1 **Title:** Selective logging effects on 'brown world' faecal-detritus pathway in tropical forests: a
2 case study from Amazonia using dung beetles
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4 **Authors**: Filipe França[1, 2*], Júlio Louzada [1, 2], and Jos Barlow [1, 2, 3]

5 [1] Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster, LA1 4YQ, UK.

6 [2] Departamento de Biologia, Universidade Federal de Lavras, Lavras-MG, 37200-000, Brazil.

7 [3] Museu Paraense Emilio Goeldi, Av. Magalhães Barata, 376, Belém-PA, 66040-170, Brazil.

8 *Correspondence author:* Filipe M. França (filipeufla@gmail.com, +553538291923).

9 Departamento de Biologia, Setor de Ecologia, Universidade Federal de Lavras, Lavras-MG,

10 37200-000, Brazil.

Abstract:

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

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

Abbreviations:

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

DBH: Diameter at breast height

FSC: Forest Stewardship Council

FAO: Food and Agriculture Organization of the United Nations

GLM: Generalised Linear Model

RIL: Reduced-Impact Logging

1. Introduction

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

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

68 impacts on ecosystem processes, with dramatic implications for both 'green' and 'brown'

69 worlds (Wu et al., 2011).

70   Dung beetles (Coleoptera: Scarabaeinae) are a focal group of detritivores that are

71 frequently used in ecological research linking biodiversity to ecosystem functioning under

72 changing environmental conditions (e.g. Braga et al., 2013; Slade et al., 2011). Through dung

73 manipulation for feeding and nesting purposes (Hanski and Cambefort, 1991), dung beetles

74 play a vital role in facilitating the transfer of energy and matter through dung-based pathways

75 (Nichols and Gardner, 2011). They influence a range of specific detritus processes (Fig. 1),

76 such as faecal consumption and soil bioturbation (Nichols et al., 2007), dung beetle biomass

77 production for predators (Young, 2015), secondary seed dispersal (Griffiths et al., 2016, 2015)

78 and microbial transport across the soil-surface (Slade et al., 2016). Although previous

79 investigation has shown that impacts of human activities in tropical forests on dung beetles are

80 mediated by habitat type and via body-size-dependent responses (Nichols et al., 2013b),

81 conclusions were based on a space-for-time design which may underestimate the impacts from

82 human disturbance (França et al. 2016a). Moreover, despite evidence highlighting the

83 importance of environmental context to predict dung beetle-mediated ecological processes

84 within undisturbed forests (Griffiths et al., 2015), we are not aware of any empirical study

85 exploring the extent to which an anthropogenic forest disturbance, such as selective logging,

86 alters the importance of environmental drivers for dung beetle-mediated faecal-detritus

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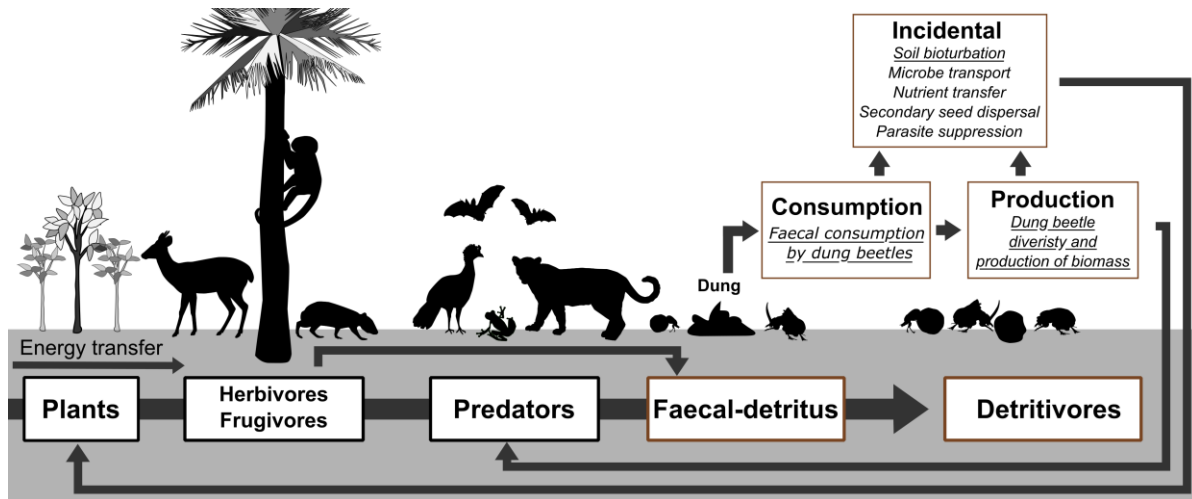
Figure 1. Dung beetle-mediated faecal detritus-pathway. The energy flow comes from Sun and other key soil elements (e.g. N and P), being assimilated by plants. Plants are consumed by herbivores and frugivorous, which in turn are consumed by predators. These animals, through defecating, produce the resources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

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

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

2. Material and methods

2.1 Study site

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

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

2.2 Experimental design

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

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

We sampled environmental variables, dung beetles and their associated detritus processes twice within each sample unit: the pre-logging survey occurred between June and July 2012, a few weeks before logging operations began. The post-logging dung beetle survey took place in 2013, approximately 10 months after logging activities ended. It also occurred in June and July, to minimize possible seasonal effects. RIL operations started in July and ended in September 2012; logging intensity ranged from 0 to 50.3 m^3 ha^{-1} of timber (or 0 to 7.9 trees ha^{-1}) that was eventually extracted within our sample units (see França et al. 2016b for logging intensity details). All data were sampled at exactly the same locations and following the same methods in both surveys. Sampling locations were relocated based on marking tape, or by GPS when disturbance from logging activities meant this could not be found.

