

1 **Logging and soil nutrients independently explain plant trait expression in tropical forests**

2 Sabine Both<sup>1,2\*</sup>, Terhi Riutta<sup>3,4</sup>, C. E. Timothy Paine<sup>2</sup>, Dafydd M. O. Elias<sup>5,6</sup>, Rudi Chino<sup>7</sup>, Annuar Jain<sup>8</sup>,  
3 David Johnson<sup>9</sup>, Ullly H. Kritzler<sup>9</sup>, Marianne Kuntz<sup>1</sup>, Noreen Majalap-Lee<sup>10</sup>, Nora Mielke<sup>1</sup>, Milenka X.  
4 Montoya Pillco<sup>1</sup>, Nicholas J. Ostle<sup>5,6</sup>, Yit A. Teh<sup>1</sup>, Yadvinder Malhi<sup>2</sup>, David F. R. P. Burslem<sup>1</sup>

5

6 <sup>1</sup> Institute of Biological and Environmental Sciences, University of Aberdeen, 23 St Machar Drive,  
7 Aberdeen, AB24 3UU, United Kingdom

8 <sup>2</sup> Environmental and Rural Science, University of New England, Armidale 2351 NSW, Australia

9 <sup>3</sup> Environmental Change Institute, School of Geography and the Environment, University of Oxford,  
10 South Parks Road, Oxford, OX1 3QY, United Kingdom

11 <sup>4</sup> Imperial College London, Department of Life Sciences, Silwood Park Campus, Buckhurst Road,  
12 Ascot, SL5 7PY, United Kingdom

13 <sup>5</sup> Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster, LA1 4YQ, United Kingdom

14 <sup>6</sup> Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster,  
15 LA1 4AP, United Kingdom

16 <sup>7</sup> Instituto de Ciencias de la Naturaleza, Territorio y Energías Renovables, Pontificia Universidad  
17 Católica del Perú, Lima, Perú

18 <sup>8</sup> The South East Asia Rainforest Research Partnership (SEARRP), Danum Valley Field Centre, PO Box  
19 60282, 91112, Lahad Datu, Sabah, Malaysia

20 <sup>9</sup> School of Earth and Environmental Sciences, The University of Manchester, Oxford Road,  
21 Manchester, M13 9PT, United Kingdom

22 <sup>10</sup> Forest Research Centre, Peti Surat 1407, 90715 Sandakan, Sabah, Malaysia

23

24 \*Author for correspondence:

25 Sabine Both

26 Tel: +61 6773 4308

27 Email: [sboth@une.edu.au](mailto:sboth@une.edu.au)

28

29 ORCID:

30 S. Both: 0000-0003-4437-5106

31 T. Riutta: 0000-0002-8308-5307

32 C.E.T. Paine: 0000-0001-8705-3719

33 D. Johnson: 0000-0003-2299-2525

34 N. Ostle: 0000-0003-3263-3702

35 Y. Malhi: 0000-0002-3503-4783

36 Y. Arn Teh: 0000-0001-7976-6794

37 D. Burslem: 0000-0001-6033-0990

38

39 Twitter Sabine Both: [@BothSabine](#)

40

41

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52

53 **Summary**

- 54 • Plant functional traits regulate ecosystem functions but little is known about how co-occurring  
55 gradients of land use and edaphic conditions influence their expression. We test how gradients  
56 of logging disturbance and soil properties relate to community-weighted mean traits in logged  
57 and old-growth tropical forests in Borneo.
- 58 • We studied 32 physical, chemical and physiological traits from 284 tree species in eight 1 ha  
59 plots and measured long-term soil nutrient supplies and plant-available nutrients.
- 60 • Logged plots had greater values for traits that drive carbon capture and growth, whilst old-  
61 growth forests had greater values for structural and persistence traits. Although disturbance was  
62 the primary driver of trait expression, soil nutrients explained a statistically independent axis of  
63 variation linked to leaf size and nutrient concentration. Soil characteristics influenced trait  
64 expression via nutrient availability, nutrient pools, and pH.
- 65 • Our finding, that traits have dissimilar responses to land use and soil resource availability,  
66 provides robust evidence for the need to consider the abiotic context of logging when predicting  
67 plant functional diversity across human-modified tropical forests. The detection of two  
68 independent axes was facilitated by the measurement of many more functional traits than have  
69 been examined in previous studies.

70

71 **Keywords:** anthropogenic disturbance, Borneo, functional diversity, functional traits, land use, Rao's  
72 Q, tropical rainforest, variance partitioning

73

## 74 **Introduction**

75 The differential expression of plant functional traits influences key ecosystem functions (Cornwell *et al.*, 2008; De Deyn *et al.*, 2008; Fortunel *et al.*, 2009; Finegan *et al.*, 2015). Trait expression varies  
76 across landscapes as a result of anthropogenic disturbance, soil characteristics, and other abiotic  
77 factors such as climate (Ordoñez *et al.*, 2009; Baraloto *et al.*, 2012; Fortunel *et al.*, 2014a; Dent &  
78 Burslem, 2016). Fertile soils are associated with traits conferring rapid nutrient acquisition and use,  
79 which support fast growth rates, whereas nutrient-poor soils are often associated with conservative  
80 strategies for the maintenance of long-lived tissues (Aerts & Chapin 2000; Ordoñez *et al.*, 2009; Jager  
81 *et al.*, 2015). Anthropogenic disturbances pervade ecosystems worldwide (Hansen *et al.*, 2013) and  
82 can affect trait expression in seeds, leaves and woody tissue (Gómez-González *et al.*, 2011; Baraloto  
83 *et al.*, 2012; Carreño-Rocabado *et al.*, 2012). Substantial effort has been dedicated to characterising  
84 the independent effects of human disturbance (McIntyre *et al.*, 1999; Mouillot *et al.*, 2013a; Buzzard  
85 *et al.*, 2016) and environmental gradients (Fortunel *et al.*, 2014b; Fyllas *et al.*, 2017) on plant trait  
86 expression and ecosystem function. However, in practice, communities are influenced by multiple  
87 factors simultaneously, and the effects of disturbance may vary along environmental gradients such  
88 as nutrient availability.  
89

90 Comprehensively analysing trait expression in response to multiple gradients is challenging but  
91 essential for predicting the ecosystem-level consequences of anthropogenic disturbance. The leaf  
92 economics spectrum (Wright *et al.*, 2004; Díaz *et al.*, 2016) suggests that the increase in resource  
93 availability associated with disturbance and soil fertility will select for similar leaf trait syndromes.  
94 Therefore, functional traits of plant communities should converge at the extremes of environmental  
95 gradients. Evidence from tropical tree communities suggests that foliar concentrations of N and P  
96 and specific leaf area increase in response to gradients of both disturbance (Baraloto *et al.*, 2012;  
97 Carreño-Rocabado *et al.*, 2012; Carreño-Rocabado *et al.*, 2016) and soil nutrient availability (Fyllas *et al.*,  
98 2009; Fortunel *et al.*, 2014a; Apaza *et al.*, 2015; Jager *et al.*, 2015; Turnbull *et al.*, 2016; Van der  
99 Sande *et al.*, 2016). Similarly, leaf dry matter content and branch and stem wood density decrease  
100 with both disturbance (Verburg & van Eijk-Bos, 2003; Baraloto *et al.*, 2012; Carreño-Rocabado *et al.*,  
101 2012; Carreño-Rocabado *et al.*, 2016) and soil nutrients (Ordoñez *et al.*, 2009; Fortunel *et al.*, 2014b;  
102 Jager *et al.*, 2015). All these studies, however, share two weaknesses: they did not examine the  
103 influence of multiple factors on trait expression, and they used a limited set of traits. Moreover,  
104 many did not consider traits associated with ecologically important processes, such as structural and  
105 defence compounds (important for herbivory and hence trophic interactions); photosynthetic  
106 activity (essential for biomass production); and leaf  $\delta^{15}\text{N}$  values (provides insight into sources and  
107 use of nitrogen). Our understanding about the links between trait sensitivity to anthropogenic

108 disturbance, soil properties, and ecosystem processes in tropical forests therefore remains  
109 incomplete.

110       The consequences of changes in community structure and diversity for ecosystem service  
111 provision are determined by the impacts of disturbance on community-level trait expression, which  
112 is a function of the type and intensity of disturbance. For example, in South American tropical  
113 forests, disturbance due to logging and silvicultural activity increases light availability and triggers  
114 the recruitment of species with traits that promote rapid growth rates (Baraloto *et al.*, 2012;  
115 Carreño-Rocabado *et al.*, 2012). We expect a similar response to logging in Southeast Asian tropical  
116 forest. We build upon these studies to additionally determine the influence of soil properties  
117 including nutrient availability on functional traits.

118       Tropical lowland forests in Southeast Asia are amongst the most species-rich communities  
119 worldwide, but are also the most threatened by logging and conversion to agriculture (Hansen *et al.*,  
120 2013; Edwards *et al.*, 2014; Stibig *et al.*, 2014). The high density of commercially valuable species  
121 explains the high intensity of logging in Southeast Asian forests (Osman *et al.*, 2012; Gaveau *et al.*,  
122 2014), which suffer rates of extraction that far exceed those in tropical forests elsewhere (see Asner  
123 *et al.*, 2005 for the Brazilian Amazon and Rutishauser *et al.*, 2015 for various sites in the Amazon  
124 Basin). Logging creates a spatially patchy disturbance, with gaps and skid trails characterised by high  
125 light and temperature distributed among fragments of relatively unmodified forest (Johns 1997). The  
126 selective removal of target species, logging-induced mortality and recruitment of pioneer species in  
127 disturbed areas affects tree species composition and the pools and fluxes of biomass and nutrients  
128 (Cannon *et al.*, 1998; Verburg & van Eijk-Bos 2003; Pfeifer *et al.*, 2016; Riutta *et al.*, 2018). Although  
129 the magnitude of anthropogenic disturbance is much greater in forests in Southeast Asia than in  
130 South America, they have received far less attention regarding the modification of plant functional  
131 traits. Specifically, the potential for intense logging to override the effects of environmental  
132 gradients, including soil properties, has not been investigated.

