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Key Words:	anthropogenic disturbance, Borneo, functional diversity, functional traits, land use, Rao's Q, tropical rainforest, variance partitioning

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

2 Sabine Both[1*], Terhi Riutta[2,3], C. E. Timothy Paine[4], Dafydd M. O. Elias[5,6], Rudi Chino[7], Annuar Jain[8],

3 David Johnson[9], Ully H. Kritzler[9], Marianne Kuntz[1], Noreen Majalap-Lee[10], Nora Mielke[1], Milenka X.

4 Montoya Pillco[1], Nicholas J. Ostle[5,6], Yit A. Teh[1], Yadvinder Malhi[2], David F. R. P. Burslem[1]

5

6 [1] Institute of Biological and Environmental Sciences, University of Aberdeen, 23 St Machar Drive,

7 Aberdeen, AB24 3UU, United Kingdom

8 [2] Environmental Change Institute, School of Geography and the Environment, University of Oxford,

9 South Parks Road, Oxford, OX1 3QY, United Kingdom

10 [3] Imperial College London, Department of Life Sciences, Silwood Park Campus, Buckhurst Road,

11 Ascot, SL5 7PY, United Kingdom

12 [4] Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA, United Kingdom

13 [5] Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster, LA1 4YQ, United Kingdom

14 [6] Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster,

15 LA1 4AP, United Kingdom

16 [7] Instituto de Ciencias de la Naturaleza, Territorio y Energías Renovables, Pontificia Universidad

17 Católica del Perú, Lima, Perú

18 [8] The South East Asia Rainforest Research Partnership (SEARRP), Danum Valley Field Centre, PO Box

19 60282, 91112, Lahad Datu, Sabah, Malaysia

20 [9] School of Earth and Environmental Sciences, The University of Manchester, Oxford Road,

21 Manchester, M13 9PT, United Kingdom

22 [10] Forest Research Centre, Peti Surat 1407, 90715 Sandakan, Sabah, Malaysia

23

24 *Author for correspondence:

25 Sabine Both

26 Tel: +44 1224274257

27 Email: s.both@abdn.ac.uk

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Summary

- Plant functional traits regulate ecosystem functions but little is known about how co-occurring gradients of land use and edaphic conditions influence their expression. We test how gradients of logging disturbance and soil properties relate to community-weighted mean traits in logged and old-growth tropical forests in Borneo.

- In eight 1 ha plots, we studied 32 physical, chemical and physiological traits from 284 tree species and measured long-term soil nutrient supplies and plant-available nutrients.

- Logged plots had greater values for traits that drive carbon capture and growth, whilst old-growth forests had greater values for structural and persistence traits. Although disturbance was the primary driver of trait expression, soil nutrients explained a statistically independent axis of variation linked to leaf size and nutrient concentration. Soil characteristics influenced trait expression via nutrient availability, and through nutrient pools and pH.

- Our finding, that traits have contrasting responses to land use and soil resource availability, provides robust evidence for the need to consider the abiotic context of logging when predicting plant functional diversity across human-modified tropical forests. The detection of two independent axes was made possible by the measurement of many more functional traits than have been examined in previous studies.

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

Introduction

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

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

95 disturbance, soil properties, and ecosystem processes in tropical forests therefore remains
96 incomplete.

97   The consequences of changes in community structure and diversity for ecosystem service
98 provision are determined by the impacts of disturbance on community-level trait expression, which
99 is a function of the type and intensity of disturbance. For example, in South American tropical
100 forests, disturbance due to logging and silvicultural activity increases light availability and triggers
101 the recruitment of species with traits that promote rapid growth rates (Baraloto *et al.* 2012;
102 Carreño-Rocabado *et al.* 2012). We expect a similar response to logging in Southeast Asian tropical
103 forest but additionally aim to determine the influence of soil properties including nutrient
104 availability.