2.3 Environmental drivers of ecosystem processes

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

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

161   using optimum exposure for each site (Zhang et al., 2005). The Gap Light Analyser software

162   (GLA version 2.0; Frazer et al., 1999) was used to estimate the 'canopy openness %' factor,

163   which represents the ratio of the total amount of open space to the total area of the

164   hemispherical photograph (Frazer et al., 1999). This approach has been widely used to account

165   for the canopy openness (Medjibe et al., 2014; Niemczyk et al., 2015; Silveira et al., 2010). In

166   addition, leaf litter was collected from the forest floor within a 25×25 cm square randomly

167   placed ~1 m from each pitfall trap (Appendix B, Fig. B1). We used a *Shimatzu* AY220 balance

168   scale (*Shimadzu Corporation, Kyoto, Japan*) accurate to within ±0.001g to obtain the leaf litter

169   weight after drying it at 60 °C for 96-h. For analysis purpose and to get an aggregate value,

170   canopy openness and leaf litter metrics were the averages among the six samples taken within

171   each of the sample units. Lastly, we also took a soil sample (~10 cm depth) at the six trap

172   locations, forming a composite soil sample to represent the soil texture (clay, silt and coarse

173   sand fractions) within the sample units at each survey. Granulometric analyses were conducted

174   in the soil laboratory of *Jari Celulose S.A*. In the same way as previous dung beetle-research,

175   we also considered the sand proportion as our soil texture measure (Gries et al., 2012; Griffiths

176   et al., 2015).

2.4 Detritivore communities and faecal-detritus processes

178   We addressed our research questions by exploring the logging impacts on dung beetle

179   communities, assessed by using the relative dung beetle species richness and biomass, which

180   were considered as a proxy of the production available for dung beetle predators (Young,

181   2015); and two processes associated with the faecal-detritus pathway (Fig. 1): (1) faecal

182   consumption and (2) incidental detrital processes, evaluated by sampling the dung beetle-

183   mediated faecal removal and soil bioturbation, respectively.

2.4.1 Faecal consumption and incidental soil bioturbation

The day before dung beetles were sampled, we established two circular, 1-m diameter

mesocosm arenas (Braga et al., 2013), spaced 100 m apart, and located at least 75 m from the

edge of the sample units (Appendix A, Fig. A2). Each mesocosm was delimited by a nylon-

mesh fence (~15 cm tall) held by bamboo sticks (Appendix A, Fig. A3). To facilitate the

evaluation of these processes, we cleared the soil surface of any leaf litter and vegetation

before placing a single 200-g experimental faecal deposit (4:1 pig to human ratio following

Marsh et al., 2013) at the centre of each mesocosm (Braga et al., 2013, 2012).

This mesocosm design allows dung beetles to freely enter the arena, and perform their

feeding and nesting activities that result in further underground relocation of faecal resources

while limiting the horizontal dung removal of brood balls by roller species to the contained

area (~0.785 m^2). After 24-h exposure period to the dung beetle communities, we weighed the

remaining dung (when present) and calculated the faecal consumptions rates. This 24-h period

of exposition was the same as previous studies following this protocol (Braga et al., 2013,

2012; Nichols et al., 2013b) and was chosen based on known movements of dung beetles

(Silva and Hernández, 2015) to avoid the risk of beetles from outside the unit perform the

faecal-detritus processes measured within the mesocosm. A parallel humidity control

experiment was set aside each arena (Appendix A, Fig. A3). Thus, changes in humidity of each

experimental faecal deposit were considered to calculate the faecal consumption rates (see

Appendix B for details). To quantify the incidental soil bioturbation rates as consequence of

excavations by dung beetles, we collected the loose soil clearly found above the soil surface

and weighed it after drying it at 60 ^{o}C for a week (Braga et al., 2013, 2012). We pooled the

data from the two arenas to get an aggregate value of dung beetle-mediated functional

processes for each sample unit.

2.4.2 Detritivore biomass and richness

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

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

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

2.5 Statistical analyses

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

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

identify the most likely predictors while minimizing the influence of multicollinearity and

providing the independent contribution of each predictor (Chevan and Sutherland, 1991).

Competing models were evaluated based on R^2 goodness of fit statistic, which allowed us to

interpret the independent effects as proportion of explained variance. Significance ($\alpha = 0.05$) of

independent effects of each predictor was calculated using a randomization test with 1000

iterations (Mac Nally, 2002; Walsh and Nally, 2013).

We analysed each response variable separately at each survey (pre and post-logging) to

evaluate whether these faecal-detritus processes are influenced by similar drivers after logging

operations. Gaussian distributions were tested using the Shapiro-Wilk normality test through

the *Shapiro.test()* function (*stats* package, Patrick Royston 1995). Hierarchical partitioning and

further randomization-significance tests were executed using the *hier.part* package (Walsh and

Nally, 2013). Table C1 (Appendix C) demonstrates the data used for GLM's and HP analyses.