133       Here, we measured 32 leaf, wood and physiological traits of 284 tropical tree species to  
134 capture community level trait expression in response to selective logging across a gradient of soil  
135 properties in species-rich tropical rainforest in Sabah, northern Borneo. We consider traits reflecting  
136 nutrient status, light capture, photosynthesis, and allocation to structure and defence, to provide a  
137 whole-plant perspective and assess many aspects of functional diversity. We tested the hypothesis  
138 that functional trait values and functional diversity shift in response to anthropogenic disturbance  
139 and soil properties. We used community-weighted mean (CWM) values of traits to quantify average  
140 trait values, and a multi-trait index of functional diversity (FD) to quantify trait variation, which can  
141 occur independent of variation in CWM trait values (Ricotta & Moretti, 2011).

142 Specifically, we predict that (1) increasing disturbance and soil nutrient availability will  
143 increase CWM traits related to tissue nutrient concentrations and carbon assimilation rates, but  
144 reduce tissue densities and investments in structural defences. Given the high logging intensity in  
145 Southeast Asia, we further predict that (2) a greater proportion of the variance in CWM traits will be  
146 explained by logging than by soil properties, emphasizing the pervasive impact of anthropogenic  
147 land use on functional trait expression. Finally, due to the high overall tree species richness, we  
148 predict that (3) functional diversity will remain high in response to disturbance, despite shifts in  
149 overall CWM traits.

150

## 151 **Material and Methods**

### 152 *Study sites*

153 Sampling was conducted in eight 1 ha plots in Sabah, Malaysian Borneo. The plots are part of the  
154 Global Ecosystems Monitoring (GEM) network of permanent sample plots with intensive, regular  
155 carbon cycle measurements (Malhi *et al.*, 2015; Riutta *et al.*, 2018) and were selected to capture  
156 variation in logging intensity across a range of lowland tropical forests in northern Borneo. Old-  
157 growth lowland mixed dipterocarp forest plots (hereafter OG) were located in the Maliau Basin  
158 Conservation Area (two plots) and the Danum Valley Conservation Area (two plots), while the other  
159 four plots were distributed between these two areas in the selectively logged Kalabakan Forest  
160 Reserve (hereafter SL). The four logged plots are part of the Stability of Altered Forest Ecosystem  
161 (SAFE) project (Ewers *et al.*, 2011). This area has been logged two times with the first round of  
162 logging in the mid-1970s and subsequent repeated logging during 1990-2008. Approximately 150–  
163 179 m<sup>3</sup> ha<sup>-1</sup> of timber was removed over this time period (Struebig *et al.*, 2013), bracketing the mean  
164 extraction volume across Sabah (152 m<sup>3</sup> ha<sup>-1</sup>, Fisher *et al.*, 2011).

165 All three areas are part of the Yayasan Sabah Forest Management Area, separated by  
166 approximately 80 km, and belong to a formerly connected area of lowland dipterocarp rainforest  
167 characterised by high species richness and many tall, emergent trees. The region has a moist tropical  
168 climate with an annual daily mean temperature of 26.7 °C and annual precipitation of approximately  
169 2600-2700 mm (Walsh & Newbery, 1999). Although the climate is aseasonal there are occasional  
170 droughts and dry spells associated with supra-annual El Niño Southern Oscillation events (Walsh &  
171 Newbery 1999; Newbery & Lingensfelder, 2009). The forest soils in Sabah are mostly orthic Acrisols or  
172 Ultisols (for more details see Marsh & Greer, 1992; Nainar *et al.*, 2015).

173

### 174 *Sampling design*

175 Thirty-two functional traits were measured on 651 individual trees  $\geq 10$  cm diameter at breast height  
176 (dbh) representing 284 species during an intensive sampling campaign from July to December 2015.  
177 We combined two strategies to sample the functional trait values in each plot. In the first, weighted  
178 basal area strategy, we sampled species that most contributed to the total plot basal area. This  
179 approach assumes that species accounting for a larger proportion of plot basal area also make a  
180 greater contribution to ecosystem functioning. Species were ranked based on their contribution to  
181 total basal area at the most recent census for each plot (2011 to 2015), which ranged from 10.9–  
182 41.8  $\text{m}^2 \text{ha}^{-1}$ . All species that contributed to 70% of plot basal area (in decreasing order of species  
183 basal area) were identified for sampling. In 57% of cases only one individual per species occurred;  
184 otherwise, the individual with the greatest dbh within a species was sampled. This strategy  
185 disproportionately sampled large-statured and abundant species. To ensure that smaller and  
186 potentially rare species were also represented, we adopted a second strategy: stratified random and  
187 taxon-independent sampling of all trees  $\geq 10$  cm dbh in three randomly selected  $20 \times 20$  m subplots  
188 within each 1 ha plot. As this strategy allowed for repeated samples of the same species, as well as  
189 sampling from all height strata, it contained understory and shaded trees. This combination of  
190 different sampling strategies provided a comprehensive representation of the tree community  
191 (Paine *et al.*, 2015) and resulted in an overall representation of  $> 90\%$  of the total basal area per plot  
192 (except one plot with 65%) and 51–71% of the species  $\geq 10$  cm dbh (Fig. S1).

193

#### 194 *Soil properties*

195 We measured total nutrients and exchangeable nutrient pools to estimate both long-term nutrient  
196 supply as well as plant-available forms. Two randomly located soil cores were taken per plot in 2014–  
197 2015. Surface soil (0–10 cm) was analysed for pH, cation exchange capacity and total concentrations  
198 of P, C, N, Mg, K and Ca using the protocols of Quesada *et al.*, (2010, 2012). To assess availability of  
199 K, Ca, Mg, P,  $\text{NO}_3^-$  and  $\text{NH}_4^+$  we measured nutrient supply rates using in-situ ion exchange  
200 membranes (PRSTM Probes, Western AG, Saskatoon, Canada). To account for spatial variability we  
201 installed four probe pairs (each composed of one cation and anion probe) vertically at corners of  
202 three  $50 \times 50$  cm quadrats to 10 cm depth within each of the three subplots used in the stratified  
203 random sampling. These were collected after two weeks, washed with distilled water and sent to the  
204 manufacturer for analysis. They pooled the four probe pairs from each quadrat prior to elution with  
205 0.5M HCl for 1 hr, yielding 72 samples.  $\text{NO}_3^-$  and  $\text{NH}_4^+$  were measured colorimetrically using  
206 automated flow injection analysis (FIA). All other elements were analysed using Inductively Coupled  
207 Plasma Mass Spectrometry (ICP-MS). Results are reported as supply rates over the burial period  
208 (micrograms/ $10 \text{ cm}^2/14$  days).

209

210 *Trait measurements*

211 From each target tree, we attempted to sample a fully sunlit canopy branch and a fully shaded  
212 branch; however, branches of only one type were available for most trees (91%) because it was  
213 uncommon for large canopy trees to possess fully shaded branches and for small understorey trees  
214 to have fully sunlit branches. Branch samples were collected by tree climbing or by cutting from the  
215 ground with telescopic branch cutters. Target tree height ranged from 2.3 to 78.1 m, and sample  
216 height ranged from 2.3 m to 53 m. Branches were approximately 2-4 cm in diameter and provided  
217 sufficient leaf material for all analyses. Photosynthetic activity was only measured on trees selected  
218 by the basal area sampling strategy due to time constraints (N = 298), whereas all other functional  
219 traits were determined on all trees. Undamaged mature leaves were collected and cleaned with  
220 water for subsequent analyses. Fresh and dry leaf weight, (specific) leaf area, leaf thickness, leaf dry  
221 matter content (LDMC), (specific) force to punch and branch wood density were determined in a  
222 field laboratory. Dried bulked and milled leaf material was used for determination of Ca, K, Mg, P, C  
223 and N concentrations,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotope composition, cellulose, hemicellulose and lignin  
224 concentrations. Analyses of pigments (chlorophyll a, chlorophyll b, and carotenoids), phenols and  
225 tannins were conducted on 0.7 cm diameter leaf discs punched from fresh leaves immediately after  
226 field collection and frozen in liquid nitrogen. Herbarium voucher specimens were taken for  
227 identification of trees and were deposited in the herbarium at Danum Valley Field Centre. All trait  
228 measurements follow standardised protocols (Pérez-Harguindeguy *et al.*, 2013), and detailed  
229 methods and an overview of sampling and replication are provided in Table S1.

230

231 *Statistical analyses*

232 To generate a tree-level dataset, replicated leaf-level functional traits were averaged over sun and  
233 shade leaves for the few individuals that possessed both. Our results were not significantly different  
234 for analyses on sun leaves alone, where available, or otherwise shade leaves, so we combined data  
235 from sun and shade leaves together. Leaf chemical properties that are most relevant for  
236 photosynthetic activity (chlorophyll a, chlorophyll b, bulk carotenoids, N, and P) were expressed as  
237 mass-based as well as area-based values. For 43% of species, multiple individuals were measured  
238 and trait values were averaged to generate species-level values. For all analyses, if necessary,  
239 species-level leaf traits were log-transformed to improve the normality of residuals. A CWM was  
240 calculated for each trait, weighted by the number of individuals of each species in each plot (Pla *et al.*,  
241 2012). Values of dark respiration fluxes and  $\delta^{13}\text{C}$  were converted to positive values for ease of  
242 interpretation. To characterise soil properties in relation to land use, we performed a principal

243 component analysis (PCA) of soil chemical properties across the eight plots with the measurements  
244 of total concentrations of P, C, N, Mg, K, Ca, exchangeable Mg, K, Ca,  $\text{NH}_4^+$  and  $\text{NO}_3^-$ , extractable P,  
245 pH and cation exchange capacity (CEC). To visualise the distribution of CWM traits across forest  
246 types and test hypothesis 1, we conducted a PCA using centred and standardised CWM trait values  
247 for each study plot.

