall traps in each forest type (conserved -CF- and
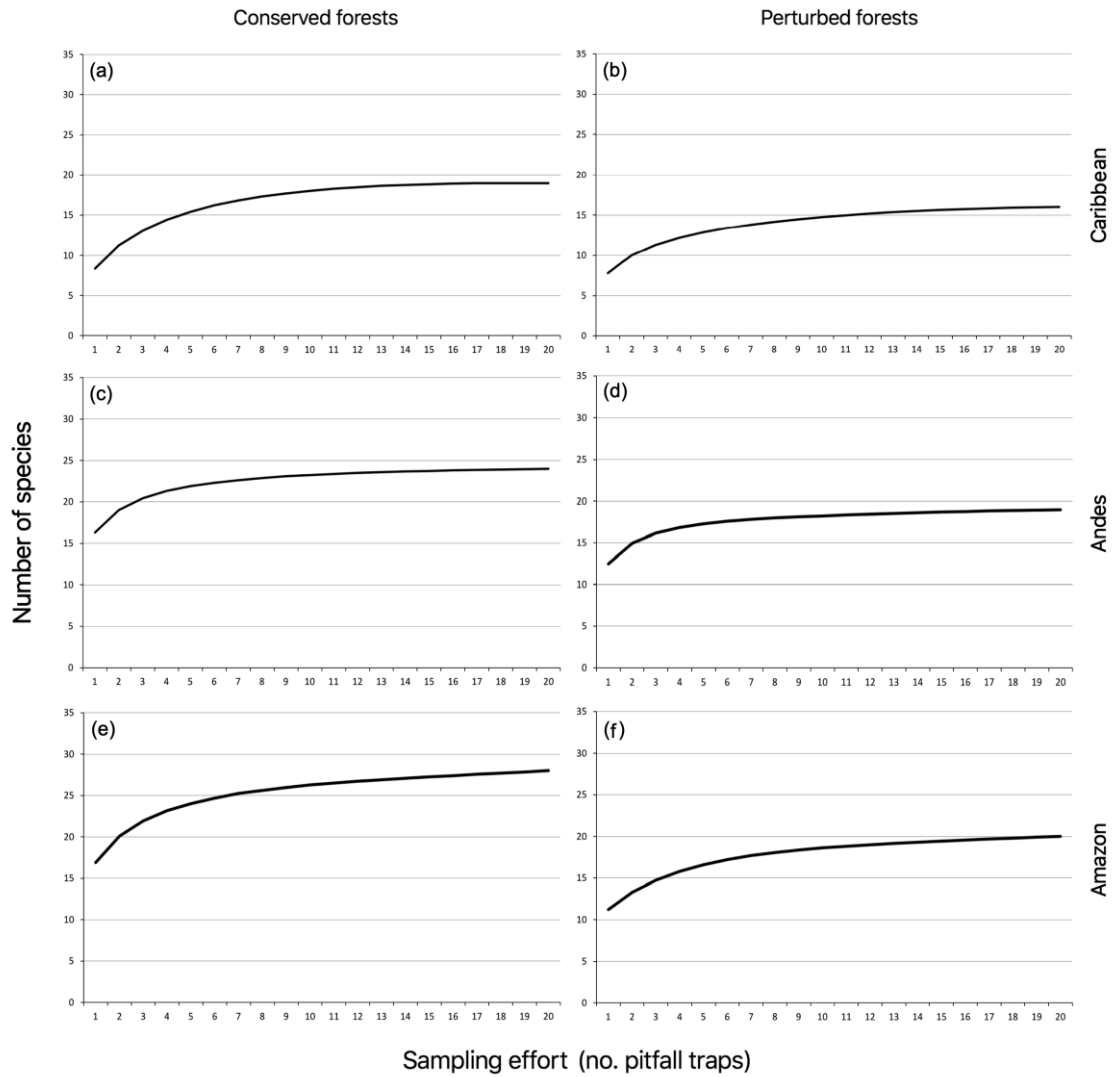
881 perturbed forest -PF).