3. Results

The canopy openness was the only environmental aspect changing between surveys (two-way

ANOVA: *survey $\times$ treatment* $F_{1, 64} = 1.4$, $p = 0.230$; *treatment* $F_{1, 65} = 3.7$, $p = 0.058$; *survey* $F_{1, 66} = 174.2$, $p < 0.001$), and increased significantly in logged forests (t-test, P-values ≤ 0.02; Fig. 2).
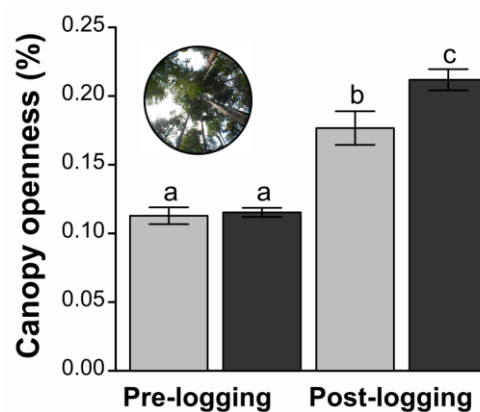
Figure 2. Canopy openness changes between control (light grey bars) and logging sites (dark grey bars) at surveys performed before (left bars in the panels) and after selective-logging

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

281 We also found negative logging impacts on dung beetle richness (two-way ANOVA:

282 *survey* × *treatment* $F_{1, 64}$ = 7.8, p = 0.006; *treatment* $F_{1, 65}$ = 3.2, p = 0.078; *survey* $F_{1, 66}$ = 70.4,

283 p < 0.001; Fig. 3A) and biomass (two-way ANOVA: *survey* × *treatment* $F_{1, 64}$ = 11.4, p =

284 0.001; *treatment* $F_{1, 65}$ = 1.7, p = 0.19; *survey* $F_{1, 66}$ = 41.8, p < 0.001; Fig. 3B), which reduced

285 up to 50% at logged forests (Fig 3A-B). However, while soil bioturbation decreased at both

286 control and logged sites in the second survey (two-way ANOVA: *survey* × *treatment* $F_{1, 64}$ =

287 0.3, p = 0.53; *treatment* $F_{1, 65}$ = 0.07, p = 0.78; *survey* $F_{1, 66}$ = 35.23, p < 0.001; Fig. 3D), no

288 significant direct logging impacts were found on dung beetle-mediated faecal consumption

289 (two-way ANOVA: *survey* × *treatment* $F_{1, 64}$ = 0.1, p = 0.750; *treatment* $F_{1, 65}$ = 1.8, p = 0.173;

290 *survey* $F_{1, 66}$ = 3.4, p = 0.069; Fig. 3C). Importantly, although a very weak spatial

291 autocorrelation was found in the pre-logging dung beetle richness and biomass (r = 0.18 and r

292 = 0.12, respectively; all P-values ≤ 0.03), these metrics were not spatially structured in the

293 post-logging survey (r = -0.41 and r = -0.42, respectively; all P-values = 0.999), even when the

294 control units were excluded from analysis (Appendix B).
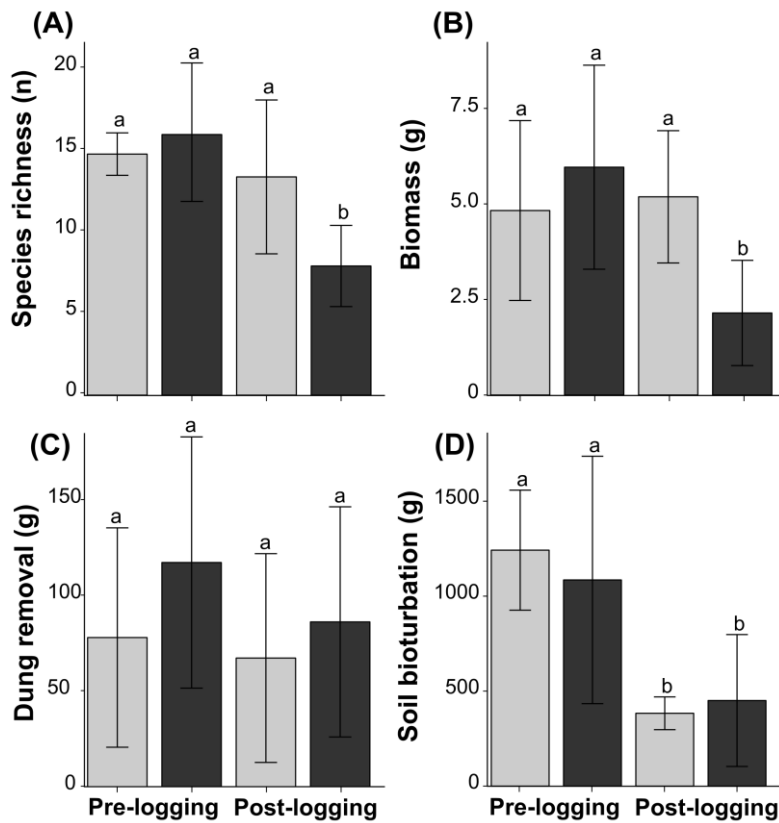
Figure 3. Dung beetle species richness (A), biomass (B), and rates of dung removal (C) and incidental soil bioturbation (D) sampled in control (light grey bars) and logging sites (dark grey bars) at surveys performed before (left bars in the panels) and after selective-logging (right bars). Means ± standard deviation (SD) followed by the same letter indicate post hoc zero difference at 5%.