248 In order to test hypothesis 2, site scores from the first two PCA axes of soil properties, along with a  
249 binary variable representing logging history, were used as predictors in linear models to partition the  
250 variance in each CWM trait. The first two principal components from the soil PCA were both  
251 statistically independent of logging history (linear model:  $p \geq 0.48$ ). Nevertheless, because the three  
252 predictors were weakly but non-significantly inter-correlated ( $R^2 \leq 0.29$ ), we used the hierarchical  
253 partitioning method of Chevan and Sutherland (1991), as implemented in the hier.part library of R,  
254 to estimate the variance in functional traits explained by each. This technique calculates the  $R^2$  of  
255 every possible model, then averages over this set of models to allocate the variance explained by  
256 each predictor variable. It thereby overcomes the effect of the order that inter-correlated variables  
257 enter a model on the inference of variance explained by each variable (Chevan & Sutherland, 1991).  
258 Tests of significance are less informative than partitioning the variance in CWM trait values in this  
259 analysis. Nevertheless, given that this analysis generated 99 p-values (3 tests on each of 32  
260 functional traits, plus functional diversity), we corrected the p-values using the false discovery rate  
261 (García 2004).

262 To address hypothesis 3, we computed plot-level values of functional diversity (FD) as Rao's  
263 quadratic entropy (Rao's Q), which is the sum of the pairwise distances between species in  
264 multidimensional trait space weighted by their relative abundance (Rao 1982). It is the functional  
265 equivalent of Simpson's diversity index. We compared Rao's Q among forest types with ANOVA.

266 All analyses were performed using R 3.4.0 (R Core Team 2017).

267

## 268 **Results**

### 269 *Forest structure, species composition and soil properties of plots*

270 The study plots varied substantially in basal area (BA) and stem density, with BA varying fourfold  
271 ( $10.9 \text{ m} - 41.8 \text{ m}^2 \text{ ha}^{-1}$ , Table 1). Basal area was significantly less in the SL plots but the range among  
272 plots within each forest type was similar (means: SL  $17.8 \pm 12.7$ , OG  $34.8 \pm 14.9 \text{ m}^2 \text{ ha}^{-1}$ ; ANOVA:  $F_{1,6}$   
273  $= 15.26$ ,  $p = 0.008$ ). Stem density ranged from 331 to 565  $\text{ha}^{-1}$ , peaking in plots with intermediate BA  
274 but was not associated with logging ( $F_{1,6} = 0.02$ ,  $p = 0.90$ ). Species richness was similar in OG and SL  
275 plots, ranging from 124 to 211 tree species  $\text{ha}^{-1}$  ( $F_{1,6} = 0.55$ ,  $p = 0.49$ ).

276 A PCA of soil chemical properties explained 69.5% on the first two principal axes (Fig. 1). The  
277 strongest gradient was defined by variation in total Mg, total P and CEC, whereas the second axis  
278 represented a gradient of total C, total N and exchangeable Ca to exchangeable K and  $\text{NH}_4^+$ . Nutrient  
279 concentrations varied markedly among plots, including 10-fold and 5-fold variation in total Mg and  
280 total P concentrations, and 9-fold and 10-fold variation in exchangeable K and  $\text{NH}_4^+$  (Table 1). Soil  
281 properties differed among plots, but were independent of logging history, indicated by the  
282 overlapping distribution of OG and SL plots in the PCA (Fig. 1).

283

#### 284 *Community-weighted mean traits*

285 Major gradients in CWM trait expression were visualised by PCA, with the first two axes  
286 explaining 77.7% of the variance in functional traits (Fig. 2). There was a clear differentiation of  
287 functional composition between OG and SL plots along the first principal component, indicated by a  
288 distinct clustering of the study plots. Tree communities in OG plots were characterised by greater  
289 investment in defence and tissue density, whereas SL tree communities expressed higher  
290 photosynthetic activity and reduced investment into structural components (Table 2). Old-growth  
291 forests were characterized by denser wood and tougher leaves. These traits reflect enhanced  
292 structural investment, implying longer leaf life span and slower growth rates. Tree communities in SL  
293 forest had higher photosynthetic activity represented by higher CWM values of  $A_{\text{max}}$ ,  $A_{\text{sat}}$ , and  $R_d$ .  
294 These higher rates of gas exchange were supported by the expression of higher CWM area-based  
295 pigment concentrations in SL communities and higher  $N_a$ ,  $N_m$  and  $P_a$  concentrations. Tree  
296 communities in SL were enriched in  $^{13}\text{C}$  compared to OG communities, indicating greater water-use  
297 efficiency.

298 The second axis of functional trait space represented tissue nutrient concentrations and leaf  
299 area, but was independent of logging history (Fig. 2). This axis reflects covariation among CWM  
300 values of leaf area, leaf  $P_m$ ,  $N_m$ ,  $\text{Mg}_m$  and  $\text{Ca}_m$  concentrations, and a negative association of these  
301 traits with leaf  $\text{C}_m$  and tannin concentrations. Variability of these traits within both logged and  
302 unlogged forests was high, which suggests that the expression of these traits is driven by underlying  
303 soil properties rather than logging history.

#### 304 *Variance partitioning*

305 Partitioning the community level response of traits to logging and the first two principal components  
306 of soil properties showed that these factors explained up to 90% of the variation in traits. Overall,  
307 the proportion of variance explained was on average 74.4%. (Fig. 3, Table S4). To present these  
308 results, we group the functional traits based on their main association with leaf nutrients,  
309 photosynthesis or structure. Variation in mass-based concentrations of leaf  $\text{Ca}_m$ ,  $P_m$ ,  $N_m$  and  $K_m$  and  
310 to a lesser extent  $\text{Mg}_m$  were associated with variation in soil properties, both with soil PC1 and 2.

311 Particularly soil PC1, enveloping a gradient from exchangeable Mg to cation exchange capacity (CEC)  
312 and total P, strongly affected the variance in leaf  $C_m$ ,  $P_m$ ,  $C_m$ . However, expressed on area basis,  
313 foliar  $P_a$  and  $N_a$  concentrations were mainly explained by logging. Variation in SLA and leaf thickness  
314 appears to underlie the contrasting response of mass and area based traits. For leaf traits related to  
315 photosynthesis, 33.5–78.6% of variance was explained by logging and a much smaller proportion by  
316 soil PC1 (1.5–21.8%) or soil PC2 (0.9–35.6%; Table S4). Structural traits were explained by a  
317 combination of both logging history and the independent effects of soil properties. Logging  
318 explained on average 39.2% of variance in traits reflecting tissue density and structural investment,  
319 such as specific force to punch and branch wood density, which had consistently lower values in  
320 logged forest plots. Community-weighted mean LDMC was unusual in that it was poorly explained by  
321 the predictor variables. In contrast, leaf size, expressed as CWM leaf area and leaf mass, increased  
322 with increasing values of soil PC1, which was linked to plots with higher total N and exchangeable Ca  
323 concentrations (Fig. 1). There was an increase in CWM tannin concentrations in logged forest plots  
324 and at higher values of soil PC1. The CWM values of  $C_m$  and  $N_a$  were significantly explained by the  
325 first principal component of soil properties, and forest type, respectively, whereas other traits were  
326 statistically independent of the predictors (Fig. 3)

327

### 328 *Functional diversity*

329 Functional diversity, expressed as Rao's Q, was did not differ between forest types (Fig. 4;  $F_{1,6} = 0.16$ ,  
330  $p = 0.70$ ), and neither logging nor soil properties explained a significant proportion of its variance  
331 (Fig. 3). The main proportion of variance was explained by soil PC2, but the interpretation of this  
332 relationship is unclear. Variability in FD was greater among SL than OG forests (Fig. 4), potentially  
333 hinting at the heterogeneous conditions resulting from logging.

334

### 335 **Discussion**

336 Logging profoundly affected the expression of plant functional traits in Bornean tropical forests.  
337 Logging was the primary driver of variation in community-weighted mean (CWM) values of  
338 functional traits (Fig. 2), and explained more variation than soil properties for 20 of 32 traits (Fig. 3).  
339 Similar impacts of logging on functional trait expression have been demonstrated in Neotropical  
340 forests (Baraloto *et al.*, 2012; Carreño-Rocabado *et al.*, 2012), although those studies did not analyse  
341 soil-related factors. Together, these studies confirm that CWM traits are highly sensitive to land-use  
342 change in tropical forests, but results from our study additionally highlight the considerable  
343 relevance of the environmental context for trait expression. This is an important outcome in the light  
344 of the fact that logging has impacted over half of all tropical forests globally, and over 70% of forests

345 in Sabah (Bryan *et al.*, 2013; Potapov *et al.*, 2017). Therefore, the effect of logging on the expression  
346 of functional traits is likely to pervade tropical forest landscapes and impact ecosystem processes  
347 with cascading effects on other trophic levels . Moreover, logging-associated changes in forest  
348 structure and CWM traits drive altered patterns of productivity in tropical forests (Pfeifer *et al.*,  
349 2016; Riutta *et al.*, 2018).