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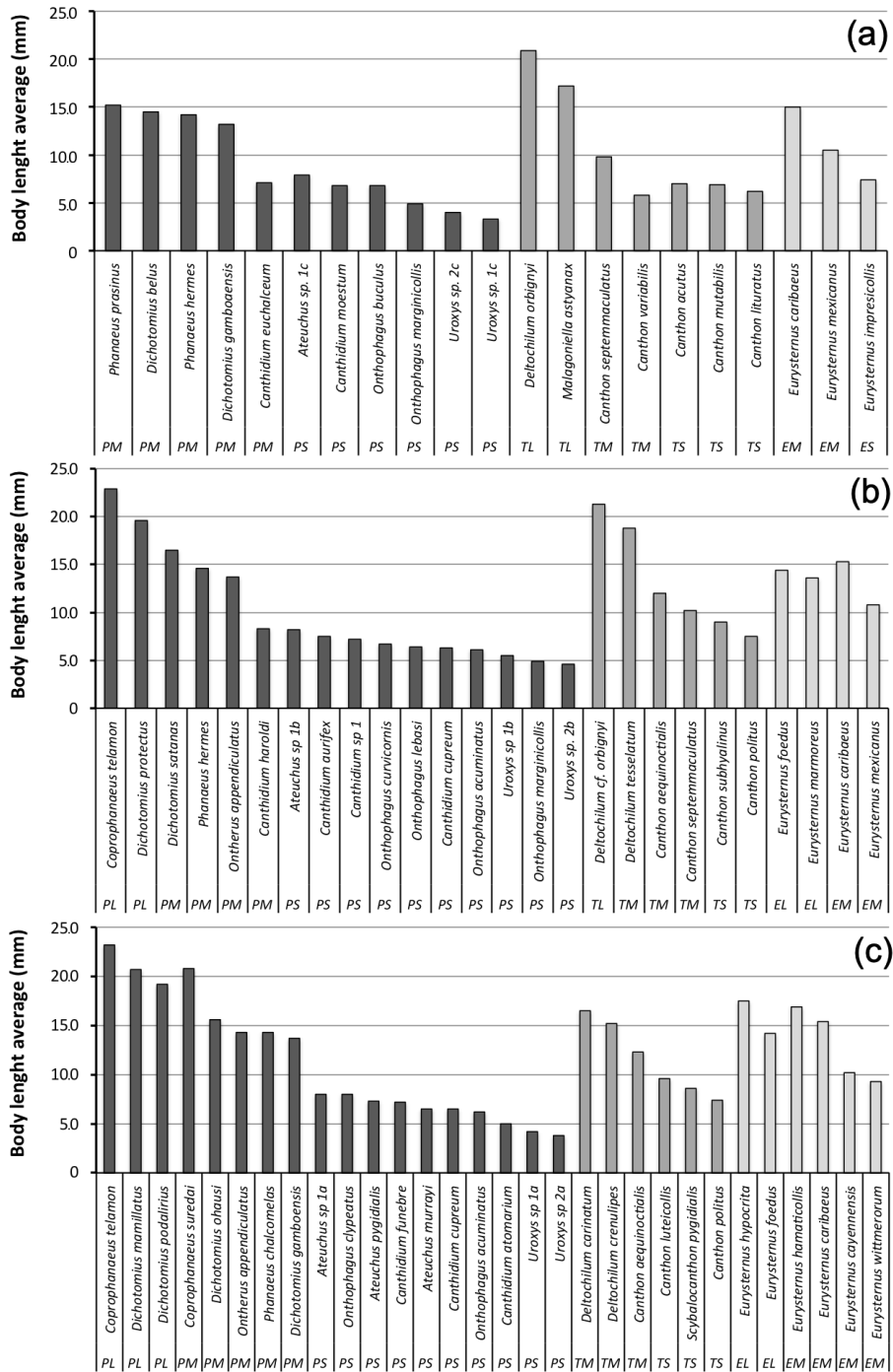
FIGURE S2 Species assignment to different functional groups, that were defined based

on dung relocation behavior and average body length (P: paracoprids, dark grey bars; T:

telecoprids, medium gray bars; and E: endocoprids, light gray bars; and the average