Relating faecal-detritus pathways to environmental conditions before and after logging

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

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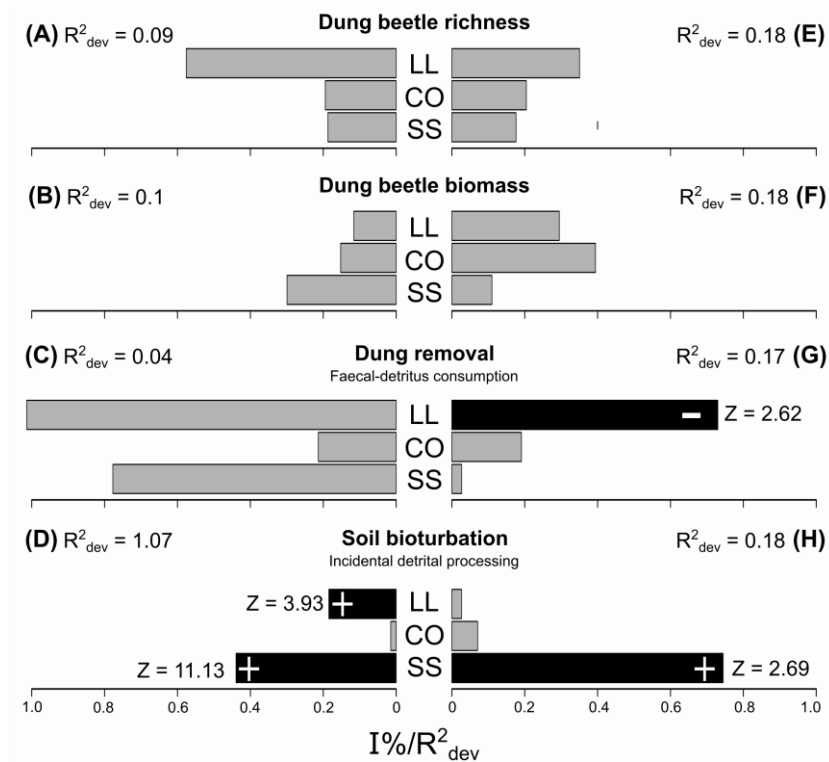
Figure 4. Distribution of the percentage of the independent effects of different predictors on dung beetle-mediated faecal detritus-processes. Left panels show pre-logging results (A-D) and right panels the post-logging ones (E-H). The x-axis shows the percentage of the independent effects (I %) divided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

4. DISCUSSION

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

15

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

4.1 Selectively logged forests can retain belowground functional processes

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

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

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

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

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

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

4.4 Conclusions

This investigation addressed to better understand the role that environmental conditions have in mediating the logging impacts on belowground functional processes. We found no support that our measures of canopy openness mediated dung beetle responses to logging, but we provide evidence that forest disturbances may alter the environmental importance for ecosystem functioning in tropical forests. While the dung beetle patterns reported here highlight the importance of within-forest disturbance (Barlow et al., 2016) and the irreplaceable role that pristine forests have to retain tropical biodiversity (Gibson et al., 2011), we demonstrate that carefully managed and certified selectively logged forests nevertheless can retain ecosystem processes such as detrital consumption and soil bioturbation (D. P. Edwards et al., 2014; Ewers et al., 2015).

Supplementary material:
Additional supplementary material may be found in the online version of this article:
Appendix A. Supplementary figures.
Appendix B. Supplementary experimental procedures.
Appendix C. Supplementary tables.

LITERATURE CITED

Asner, G.P., Broadbent, E.N., Oliveira, P.J.C., Keller, M., Knapp, D.E., Silva, J.N.M., 2006. Condition and fate of logged forests in the Brazilian Amazon. Proc. Natl. Acad. Sci. U. S. A. 103, 12947–12950. doi:10.1073/pnas.0604093103

Asner, G.P., Keller, M., Pereira, Jr, R., Zweede, J.C., Silva, J.N.M., 2004a. Canopy damage and recovery after selective logging in Amazonia: Field and stellite studies. Ecol. Appl. 14, 280–298. doi:10.1890/01-6019

435 Asner, G.P., Keller, M., Silva, J.N.M., 2004b. Spatial and temporal dynamics of forest canopy
436   gaps following selective logging in the eastern Amazon. Glob. Chang. Biol. 10, 765–783.
437   doi:10.1111/j.1529-8817.2003.00756.x

438 Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Nally, R. Mac, Thomson,
439   J.R., Ferraz, S.F. de B., Louzada, J., Oliveira, V.H.F., Parry, L., Ribeiro de Castro Solar,
440   R., Vieira, I.C.G., Aragão, L.E.O.C., Begotti, R.A., Braga, R.F., Cardoso, T.M., Jr, R.C.
441   de O., Souza Jr, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira,
442   J.M., Vaz-de-Mello, F.Z., Veiga, R.C.S., Venturieri, A., Gardner, T.A., 2016.
443   Anthropogenic disturbance in tropical forests can double biodiversity loss from
444   deforestation. Nature 535, 144–147. doi:10.1038/nature18326