350 In our study, the principal axis of functional trait space defined a clear gradient from values of traits  
351 that maximise carbon capture and growth, which were predominantly expressed in selectively  
352 logged forests, to greater allocation to tissue persistence and stability, which were predominantly  
353 expressed in old-growth forests. This strong signal of anthropogenic disturbance is partly congruent  
354 with the leaf economics spectrum, which differentiates species along a gradient based on leaf traits  
355 contributing to resource acquisition and conservation (Wright *et al.*, 2004; Díaz *et al.*, 2016). Thus,  
356 species in logged forest communities expressed higher CWM values of area-based measures of N, P  
357 and pigments, whereas old-growth forest communities expressed low CWM values of these traits  
358 and higher values of traits conferring structural stability and resistance to herbivory, such as branch  
359 wood density and leaf toughness. Supporting hypothesis 1, disturbance enhanced the occurrence of  
360 species possessing traits that confer rapid carbon capture and investment in fast growth rates  
361 (Baraloto *et al.*, 2012; Carreño-Rocabado *et al.*, 2012, 2016). We amplify previous results by  
362 additionally demonstrating that logged forest communities expressed higher CWM values of  $A_{\text{sat}}$ ,  
363  $A_{\text{max}}$  and  $R_{\text{d}}$ , whereas old-growth forest communities were characterised by higher values of traits  
364 conferring structural stability of wood and leaves. The inclusion of these physiological traits related  
365 to rates of photosynthesis and respiration allows us to make inferences about ecosystem function  
366 stronger than those that can be derived from structural traits. Moreover, we examined the chemical  
367 traits of phenol and tannin concentrations, the distributions of which were incongruent with the  
368 traditional resource conserving – resource acquisition view of trait syndromes. In these ways, our  
369 study expands upon previous examinations of trait associations.

370 We observed lower CWM values of specific leaf area (SLA) in logged forests, in contrast to  
371 results from French Guiana (Baraloto *et al.*, 2012), and contrary to the expectation that SLA scales  
372 positively with  $A_{\text{max}}$ , foliar  $N_{\text{a}}$ , and foliar  $P_{\text{a}}$  concentrations among species (Wright *et al.*, 2004). The  
373 lack of association between SLA and other leaf-economic traits is surprising and deserves further  
374 study. Microclimatic changes resulting from logging (Hardwick *et al.*, 2015) may filter for species to  
375 be adapted to resist the more exposed and potentially desiccating conditions created by logging  
376 gaps and decreased canopy height. A reduction in SLA may contribute to photosynthetic water-use  
377 efficiency, especially when combined with enhanced investment in photosynthetic enzymes, to  
378 ensure draw-down of internal  $\text{CO}_2$  concentrations at a given stomatal conductance (Reich *et al.*,

379 2003). The greater enrichment of CWM  $\delta^{13}\text{C}$  of logged forest tree communities demonstrates lower  
380 discrimination for the heavier  $^{13}\text{C}$  isotope and provides independent evidence of enhanced  
381 integrated water-use efficiency for trees in this hotter and drier environment (Farquhar *et al.*, 1989;  
382 Rumman *et al.*, 2018). The absence of a shift in SLA in response to logging in French Guianan forests  
383 (Baraloto *et al.*, 2012) suggests that logging imposes a more extreme environmental contrast for  
384 trees occurring in the less seasonal climate of Borneo. Species that have evolved in a seasonal  
385 climate such as in French Guiana, may be better adapted to changes in microclimatic conditions, like  
386 those driven by logging (B. Blonder *et al.*, unpublished data). The impact of logging may be more  
387 severe in tree communities not adapted to drought and emphasises the potential sensitivity of  
388 Bornean forests to future climatic change. Mean temperature for Borneo is predicted to rise by 0.9  
389 – 3.2 °C, annual precipitation is predicted to become increasingly less, hence drier, in central to  
390 western Borneo and more, i.e. wetter, in northern and north-western Borneo (ICCP 2013; Scriven *et al.*,  
391 2015).

392 We show that trait expression responded independently to logging disturbance and soil  
393 properties. Variation in soil properties can be attributed to interactions between underlying soil  
394 texture and mineralogy, on one hand, and the impacts of logging disturbances including soil  
395 inversion, removal, and compaction on the other (Pinard *et al.*, 2000). However, soil properties did  
396 not differ systematically between old-growth and selectively logged forests (Fig. 1), owing to  
397 variation in underlying soil types and the heterogeneous nature of logging. This allowed us to assess  
398 their independent effects on the expression of CWM functional traits. For most of the mass-based  
399 nutrient concentrations, variation in soil properties explained more variation in CWM trait values  
400 than did logging, whereas traits linked to photosynthesis and carbon capture were more sensitive to  
401 logging than to variation in soil properties (Fig. 3). The mechanisms underlying these associations  
402 deserve further study. An obvious field of research should be the study of post-logging alterations in  
403 the fungal community, in particular the occurrence and diversity of ectomycorrhizal fungi (McGuire  
404 *et al.*, 2015). In SE Asia, they are almost exclusively associated with tree species of the family  
405 Dipterocarpaceae, which are also the main family logged for timber (but see Essene *et al.*, 2017). The  
406 interacting effects between tree species dominance, logging and below-ground microbial diversity  
407 and ecosystem functions are largely unknown.

408 We provide clear evidence that soil properties act on trait expression in two independent  
409 ways; the first axis reflected total pools of nutrients, and the second reflected nutrient availability  
410 (Fig. 1). Community-weighted mean values of leaf area, leaf dry mass and foliar concentrations of  $P_m$ ,  
411  $P_a$ ,  $N_m$  and  $Ca_m$  all increased in response to the first axis of variation in soil properties, whereas leaf  
412  $C_m$  and tannin concentrations decreased along this gradient (Fig. 3). The second component of soil

413 variation also influenced some leaf traits, particularly  $\delta^{13}\text{C}$ ,  $\text{N}_a$  and  $\text{P}_a$  concentrations (Table 2, Table  
414 S4). Moreover, most traits were influenced either by the first or second axis of variation in soil  
415 properties, but rarely both. This finding may reflect a trade-off in how plants interact with local  
416 edaphic conditions, as suggested in other systems (Laliberte *et al.*, 2015); a key future challenge will  
417 be to disentangle the mechanisms underpinning these contrasting responses of functional traits to  
418 the soil environment. Our results highlight the need to consider the context dependency of drivers  
419 of variation in functional traits. Landscape-level predictions of change in functional trait expression  
420 in response to anthropogenic disturbance will need to account for the additional effects of soil  
421 properties. Our work therefore provides valuable data to the modelling community, and will help  
422 address recent calls to integrate empirical data into biogeochemical cycling models (Baker *et al.*,  
423 2017). Recently, it was shown that plant trait diversity permits forests in the Amazon to adapt to  
424 new climatic conditions (Sakschewski *et al.*, 2016), and a new trait-based model has explored the  
425 influence of climate and soil nutrient availability on primary production and carbon use efficiency of  
426 trees (Fyllas *et al.*, 2014). Our data offers potential to extend the scope of these models to other  
427 critical regions and explore the effects of land use change on key ecosystem functions.

428         Despite the large variation in CWM traits, functional diversity (FD) did not differ between  
429 selectively logged and old-growth forest, which is consistent with our third hypothesis and with  
430 results from Neotropical forests (Fig. 4; Baraloto *et al.*, 2012; Carreño-Rocabado *et al.*, 2012). This  
431 finding emphasises that forests can retain species richness and trait variation, yielding similar FD,  
432 despite logging. In line with Mayfield *et al.*, (2010), logging did not result in loss of FD but in shifts of  
433 numerous CWM trait values, indicating a lower sensitivity of multi-trait FD to these changes (Ricotta  
434 & Moretti, 2011). FD was more variable among logged forests than old-growth forests (Fig. 4),  
435 probably owing to variation in logging history and intensity, which affect forest structure (Cannon *et al.*,  
436 1994; Berry *et al.*, 2008), microclimatic conditions (Hardwick *et al.*, 2015) and ecosystem  
437 functions (Mayfield *et al.*, 2006; Both *et al.*, 2017; Riutta *et al.*, 2018). The substantial variance in FD  
438 among the disturbed plots highlights the challenge of predicting the impacts of anthropogenic  
439 modification on FD in environments where the outcomes may be highly context-dependent  
440 (Costantini *et al.*, 2016).

441         Assessments of functional composition and diversity at a community scale are critical as  
442 human-modified landscapes become more extensive and play an increasing role in the provision of  
443 ecosystem services (Berry *et al.*, 2010; Gibson *et al.*, 2011). However, uncertainty remains over how  
444 changes in community trait expression will affect ecosystem functioning and resilience after  
445 selective logging and other forms of disturbance (Laliberté *et al.*, 2010; Mayfield *et al.*, 2010;  
446 Edwards *et al.*, 2014). Part of that uncertainty arises because rare tree species may contribute

447 substantially to resilience (Mouillot *et al.*, 2013b), but tend to be under-represented in traditional  
448 sampling designs adopted for measuring ecosystem functions. Our nested sampling design explicitly  
449 resolved this issue by selecting both common and rare, big and small tree species across the full  
450 range of size classes. We therefore advocate this approach in future assessments of trait expression  
451 at the community scale.

452 We demonstrate a consistent shift in community-level trait expression in response to logging,  
453 reflecting a transition from an old-growth forest dominated by individuals with resource conserving,  
454 structurally persistent tissues to logged forests manifesting greater capacity for carbon assimilation  
455 and vegetative growth. Strikingly, there was a second, independent, axis of functional trait variation  
456 reflecting variation in soil properties (i.e. nutrient availability and chemistry including pH), which  
457 explained variation in leaf size and mass-based foliar nutrient concentrations. The elucidation of  
458 these orthogonal dimensions of plant trait variation was made possible by the measurement of  
459 numerous functionally relevant traits and by their consideration at the community level, as well as  
460 by the inclusion of rare species. These results provide a basis for predicting how pervasive logging  
461 disturbance combines with natural gradients to determine trait expression and ecosystem  
462 functioning across human-modified tropical landscapes.