body length in mm: L: large, M: medium, and S: small), in each study area: (a)
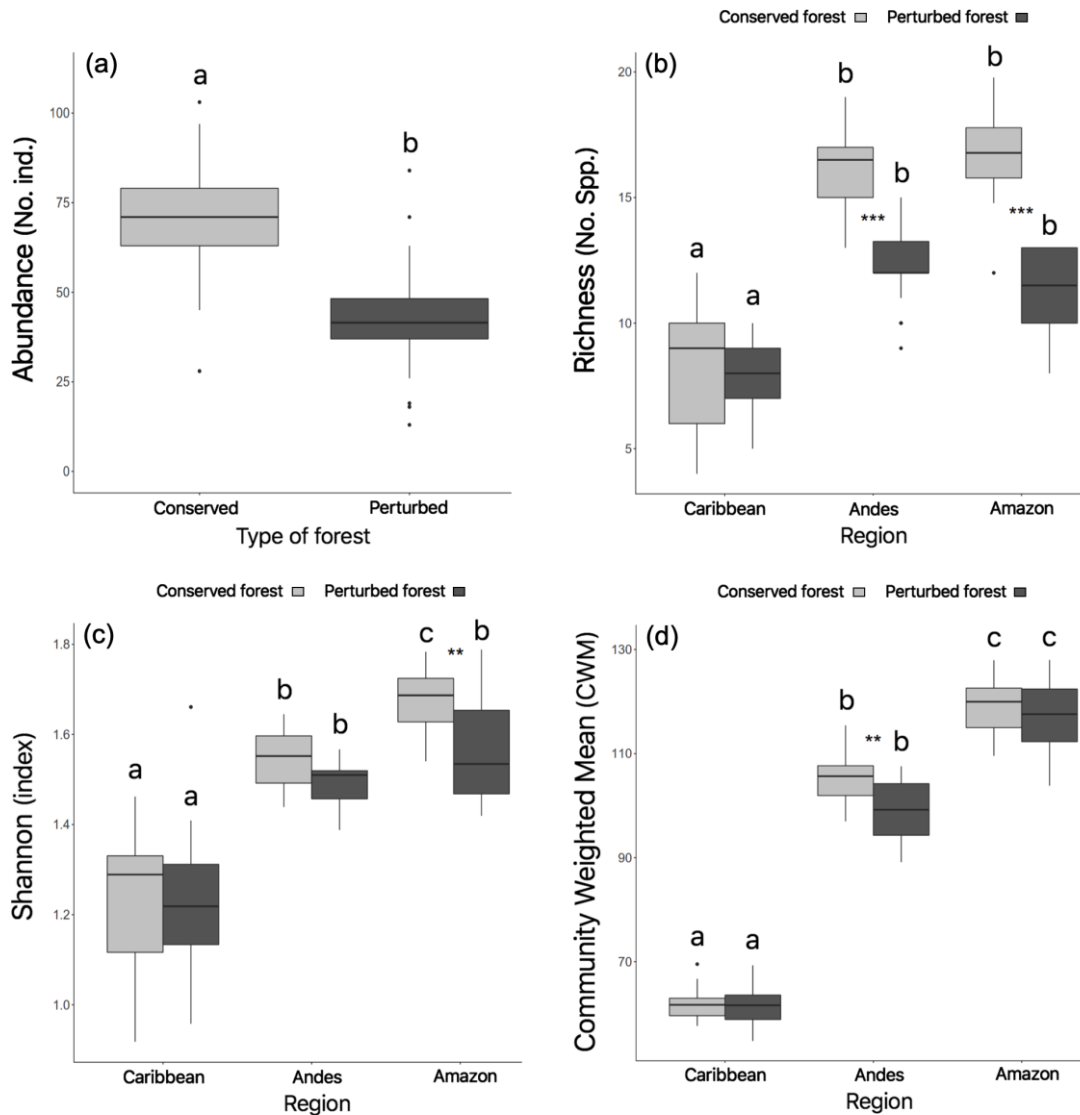
Caribbean, (b) Andes, and (c) Amazon.

889

FIGURE S3 Species accumulation curves for each type of forest and study area: (a) Caribbean – Conserved Forest, (b) Caribbean – Perturbed Forest, (c) Andes - Conserved Forest, (d) Andes - Perturbed Forest, (e) Amazon – Conserved Forest, and (f) Amazon – Perturbed Forest.

FIGURE S4 Dung beetle assemblage diversity and structure per study area (Caribbean, Andes, and Amazon sites) and type of forest (conserved and perturbed). (a) Abundance, (b) species richness, (c) Shannon index, and (d) Community Weighted Mean (CWM). Different letters above and below boxes represent post-hoc contrast differences between study areas when considering the same type of forest, and asterisks indicate significant differences (*** $p<0.001$) between conserved and perturbed forests within the same study area.