445 Barlow, J., Louzada, J., Parry, L., Hernández, M.I.M., Hawes, J., Peres, C.A., Vaz-de-Mello,
446   F.Z., Gardner, T.A., 2010. Improving the design and management of forest strips in
447   human-dominated tropical landscapes: A field test on Amazonian dung beetles. J. Appl.
448   Ecol. 47, 779–788. doi:10.1111/j.1365-2664.2010.01825.x

449 Berenguer, E., Ferreira, J., Gardner, T.A., Aragão, L.E.O.C., De Camargo, P.B., Cerri, C.E.,
450   Durigan, M., Oliveira, R.C. De, Vieira, I.C.G., Barlow, J., 2014. A large-scale field
451   assessment of carbon stocks in human-modified tropical forests. Glob. Chang. Biol.
452   2005, 1–14. doi:10.1111/gcb.12627

453 Bicknell, J.E., Phelps, S.P., Davies, R.G., Mann, D.J., Struebig, M.J., Davies, Z.G., 2014.
454   Dung beetles as indicators for rapid impact assessments: Evaluating best practice forestry
455   in the neotropics. Ecol. Indic. 43, 154–161. doi:10.1016/j.ecolind.2014.02.030

456 Bicknell, J.E., Struebig, M.J., Davies, Z.G., 2015. Reconciling timber extraction with
457   biodiversity conservation in tropical forests using reduced-impact logging. J. Appl. Ecol.
458   52, 379–388. doi:10.1111/1365-2664.12391

459 Blaser, J., Sarre, A., Poore, D., Johnson, S., 2011. Status of Tropical Forest Maganement 2011,
460   International Tropical Timber Organization. International Tropical Timber Organization,
461   Yokohama, Japan.

462 Block, W.M., Franklin, A.B., Ward-Jr., J.P., Ganey, J.L., White, G.C., 2001. Design and
463   implementation of monitoring studies to evaluate the success of ecological restoration on
464   wildlife. Restor. Ecol. 9, 293–303. doi:10.1046/j.1526-100X.2001.009003293.x

465 Braga, R.F., Korasaki, V., Andresen, E., Louzada, J., 2013. Dung Beetle Community and
466   Functions along a Habitat-Disturbance Gradient in the Amazon: A Rapid Assessment of
467   Ecological Functions Associated to Biodiversity. PLoS One 8, e57786.
468   doi:10.1371/journal.pone.0057786

469   Braga, R.F., Korasaki, V., Audino, L.D., Louzada, J., 2012. Are Dung Beetles Driving Dung-
470   Fly Abundance in Traditional Agricultural Areas in the Amazon? Ecosystems 15, 1173–
471   1181. doi:10.1007/s10021-012-9576-5

472   Chevan, A., Sutherland, M., 1991. Hierarchical Partitioning. Am. Stat. 25, 90–96.

473   Crawley, M.J., 2002. Statistical Computing: An Introduction to Data Analysis using S-Plus.
474   John Wiley & Sons, Ltd, London.

475   Dangles, O., Carpio, C., Woodward, G., 2012. Size-dependent species removal impairs
476   ecosystem functioning in a large-scale tropical field experiment. Ecology 93, 2615–2625.
477   doi:10.1890/12-0510.1

478   Davis, A.J., Holloway, J.D., Huijbregts, H., Krikken, J., Ashley, H., Sutton, S.L., Huijbregtst,
479   H., Davis, J., Hollowayt, J.D., 2001. Dung beetles as indicators of change in the Forests
480   of Northern Borneo. J. Anim. Ecol. 38, 593–616.

481   Dykstra, D., Heinrich, R., 1996. FAO Model Code of Forest Harvesting Practice. Food and
482   Agriculture Organization of the United Nations, Rome.

483   Edwards, D.P., Magrach, A., Woodcock, P., Ji, Y., Lim, N.T.-L., Edwards, F.A., Larsen, T.H.,
484   Hsu, W.W., Benedick, S., Khen, C.V., Chung, A.Y.C., Reynolds, G., Fisher, B.,
485   Laurance, W.F., Wilcove, D.S., Hamer, K.C., Yu, D.W., 2014. Selective-logging and oil
486   palm: multitaxon impacts, biodiversity indicators, and trade-offs for conservation
487   planning. Ecol. Appl. 24, 2029–2049. doi:10.1890/14-0010.1

488   Edwards, D.P., Tobias, J.A., Sheil, D., Meijaard, E., Laurance, W.F., 2014. Maintaining
489   ecosystem function and services in logged tropical forests. Trends Ecol. Evol. 29, 511–
490   520. doi:10.1016/j.tree.2014.07.003

491   Edwards, D.P., Woodcock, P., Edwards, F.A., Larsen, T.H., Hsu, W.W., Benedick, S.,
492   Wilcove, D.S., 2012. Reduced-impact logging and biodiversity conservation: a case
493   study from Borneo. Ecol. Appl. 22, 561–571. doi:10.1890/11-1362.1

494   Edwards, F.A., Edwards, D.P., Larsen, T.H., Hsu, W.W., Benedick, S., Chung, A., Vun Khen,
495   C., Wilcove, D.S., Hamer, K.C., 2014. Does logging and forest conversion to oil palm
496   agriculture alter functional diversity in a biodiversity hotspot? Anim. Conserv. 17, 163–
497   173. doi:10.1111/acv.12074

498   Estrada, A., Coates-Estrada, R., 2002. Dung beetles in continuous forest, forest fragments and
499   in an agricultural mosaic habitat island at Los Tuxtlas, Mexico. Biodivers. Conserv. 11,
500   1903–1918.