463

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479

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485

486 **References**487 **References**

- 488 **Aerts R, Chapin III FS. 2000.** The Mineral Nutrition of Wild Plants Revisited: A Re-evaluation of  
489 Processes and Patterns. *Advances in Ecological Research* **30**: 26–27.
- 490 **Apaza-Quevedo A, Lippok D, Hensen I, Schleuning M, Both S. 2015.** Elevation, Topography, and  
491 Edge Effects Drive Functional Composition of Woody Plant Species in Tropical Montane Forests.  
492 *Biotropica* **47**: 449–458.
- 493 **Asner GP, Knapp DE, Broadbent EN, Oliveira PJC, Keller M, Silva JN. 2005.** Selective Logging in the  
494 Brazilian Amazon. *Science* **310**: 480–482.
- 495 **Baker TR, Pennington RT, Dexter KG, Fine PV, Fortune-Hopkins H, Honorio EN, Huamantupa-**  
496 **Chuquimaco I, Klitgård BB, Lewis GP, de Lima HC et al. 2017.** Maximising synergy among tropical  
497 plant systematists, ecologists, and evolutionary biologists. *Trends in Ecology and Evolution* **32(4)**:  
498 258–67.
- 499 **Baraloto C, Hérault B, Paine CET, Massot H, Blanc L, Bonal D, Molino J-F, Nicolini EA, Sabatier S.**  
500 **2012.** Contrasting taxonomic and functional responses of a tropical tree community to selective  
501 logging. *Journal of Applied Ecology* **49**: 861–870.
- 502 **Berry NJ, Phillips OL, Ong RC, Hamer KC. 2008.** Impacts of selective logging on tree diversity across a  
503 rainforest landscape: the importance of spatial scale. *Landscape Ecology* **23**: 915–929.
- 504 **Berry NJ, Phillips OL, Lewis SL, Hill JK, Edwards DP, Tawatao NB, Ahmad N, Magintan D, Khen CV,**  
505 **Maryati M et al. 2010.** The high value of logged tropical forests: Lessons from northern Borneo.  
506 *Biodiversity and Conservation*, **19**: 985–997.
- 507 **Both S, Elias DMO, Kritzler UH, Ostle NJ, Johnson D. 2017.** Land use not litter quality is a stronger  
508 driver of decomposition in hyper-diverse tropical forest. *Ecology and Evolution* **7**: 9307–9318.
- 509 **Bryan JE, Shearman PL, Asner GP, Knapp DE, Aoro G, Lokes B. 2013.** Extreme differences in forest  
510 degradation in Borneo: comparing practices in Sarawak, Sabah, and Brunei. *PloS One* **8(7)**:  
511 p.e69679
- 512 **Buzzard V, Hulshof CM, Birt T, Violle C, Enquist BJ. 2016.** Re-growing a tropical dry forest: functional  
513 plant trait composition and community assembly during succession. *Functional Ecology* **30**: 1006–  
514 1013.
- 515 **Cannon C, Kartawinata K, Leighton M, Peart DR. 1994.** The structure of lowland rainforest after  
516 selective logging in West Kalimantan, Indonesia. *Forest Ecology and Management* **67**: 49–68.
- 517 **Cannon CH, Peart DR, Leighton M. 1998.** Tree Species Diversity in Commercially Logged Bornean  
518 Rainforest. *Science* **281**: 1366–1368

- 519 **Carreño-Rocabado G, Peña-Claros M, Bongers F, Alarcón A, Licona JC, Poorter L. 2012.** Effects of  
520 disturbance intensity on species and functional diversity in a tropical forest. *Journal of Ecology*  
521 **100**: 1453–1463.
- 522 **Carreño-Rocabado G, Peña-Claros M, Bongers F, Díaz S, Quétier F, Chuvíña J, Poorter L. 2016.** Land-  
523 use intensification effects on functional properties in tropical plant communities. *Ecological*  
524 *Applications* **26**: 174–189.
- 525 **Chevan A, Sutherland M. 1991.** Hierarchical Partitioning. *The American Statistician* **45**: 90–96.
- 526 **Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE,**  
527 **Hoorens B, Kurokawa H, Perez-Harguindeguy N et al. 2008.** Plant species traits are the  
528 predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* **11**:  
529 1065–1071.
- 530 **Costantini D, Edwards DP, Simons MJP. 2016.** Life after logging in tropical forests of Borneo: A  
531 meta-analysis. *Biological Conservation* **196**: 182–188.
- 532 **Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Prentice IC**  
533 **et al. 2016.** The global spectrum of plant form and function. *Nature* **529**: 167–171.
- 534 **Dent DH, Burslem DFRP. 2016.** Leaf traits of dipterocarp species with contrasting distributions  
535 across a gradient of nutrient and light availability. *Plant Ecology and Diversity* **9**: 1–13.
- 536 **De Deyn GB, Cornelissen JHC, Bardgett RD. 2008.** Plant functional traits and soil carbon  
537 sequestration in contrasting biomes. *Ecology Letters* **11**: 516–531.
- 538 **Edwards FA, Edwards DP, Larsen TH, Hsu WW, Benedick S, Chung A, Khen CV, Wilcove DS, Hamer**  
539 **KC. 2014.** Does logging and forest conversion to oil palm agriculture alter functional diversity in a  
540 biodiversity hotspot? *Animal Conservation* **17**: 163–173.
- 541 **Essene AL, Shek KL, Lewis JD, Peay K, McGuire KL. 2017.** Soil type has a stronger role than  
542 dipterocarp host species in shaping the ectomycorrhizal fungal community in a Bornean lowland  
543 tropical rain forest. *Frontiers in Plant Science* **8**: 1828.
- 544 **Ewers RM, Didham RK, Fahrig L., Ferraz G, Hector A, Holt RD, Kapos V, Reynolds G, Sinun W. et al.**  
545 **2011.** A large-scale forest fragmentation experiment: the Stability of Altered Forest Ecosystems  
546 Project. *Philosophical Transactions of the Royal Society B* **366**: 3292–3302.
- 547 **Farquhar GD, Ehleringer JR, Hubick KT. 1989.** Carbon Isotope Discrimination and Photosynthesis.  
548 *Annual Review of Plant Physiology and Plant Molecular Biology* **40**: 503–537.
- 549 **Finegan B, Pena-Claros M, de Oliveira A, Ascarrunz N, Bret-Harte MS, Carreño-Rocabado G,**  
550 **Casanoves F, Díaz S, Eguiguren Velepucha P, Fernandez F. et al. (2015).** Does functional trait  
551 diversity predict above-ground biomass and productivity of tropical forests? Testing three  
552 alternative hypotheses. *Journal of Ecology* **103**: 191–201.

- 553 **Fisher B, Edwards DP, Giam X, Wilcove DS. 2011.** The high costs of conserving Southeast Asia's  
554 lowland rainforests. *Frontiers in Ecology and the Environment* **9**: 329–334.
- 555 **Fortunel C, Garnier E, Joffre R. 2009.** Leaf traits capture the effects of land use changes and climate  
556 on litter decomposability of grasslands across Europe. *Ecology* **90**: 598–611.
- 557 **Fortunel C, Paine CET, Fine PVA, Kraft NJB, Baraloto C. 2014a.** Environmental factors predict  
558 community functional composition in Amazonian forests. *Journal of Ecology* **102**: 145–155.
- 559 **Fortunel C, Ruelle J, Beauchêne J, Fine PVA, Baraloto C. 2014b.** Wood specific gravity and anatomy  
560 of branches and roots in 113 Amazonian rainforest tree species across environmental gradients.  
561 *New Phytologist* **202**: 79–94.
- 562 **Fyllas NM, Patiño S, Baker TR, Nardoto GB, Martinelli LA, Quesada CA, Paiva R, Schwarz M, Horna  
563 V, Mercado LM et al. 2009.** Basin-wide variations in foliar properties of Amazonian forest:  
564 phylogeny, soils and climate. *Biogeosciences* **6**: 2677–2708.
- 565 **Fyllas NM, Bentley LP, Shenkin A, Asner GP, Atkin OK, Farfan-Rios W, Gloor E, Guerrieri R, Huaraca  
566 Huasco W, Ishida Y et al. 2017.** Solar radiation and functional traits explain the decline of forest  
567 primary productivity along a tropical elevation gradient. *Ecology Letter* **20**: 730–740.
- 568 **Fyllas NM, Gloor E, Mercado LM, Sitch S, Quesada CA, Domingues TF, Galbraith DR, Torre-Lezama  
569 A, Vilanova E, Ramírez-Angulo H et al. 2014.** Analysing Amazonian forest productivity using a new  
570 individual and trait-based model (TFS v. 1). *Geoscientific Model Development* **7(4)**: 1251–1269.
- 571 **García LV. 2004.** Escaping the Bonferroni iron claw in ecological studies. *Oikos* **105**: 657–663.
- 572 **Gaveau DLA, Sloan S, Molidena E, Yaen H, Sheil D, Abram NK, Ancrenaz M, Nasi R, Quinones M,  
573 Wielaard N et al. 2014.** Four Decades of Forest Persistence, Clearance and Logging on Borneo.  
574 *PLoS One* **9**: 1–11.
- 575 **Gibson L, Lee TM, Koh LP, Brook BW, Gardner TA, Barlow J, Peres CA, Bradshaw CJA, Laurance WF,  
576 Lovejoy TE et al. 2011.** Primary forests are irreplaceable for sustaining tropical biodiversity.  
577 *Nature* **478**: 378–381.
- 578 **Gómez-González S, Torres-Díaz C, Bustos-Schindler C, Gianoli E. 2011.** Anthropogenic fire drives the  
579 evolution of seed traits. *Proceedings of the National Academy of Sciences, USA* **108**: 18743–18747.
- 580 **Hansen MCC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman  
581 SV, Goetz SJ, Loveland TR et al. 2013.** High-Resolution Global Maps of 21st-Century Forest Cover  
582 Change. *Science* **342**: 850–854.
- 583 **Hardwick SR, Toumi R, Pfeifer M, Turner EC, Nilus R, Ewers RM. 2015.** The relationship between  
584 leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance  
585 drives changes in microclimate. *Agricultural and Forest Meteorology* **201**: 187–195.