501   Ewers, R.M., Boyle, M.J.W., Gleave, R.A., Plowman, N.S., Benedick, S., Bernard, H., Bishop,
502   T.R., Bakhtiar, E.Y., Chey, V.K., Chung, A.Y.C., Davies, R.G., Edwards, D.P.,

503   Eggleton, P., Fayle, T.M., Hardwick, S.R., Homathevi, R., Kitching, R.L., Khoo, M.S.,

504   Luke, S.H., March, J.J., Nilus, R., Pfeifer, M., Rao, S. V, Sharp, A.C., Snaddon, J.L.,

505   Stork, N.E., Struebig, M.J., Wearn, O.R., Yusah, K.M., Turner, E.C., 2015. Logging cuts

506   the functional importance of invertebrates in tropical rainforest. Nat. Commun. 6, 6836.

507   doi:10.1038/ncomms7836

508 Forest Stwardship Council, 2014. FSC [WWW Document]. URL https://us.fsc.org/ (accessed

509   4.29.14).

510 França, F., Barlow, J., Araújo, B., Louzada, J., 2016c. Does selective logging stress tropical

511   forest invertebrates? Using fat stores to examine sublethal responses in dung beetles.

512   Ecol. Evol. 6, 8526–8533. doi:10.1002/ece3.2488

513 França, F., Louzada, J., Korasaki, V., Griffiths, H., Silveira, J., Barlow, J., 2016b. Data from:

514   Do space-for-time assessments underestimate the impacts of logging on tropical

515   biodiversity? An Amazonian case study using dung beetles. Dryad Digit. Repos.

516   doi:10.5061/dryad.1536g

517 França, F., Louzada, J., Korasaki, V., Griffiths, H., Silveira, J.M., Barlow, J., 2016a. Do space-

518   for-time assessments underestimate the impacts of logging on tropical biodiversity? An

519   Amazonian case study using dung beetles. J. Appl. Ecol. doi:10.1111/1365-2664.12657

520 Frazer, G., Canham, C., Lertzman, K., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging

521   software to extract canopy structure and gap light transmission indices from true-colour

522   fisheye photographs, users manual and program documentation. Program 36.

523   doi:citeulike-article-id:4887176

524 Gardner, T.A., Barlow, J., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito,

525   M.C., Ferreira, L. V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-

526   Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R.,

527   Overal, W.L., Parry, L., Peters, S.L., Ribeiro, M.A., Da Silva, M.N.F., Da Silva Motta,

528   C., Peres, C.A., 2008a. The cost-effectiveness of biodiversity surveys in tropical forests.

529   Ecol. Lett. 11, 139–150. doi:10.1111/j.1461-0248.2007.01133.x

530 Gardner, T.A., Hernández, M.I.M., Barlow, J., Peres, C.A., 2008b. Understanding the

531   biodiversity consequences of habitat change: The value of secondary and plantation

532   forests for neotropical dung beetles. J. Appl. Ecol. 45, 883–893. doi:10.1111/j.1365-

533   2664.2008.01454.x

534 Gatti, R.C., Castaldi, S., Lindsell, J.A., Coomes, D.A., Marchetti, M., Maesano, M., Di Paola,

535   A., Paparella, F., Valentini, R., 2015. The impact of selective logging and clearcutting on

536   forest structure, tree diversity and above-ground biomass of African tropical forests.

537   Ecol. Res. 30, 119–132. doi:10.1007/s11284-014-1217-3

538 Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A.,

539   Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are

540   irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381.

541   doi:10.1038/nature10425

542 Gregory, N., Gómez, A., Oliveira, T.M.F. de S., Nichols, E., 2015. Big dung beetles dig

543   deeper: trait-based consequences for faecal parasite transmission. Int. J. Parasitol. 45,

544   101–105. doi:10.1016/j.ijpara.2014.10.006

545 Gries, R., Louzada, J., Almeida, S., Macedo, R., Barlow, J., 2012. Evaluating the impacts and

546   conservation value of exotic and native tree afforestation in Cerrado grasslands using

547   dung beetles. Insect Conserv. Divers. 5, 175–185. doi:10.1111/j.1752-4598.2011.00145.x

548 Griffiths, H.M., Louzada, J., Bardgett, R.D., Barlow, J., 2016. Assessing the Importance of

549   Intraspecific Variability in Dung Beetle Functional Traits. PLoS One 11, e0145598.

550   doi:10.1371/journal.pone.0145598

551 Griffiths, H.M., Louzada, J., Bardgett, R.D., Beiroz, W., França, F., Tregidgo, D., Barlow, J.,

552   2015. Biodiversity and environmental context predict dung beetle-mediated seed

553   dispersal in a tropical forest field experiment. Ecology 96, 1607–1619. doi:10.1890/14-

554   1211.1

555 Griscom, B.W., Goodman, R.C., Burivalova, Z., Putz, F.E., 2017. Carbon and Biodiversity

556   Impacts of Intensive Versus Extensive Tropical Forestry. Conserv. Lett. 1–16.

557   doi:10.1111/conl.12362

558 Guariguata, M.R., García-Fernández, C., Sheil, D., Nasi, R., Herrero-Jáuregui, C., Cronkleton,

559   P., Ingram, V., 2010. Compatibility of timber and non-timber forest product management

560   in natural tropical forests: Perspectives, challenges, and opportunities. For. Ecol.