- 586 **IPCC. 2013.** Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Nauels JA, Xia Y, Bex V, Midgley PM,  
587 eds. *Climate Change 2013 – The Physical Science Basis. Contribution of Working Group I to the*  
588 *Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University  
589 Press, UK, Cambridge.
- 590 **Jager MM, Richardson SJ, Bellingham PJ, Clearwater MJ, Laughlin DC. 2015.** Soil fertility induces  
591 coordinated responses of multiple independent functional traits. *Journal of Ecology* **103**: 374–385.
- 592 **Laliberté E, Legendre P. 2010.** A distance-based framework for measuring functional diversity from  
593 multiple traits. *Ecology* **91**: 299–305.
- 594 **Laliberté E, Lambers H, Burgess TI, Wright SJ. 2015.** Phosphorus limitation, soil-borne pathogens  
595 and the coexistence of plant species in hyperdiverse forests and shrublands. *New Phytologist*  
596 **206(2)**: 507–521.
- 597 **Malhi Y, Doughty CE, Goldsmith GR, Metcalfe DB, Girardin CA, Marthews TR, del Aguila-Pasquel J,**  
598 **Aragão LE, Araujo-Murakami A, Brando P et al. (2015).** The linkages between photosynthesis,  
599 productivity, growth and biomass in lowland Amazonian forests. *Global Change Biology* **21(6)**:  
600 2283–2295.
- 601 **Marsh W, Greer AG. 1992.** Forest land-use in Sabah, Malaysia: an introduction to Danum Valley.  
602 *Philosophical Transactions of the Royal Society B* **335**: 331–339.
- 603 **Mayfield MM, Ackerly D, Daily GC. 2006.** The diversity and conservation of plant reproductive and  
604 dispersal functional traits in human-dominated tropical landscapes. *Journal of Ecology* **94**: 522–  
605 536.
- 606 **Mayfield MM, Bonser SP, Morgan JW, Aubin I, McNamara S, Vesik PA. 2010.** What does species  
607 richness tell us about functional trait diversity? Predictions and evidence for responses of species  
608 and functional trait diversity to land-use change. *Global Ecology and Biogeography* **19**: 423–431.
- 609 **McGuire KL, D’Angelo H, Brearley FQ, Gedallovich SM, Babar N, Yang N, Gillikin CM, Gradoville R,**  
610 **Bateman C, Turner BL et al. 2015.** Responses of soil fungi to logging and oil palm agriculture in  
611 Southeast Asian tropical forests. *Microbial Ecology* **69(4)**: 733–747.
- 612 **McIntyre S, Lavorel S, Landsberg J, Forbes TDA. 1999.** Disturbance response in vegetation – towards  
613 a global perspective on functional traits. *Journal of Vegetation Science* **10**: 621–630.
- 614 **Mouillot D, Graham NAJ, Villéger S, Mason NWH, Bellwood DR. 2013a.** A functional approach  
615 reveals community responses to disturbances. *Trends in Ecology and Evolution* **28**: 167–177.
- 616 **Mouillot D, Bellwood DR, Baraloto C, Chave J, Galzin R, Harmelin-Vivien M, Kulbicki M, Lavergne S,**  
617 **Lavorel S, Mouquet N et al. 2013b.** Rare Species Support Vulnerable Functions in High-Diversity  
618 Ecosystems. *PLoS Biology* **11(5)**: 1–11.

- 619 **Nainar A, Bidin K, Walsh RP, Ewers RM, Reynolds G. 2015.** Variations in suspended sediment yield  
620 and dynamics in catchments of differing land-use in Sabah. *Transactions on Science and*  
621 *Technology* **2(1)**: 1–19.
- 622 **Newbery DM, Lingenfelder M. 2009.** Plurality of tree species responses to drought perturbation in  
623 Bornean tropical rain forest. *Plant Ecology* **201**: 147–167.
- 624 **Ordoñez JC, van Bodegom PM, Witte JM, Wright IJ, Reich PB, Aerts R. 2009.** A global study of  
625 relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology*  
626 *and Biogeography* **18**: 137–149.
- 627 **Osman R, Phua M, Ling ZY, Kamlun KU. 2012.** Monitoring of Deforestation Rate and Trend in Sabah  
628 between 1990 and 2008 Using Multitemporal Landsat Data. *Journal of Forest Science* **28**: 144–151.
- 629 **Paine CET, Baraloto C, Díaz S. 2015.** Optimal strategies for sampling functional traits in species-rich  
630 forests. *Functional Ecology* **29**: 1325–1331.
- 631 **Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS,**  
632 **Cornwell WK, Craine JM, Gurvich DE et al. 2013.** New Handbook for standardized measurement  
633 of plant functional traits worldwide. *Australian Journal of Botany* **61**: 167–234.
- 634 **Pfeifer M, Kor L, Nilus R, Turner E, Cusack J, Lysenko I, Khoo M, Chey VK, Chung AC, Ewers RM.**  
635 **2016.** Mapping the structure of Borneo's tropical forests across a degradation gradient. *Remote*  
636 *Sensing of Environment* **176**: 84–97.
- 637 **Pinard MA, Barker MG, Tay J. 2000.** Soil disturbance and post-logging forest recovery on bulldozer  
638 paths in Sabah, Malaysia. *Forest Ecology and Management* **130(1-3)**: 213–225.
- 639 **Pla L, Casanoves F, Di Rienzo J. 2012.** Functional diversity indices. In Pla L, Casanoves F, Di Rienzo J,  
640 eds. Quantifying functional biodiversity. Dordrecht, The Netherlands: Springer, 27–51.
- 641 **Potapov P, Hansen MC, Laestadius L, Turubanova S, Yaroshenko A, Thies C, Smith W, Zhuravleva I,**  
642 **Komarova A, Minnemeyer S et al. 2017.** The last frontiers of wilderness: Tracking loss of intact  
643 forest landscapes from 2000 to 2013. *Science Advances* **3**: 1–13.
- 644 **Quesada CA, Lloyd J, Schwarz M, Patiño S, Baker TR, Czimczik CI, Fyllas NM, Martinelli M, Nardoto**  
645 **GB, Schmerler J et al. 2010.** Variations in chemical and physical properties of Amazon forest soils  
646 in relation to their genesis. *Biogeosciences* **7**: 1515–1541.
- 647 **Quesada CA, Phillips OL, Schwarz M, Czimczik CI, Baker TR, Patiño S, Fyllas NM, Hodnett MG,**  
648 **Herrera R, Almeida S et al. 2012.** Basin-wide variations in Amazon forest structure and function  
649 are mediated by both soils and climate. *Biogeosciences* **9**: 2203–2246.
- 650 R Core Team 3.5.1 (2017). R: A language and environment for statistical computing. R Foundation for  
651 Statistical Computing, Vienna, Austria

- 652 **Rao RC. 1982.** Diversity and Dissimilarity Coefficients: A Unified Approach. *Theoretical Population*  
653 *Biology* **21**: 24–43.
- 654 **Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB. 2003.** The  
655 evolution of plant functional variation: traits, spectra, and strategies. *International Journal of*  
656 *Plant Sciences* **164(S3)**: S143–S164.
- 657 **Ricotta C, Moretti M. 2011.** CWM and Rao’s quadratic diversity: a unified framework for functional  
658 ecology. *Oecologia* **167(1)**: 181–188.
- 659 **Riutta T, Malhi Y, Kho LK, Marthews TR, Huaraca Huasco W, Khoo M, Tan S, Turner E, Reynolds G,**  
660 **Both S et al. (2018).** Logging disturbance shifts net primary productivity and its allocation in  
661 Bornean tropical forests. *Global Change Biology* **24(7)**: 2913–2928.
- 662 **Rumman R, Atkin OK, Bloomfield KJ, Eamus D. 2018.** Variation in bulk-leaf <sup>13</sup>C discrimination, leaf  
663 traits and water-use efficiency–trait relationships along a continental-scale climate gradient in  
664 Australia. *Global Change Biology* **24**: 1186–1200.
- 665 **Rutishauser E, Hérault B, Baraloto C, Blanc L, Descroix L, Sotta ED, Ferreira J, Kanashiro M, Mazzei**  
666 **L, d’Oliveira MV. 2015.** Rapid tree carbon stock recovery in managed Amazonian forests. *Current*  
667 *Biology* **25(18)**: R787–R788.
- 668 **Sakschewski B, Von Bloh W, Boit A, Poorter L, Peña-Claros M, Heinke J, Joshi J, Thonicke K. 2016.**  
669 Resilience of Amazon forests emerges from plant trait diversity. *Nature Climate Change* **6(11)**:  
670 1032–1036.
- 671 **Scriven SA, Hodgson JA, McClean CJ, Hill JK. 2015.** Protected areas in Borneo may fail to conserve  
672 tropical forest biodiversity under climate change. *Biological Conservation* **184**: 414–423.
- 673 **Stibig HJ, Achard F, Carboni S, Rasi R, Miettinen J. 2014.** Change in tropical forest cover of Southeast  
674 Asia from 1990 to 2010. *Biogeosciences* **11**: 247–258.
- 675 **Struebig MJ, Turner A, Giles E, Lasmana F, Tollington S, Bernard H, Bell D. 2013.** Quantifying the  
676 biodiversity value of repeatedly logged rainforests: gradient and comparative approaches from  
677 Borneo. In *Advances in ecological research*. Academic Press. 48: 183–224.
- 678 **Turnbull MH, Griffin KL, Fyllas NM, Lloyd J, Meir P, Atkin OK. 2016.** Separating species and  
679 environmental determinants of leaf functional traits in temperate rainforest plants along a soil-  
680 development chronosequence. *Functional Plant Biology* **43**: 751–765.
- 681 **Van der Sande MT, Arets EJMM, Pena-Claros M, Luciana de Avila A, Roopsind A, Mazzei L,**  
682 **Ascarrunz N, Finegan B, Alarcón A, Cáceres-Siani Y et al. 2016.** Old-growth Neotropical forests  
683 are shifting in species and trait composition. *Ecological Monographs* **86**: 228–243.
- 684 **Verburg R, van Eijk C. 2003.** Effects of selective logging on tree diversity, composition and plant  
685 functional type patterns in a Bornean rain forest. *Journal of Vegetation Science* **14**: 99–110.