561   Manage. 259, 237–245. doi:10.1016/j.foreco.2009.11.013

562 Hanski, I., Cambefort, Y., 1991. Dung Beetle Ecology. Princeton University Press, New

563   Jersey.

564 Hosaka, T., Niino, M., Kon, M., Ochi, T., Yamada, T., Fletcher, C., Okuda, T., 2014. Impacts

565   of Small-scale Clearings due to Selective logging on Dung Beetle Communities.

566   Biotropica 46, 720–731.

567 Jones, M.O., Kimball, J.S., Nemani, R.R., 2014. Asynchronous Amazon forest canopy

568   phenology indicates adaptation to both water and light availability. Environ. Res. Lett. 9,

569   124021. doi:10.1088/1748-9326/9/12/124021

570   Kissinger, G., Herold, M., De Sy, V., 2012. Drivers of Deforestation and Forest Degradation:

571   A Synthesis Report for REDD+ Policymakers. Vancouver, Canada.

572   Laurance, W.F., 2007. Have we overstated the tropical biodiversity crisis? Trends Ecol. Evol.

573   22, 65–70. doi:10.1016/j.tree.2006.09.014

574   Legendre, P., Legendre, L.F.J., 1998. Numerical Ecology, 2nd ed. Elsevier Science BV,

575   Amsterdam.

576   Mac Nally, R., 2002. Multiple regression and inference in ecology and conservation biology:

577   further comments on identifying important predictor variables. Biodivers. Conserv. 11,

578   1397–1401. doi:10.1023/A:1016250716679

579   Marsh, C.J., Louzada, J., Beiroz, W., Ewers, R.M., 2013. Optimising Bait for Pitfall Trapping

580   of Amazonian Dung Beetles (Coleoptera: Scarabaeinae). PLoS One 8, e73147.

581   doi:10.1371/journal.pone.0073147

582   Marshall, T.J., Holmes, J.W., Rose, C.W., 1996. Soil Physics, Third. ed. Cambridge University

583   Press.

584   Medjibe, V.P., Poulsen, J.R., Clark, C.J., Mbani, O.A., 2014. Natural regeneration of selected

585   timber species in the Republic of Congo. Afr. J. Ecol. 52, 552–563.

586   doi:10.1111/aje.12167

587   Merry, F., Soares-Filho, B., Nepstad, D., Amacher, G., Rodrigues, H., 2009. Balancing

588   Conservation and Economic Sustainability: The Future of the Amazon Timber Industry.

589   Environ. Manage. 44, 395–407. doi:10.1007/s00267-009-9337-1

590   Moore, J.C., Berlow, E.L., Coleman, D.C., Ruiter, P.C., Dong, Q., Hastings, A., Johnson, N.C.,

591   McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K., Rosemond, A.D., Post, D.M.,

592   Sabo, J.L., Scow, K.M., Vanni, M.J., Wall, D.H., 2004. Detritus, trophic dynamics and

593   biodiversity. Ecol. Lett. 7, 584–600. doi:10.1111/j.1461-0248.2004.00606.x

594   Negrete-Yankelevich, S., Fragoso, C., Newton, A.C., Heal, O.W., 2007. Successional changes

595   in soil, litter and macroinvertebrate parameters following selective logging in a Mexican

596   Cloud Forest. Appl. Soil Ecol. 35, 340–355. doi:10.1016/j.apsoil.2006.07.006

597   Nichols, E., Gardner, T.A., 2011. Ecology and Evolution of Dung Beetles, Ecology and

598   Evolution of Dung Beetles. John Wiley & Sons, Ltd, Chichester, UK.

599   doi:10.1002/9781444342000

600   Nichols, E., Larsen, T., Spector, S., Davis, A.L., Escobar, F., Favila, M., Vulinec, K., 2007.

601   Global dung beetle response to tropical forest modification and fragmentation: A

602   quantitative literature review and meta-analysis. Biol. Conserv. 137, 1–19.

603   doi:10.1016/j.biocon.2007.01.023

604 Nichols, E., Uriarte, M., Bunker, D.E., Favila, M.E., Slade, E.M., Vulinec, K., Larsen, T.H.,
605   Vaz-de-Mello, F.Z., Louzada, J.N.C., Naeem, S., Spector, S.H., 2013a. Trait-dependent
606   response of dung beetle populations to tropical forest conversion at local and regional
607   scales. Ecology 94, 180–189. doi:10.1890/12-0251.1

608 Nichols, E., Uriarte, M., Peres, C.A., Louzada, J., Braga, R.F., Schiffler, G., Endo, W.,
609   Spector, S.H., 2013b. Human-Induced Trophic Cascades along the Fecal Detritus
610   Pathway. PLoS One 8, e75819. doi:10.1371/journal.pone.0075819

611 Niemczyk, M., Żółciak, A., Piotr, W., 2015. The influence of stand canopy openness on the
612   growth of common yew (Taxus baccata L.). For. Res. Pap. 76, 42–48. doi:10.1515/frp-
613   2015-0004

614 Nyeko, P., 2009. Dung Beetle Assemblages and Seasonality in Primary Forest and Forest
615   Fragments on Agricultural Landscapes in Budongo, Uganda. Biotropica 41, 476–484.
616   doi:10.1111/j.1744-7429.2009.00499.x

617 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson,
618   G., Solymos, P., Stevens, M.H.H., Wagner, H., 2015. vegan: Community Ecology
619   Package. R Packag. version 2.3-0.