686 **Walsh RPD, Newbery DM. 1999.** The ecoclimatology of Danum, Sabah, in the context of the world's  
687 rainforest regions, with particular reference to dry periods and their impact. *Philosophical*  
688 *Transactions of the Royal Society B* **354**: 1869–1883.

689 **Wright IJ, Westoby M, Reich PB, Oleksyn J, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J,**  
690 **Chapin T, Cornelissen JH et al. 2004.** The worldwide leaf economics spectrum. *Nature* **428**: 821–  
691 827.

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693 Supporting information

694 Fig. S1: Realized basal area coverage of species measured across the study plots.

695 Table S1: Overview of the function of functional traits measured in this study and sample numbers.

696 Table S2: Loadings of the soil environmental variables in the Principal Component Analysis.

697 Table S3: Loadings of the community-weighted mean traits in the Principal Component Analysis.

698 Table S4: Results from linear regression models underlying the variance partitioning.

699 Methods S1: Detailed description of the trait measurements.

**700 Figure captions**

701

702 Figure 1: Principal component analysis (PCA) of plot-level soil properties. The highest loadings on the  
703 first axis are the cation exchange capacity, CEC (12.6%), total Mg (12.3%) and total P (12.2%). The  
704 highest loadings on the second axis are exchangeable K (12.0%), total N (11.1%) and exchangeable  
705 Ca (11.1%). See Table S2 for all PCA loadings.

706

707 Figure 2: Principal component analysis (PCA) of plot-level community-weighted mean functional  
708 traits. Plots cluster by logging history, with increased values of traits that maximise carbon capture  
709 and growth in logged forest communities and greater allocation to tissue persistence and structural  
710 stability in old-growth forests. The highest loadings on the first axis are chlorophyll  $b_m$  (4.44%),  $N_a$   
711 (4.37%), branch wood density (4.25%),  $A_{sat}$  (4.25%),  $A_{max}$  (4.21%) and SLA (4.17%). The highest  
712 loadings on second axis are  $P_m$  (7.45%), LA (7.02%), tannins (6.22%),  $C_m$  (5.88%) and leaf dry weight  
713 (5.75%). Mass-based nutrients are denoted by superscript “m” and area-based values by superscript  
714 “a”. See Table S3 for all PCA loadings.

715

716 Figure 3: Proportion of variance in community-weighted mean functional trait values explained by  
717 forest type and the first two principal components of soil properties (Fig. 1). Functional traits are  
718 grouped by the ecosystem function to which they most contribute. Statistical significance is derived  
719 from linear regression models following false discovery rate correction, asterisks indicate  $p < 0.05$ ,  
720 ‘+’ and ‘-’ indicate the direction of the relationship. For forest type ‘+’ indicates that trait values were  
721 greater in selectively logged than old-growth forests (i.e. positive with first PC axis). For variance  
722 explained by soil, ‘+’ indicates positive relationship with the respective PC axis. See Table 2 and Table  
723 S4 for detailed results.

724

725 Figure 4: Box-and-whisker plots showing the median, upper and lower quartile of functional diversity  
726 calculated as Rao’s Q with no significant difference between forest type (ANOVA:  $F_{1,6} = 0.16$ ,  $p =$   
727 0.70).

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729

**730 Tables**

731 Table 1: Study plot description and soil properties  $\pm$  standard deviation. Plots are listed by  
732 decreasing basal area. Basal area, stem density and number of tree species refers to all tree  
733 individuals  $\geq 10$  cm dbh. Plot locations are Maliau Basin Conservation Area (MBCA), Danum Valley  
734 conservation Area (DVCA) and the Stability of Altered Forest Ecosystem (SAFE) project site.

735 Table 2: Results from linear regression models from which the explained variance was generated,  
736 factors are the categorical 'forest type' (OG – old-growth, SL – selectively logged), and continuous  
737 'soil PC1' and 'soil PC2'. For analyses values of dark respiration  $R_d$  fluxes and  $\delta^{13}\text{C}$  were converted to  
738 positive values for ease of interpretation, here untransformed values are shown. For abbreviations  
739 and description of the functional traits, see table S1, ns = not significant.

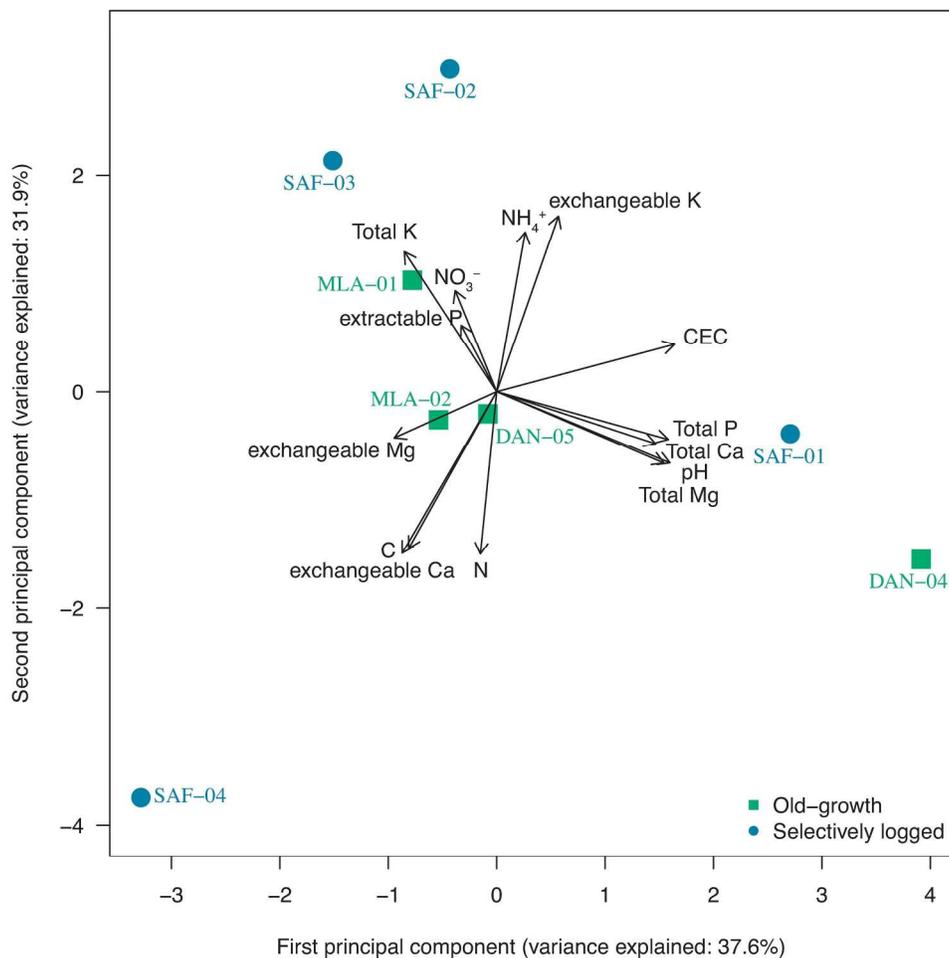


Figure 1: Principal component analysis (PCA) of plot-level soil properties. The highest loadings on the first axis are the cation exchange capacity, CEC (12.6%), total Mg (12.3%) and total P (12.2%). The highest loadings on the second axis are exchangeable K (12.0%), total N (11.1%) and exchangeable Ca (11.1%). See Table S2 for all PCA loadings.

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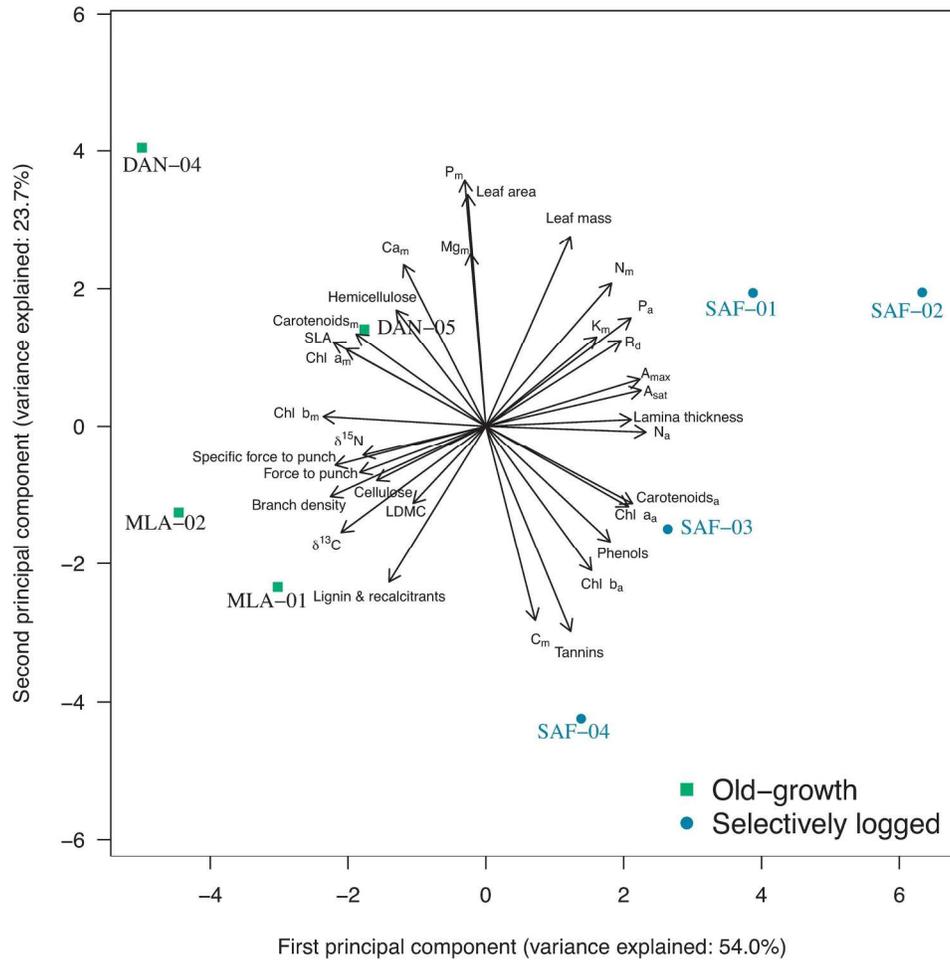


Figure 2: Principal component analysis (PCA) of plot-level community-weighted mean functional traits. Plots cluster by logging history, with increased values of traits that maximise carbon capture and growth in logged forest communities and greater allocation to tissue persistence and structural stability in old-growth forests.

The highest loadings on the first axis are chlorophyll  $b_m$  (4.44%),  $N_a$  (4.37%), branch wood density (4.25%),  $Asat$  (4.25%),  $A_{max}$  (4.21%) and  $SLA$  (4.17%). The highest loadings on second axis are  $P_m$  (7.45%),  $LA$  (7.02%), tannins (6.22%),  $C_m$  (5.88%) and leaf dry weight (5.75%). Mass-based nutrients are denoted by superscript "m" and area-based values by superscript "a". See Table S3 for all PCA loadings.

203x209mm (300 x 300 DPI)

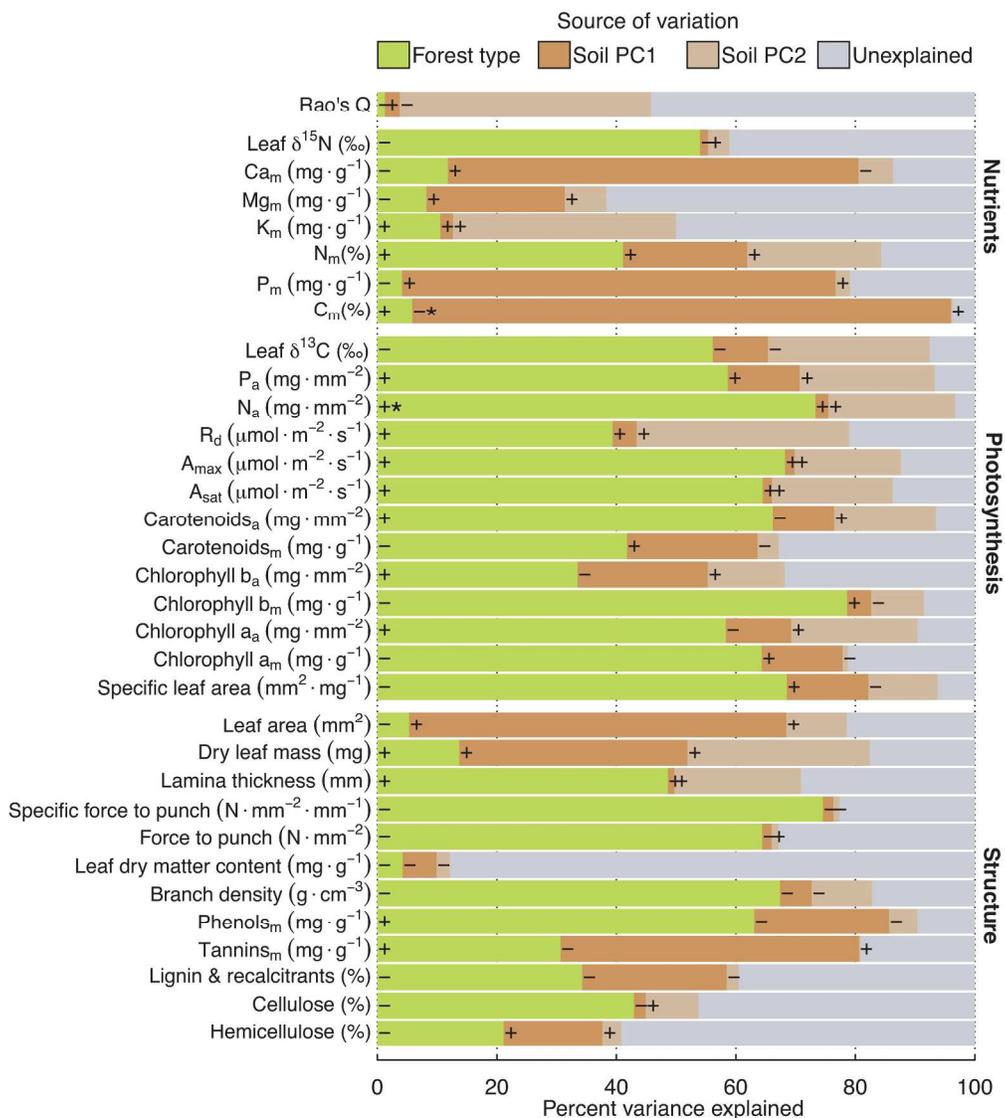


Figure 3: Proportion of variance in community-weighted mean functional trait values explained by forest type and the first two principal components of soil properties (Fig. 1). Functional traits are grouped by the ecosystem function to which they most contribute. Statistical significance is derived from linear regression models following false discovery rate correction, asterisks indicate  $p < 0.05$ , '+' and '-' indicate the direction of the relationship. For forest type '+' indicates that trait values were greater in selectively logged than old-growth forests (i.e. positive with first PC axis). For variance explained by soil, '+' indicates positive relationship with the respective PC axis. See Table 2 and Table S4 for detailed results.

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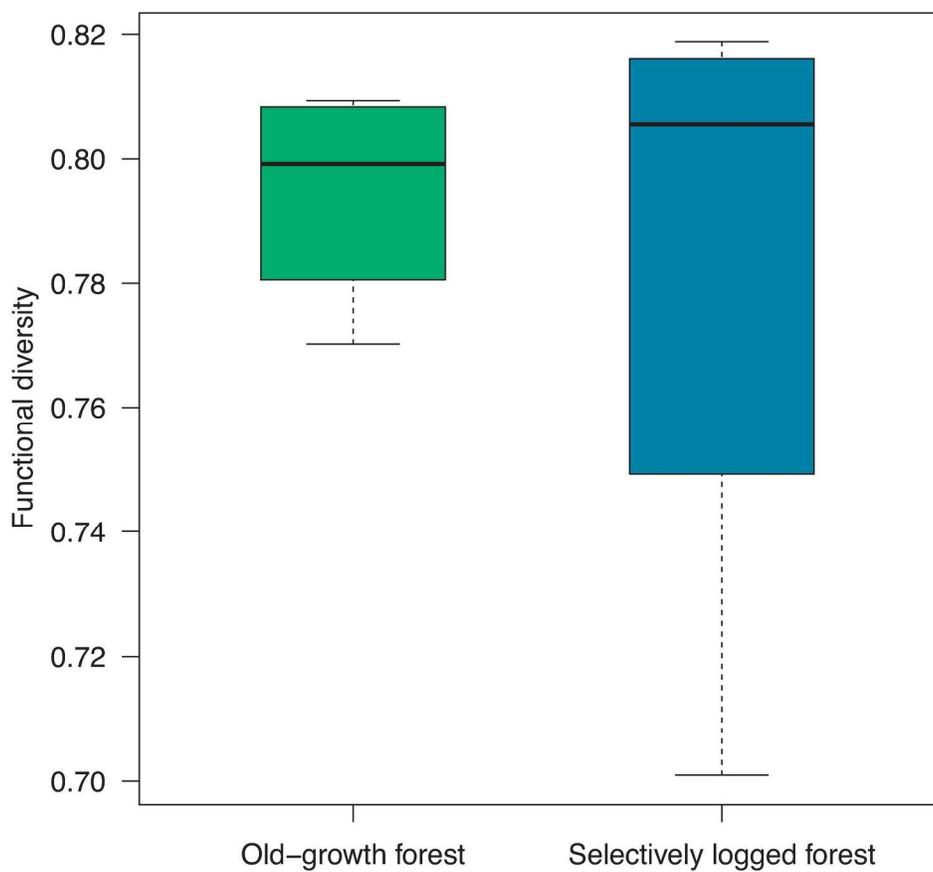


Figure 4: Box-and-whisker plots showing the median, upper and lower quartile of functional diversity calculated as Rao's Q with no significant difference between forest type (ANOVA:  $F_{1,6} = 0.16$ ,  $p = 0.70$ ).

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