620 Oliveira, V.H.F., Barlow, J., Gardner, T., Louzada, J., 2017. Are we selecting appropriate
621   metrics to assess human impacts on biodiversity? Basic Appl. Ecol.
622   doi:10.1016/j.baae.2017.03.002

623 Oliver, I., Mac Nally, R., York, A., 2000. Identifying performance indicators of the effects of
624   forest management on ground-active arthropod biodiversity using hierarchical
625   partitioning and partial canonical correspondence analysis. For. Ecol. Manage. 139, 21–
626   40. doi:10.1016/S0378-1127(99)00343-6

627 Osazuwa-Peters, O.L., Chapman, C.A., Zanne, A.E., 2015. Selective logging : does the imprint
628   remain on tree structure and composition after 45 years? Conserv. Physiol. 3, cov012.
629   doi:10.1093/conphys/cov012.Introduction

630 Parry, L., Barlow, J., Peres, C.A., 2009. Allocation of hunting effort by Amazonian
631   smallholders: Implications for conserving wildlife in mixed-use landscapes. Biol.
632   Conserv. 142, 1777–1786. doi:10.1016/j.biocon.2009.03.018

633 Patrick Royston, 1995. Remark AS R94: A remark on Algorithm AS 181: The W test for
634   normality. Appl. Stat. 44, 547–551.

635 Pearson, T.R.H., Brown, S., Murray, L., Sidman, G., 2017. Greenhouse gas emissions from
636   tropical forest degradation: an underestimated source. Carbon Balance Manag. 12, 3.
637   doi:10.1186/s13021-017-0072-2

638 R Core Team, 2017. R: A language and environment for statistical computing. R Found. Stat.

639   Comput. Vienna, Austria.

640 Richardson, V.A., Peres, C.A., 2016. Temporal Decay in Timber Species Composition and

641   Value in Amazonian Logging Concessions. PLoS One 11, e0159035.

642   doi:10.1371/journal.pone.0159035

643 Silva, P.G. Da, Hernández, M.I.M., 2015. Spatial Patterns of Movement of Dung Beetle

644   Species in a Tropical Forest Suggest a New Trap Spacing for Dung Beetle Biodiversity

645   Studies. PLoS One 10, e0126112. doi:10.1371/journal.pone.0126112

646 Silveira, J.M., Barlow, J., Louzada, J., Moutinho, P., 2010. Factors Affecting the Abundance of

647   Leaf-Litter Arthropods in Unburned and Thrice-Burned Seasonally-Dry Amazonian

648   Forests. PLoS One 5, e12877. doi:10.1371/journal.pone.0012877

649 Slade, E.M., Mann, D.J., Lewis, O.T., 2011. Biodiversity and ecosystem function of tropical

650   forest dung beetles under contrasting logging regimes. Biol. Conserv. 144, 166–174.

651   doi:10.1016/j.biocon.2010.08.011

652 Slade, E.M., Roslin, T., Santalahti, M., Bell, T., 2016. Disentangling the "brown world" faecal-

653   detritus interaction web: dung beetle effects on soil microbial properties. Oikos 125,

654   629–635. doi:10.1111/oik.02640

655 Souza, V.R.D., 2009. Avaliação do manejo florestal das Plantações da Jari Celulose S. A. na

656   região de Almerim, Estado do Pará - Brasil.

657 Uriarte, M., Turner, B.L., Thompson, J., Zimmerman, J.K., 2015. Linking Spatial Patterns of

658   Leaf Litterfall and Soil Nutrients in a Tropical Forest: a Neighborhood Approach. Ecol.

659   Appl. 25, 150313143409001. doi:10.1890/15-0112.1

660 Walsh, C., Nally, R.M., 2013. Package "hier.part."

661 Wu, X., Duffy, J.E., Reich, P.B., Sun, S., 2011. A brown-world cascade in the dung

662   decomposer food web of an alpine meadow: effects of predator interactions and

663   warming. Ecol. Monogr. 81, 313–328. doi:10.1890/10-0808.1

664 Yamada, T., Yoshioka, A., Hashim, M., Liang, N., Okuda, T., 2014. Spatial and temporal

665   variations in the light environment in a primary and selectively logged forest long after

666   logging in Peninsular Malaysia. Trees-Structure Funct. 28, 1355–1365.

667   doi:10.1007/s00468-014-1040-z

668 Young, O.P., 2015. Predation on dung beetles (Coleoptera : Scarabaeidae): A literature review.

669   Trans. Am. Entomol. Soc. 141, 111–155.

670   Zhang, Y., Chen, J.M., Miller, J.R., 2005. Determining digital hemispherical photograph

671   exposure for leaf area index estimation. Agric. For. Meteorol. 133, 166–181.

672   doi:http://dx.doi.org/10.1016/j.agrformet.2005.09.009

673   Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models

674   and extensions in ecology with R, Statistics for Biology and Health. Springer New York,

675   New York, NY. doi:10.1007/978-0-387-87458-6