105   Tropical lowland forests in Southeast Asia are amongst the most species-rich communities
106 worldwide, but are also the most threatened by intensive logging and conversion to agriculture
107 (Hansen *et al.* 2013; Edwards *et al.* 2014; Stibig *et al.* 2014). The high density of commercially
108 valuable species explains the high intensity of logging in Southeast Asian forests (Osman *et al.* 2012;
109 Gaveau *et al.* 2014), which suffer rates of extraction that far exceed those in tropical forests
110 elsewhere (Asner *et al.* 2005). Logging creates a spatially patchy disturbance, with gaps and skid
111 trails characterised by high light and temperature distributed among fragments of relatively
112 unmodified forest (Johns 1997). The selective removal of target species, logging-induced mortality
113 and recruitment of pioneer species in disturbed areas affects tree species composition and the pools
114 and fluxes of biomass and nutrients (Cannon *et al.* 1998; Verburg & van Eijk-Bos 2003; Pfeifer *et al.*
115 2016; Riutta *et al.* 2018). Although the magnitude of anthropogenic disturbance is much greater in
116 forests in Southeast Asia than in South America, they have received significantly less attention
117 regarding the modification of plant functional traits. Specifically, intense logging has the potential to
118 override the effects of other environmental gradients including soil properties.

119   Here, we measured 32 leaf, wood and physiological traits of 284 tropical tree species to
120 capture community level trait expression in response to selective logging across a gradient of soil
121 properties in species-rich tropical rainforest in Sabah, northern Borneo. We assess traits reflecting
122 nutrient status, light capture and photosynthesis, and allocation to structure and defence to provide
123 a whole-plant perspective and avoid overlooking traits that contribute to functional diversity. We
124 tested the hypothesis that CWM values of functional traits and functional diversity shift in response
125 to anthropogenic disturbance and soil properties. We used CWM traits to quantify average trait
126 values, and a multi-trait index of functional diversity (FD) to quantify trait variation, which can occur
127 independent of variation in CWM values of trait (Ricotta & Moretti 2011).

128   Specifically, we predict that (1) increasing disturbance and soil nutrient availability will

129   increase CWM traits related to tissue nutrient concentrations and carbon assimilation rates, but

130   reduce tissue densities and investments in structural defences. Given the high logging intensity in

131   Southeast Asia, we further hypothesise that (2) a greater proportion of the variance in CWM traits

132   will be explained by logging than by soil properties, emphasizing the pervasive impact of

133   anthropogenic land use on functional trait expression. Finally, due to the high overall tree species

134   richness we predict that (3) functional diversity will remain high in response to disturbance, despite

135   shifts in overall CWM traits.

136

137   **Material and Methods**

138   *Study sites*

139   Sampling was conducted in eight 1 ha plots in Sabah, Malaysian Borneo. The plots are part of the

140   Global Ecosystems Monitoring (GEM) network of permanent sample plots with intensive, regular

141   carbon cycle measurements (Malhi *et al.* 2015; Riutta *et al.* 2018) and were selected to capture

142   variation in logging intensity across a range of lowland tropical forests in northern Borneo. Old-

143   growth lowland mixed dipterocarp forest plots (hereafter OG) were located in the Maliau Basin

144   Conservation Area (MBCA, two plots) and the Danum Valley Conservation Area (DVCA, two plots),

145   while the other four plots were distributed between these two areas in the selectively logged

146   Kalabakan Forest Reserve (hereafter SL). The four logged plots are part of the Stability of Altered

147   Forest Ecosystem (SAFE) project (Ewers *et al.* 2011). This area has been logged two to four times

148   with the first round of logging in the mid-1970s and subsequent repeated logging during 1990-2008.

149   Approximately 150–179 m^3 ha^{-1} of timber was removed over this time period (Struebig *et al.* 2013),

150   bracketing the mean extraction volume across Sabah (152 m^3 ha^{-1}, Fisher *et al.* 2011).

151   All three areas are part of the Yayasan Sabah Forest Management Area and belong to a

152   formerly connected area of lowland dipterocarp rainforest characterised by high species richness

153   and many tall, emergent trees. The region has a moist tropical climate with an annual daily mean

154   temperature of 26.7 °C and annual precipitation of approximately 2600-2700 mm (Walsh & Newbery

155   1999). Although the climate is aseasonal there are occasional droughts and dry spells associated

156   with supra-annual El Niño Southern Oscillation events (Walsh & Newbery 1999; Newbery &

157   Lingenfelder 2009). The forest soils in Sabah are mostly orthic Acrisols or Ultisols (for more details

158   see Marsh & Greer 1992; Nainar *et al.* 2015).

159

160   *Sampling design*

161   Thirty-two functional traits were measured on 651 individual trees ≥ 10 cm diameter at breast height

162   (dbh) representing 284 species during an intensive sampling campaign from July to December 2015.

163   We combined two strategies to sample the functional trait values in each plot. In the first, weighted

164   basal area strategy, we sampled species that most contributed to the total plot basal area. This

165   approach assumes that species accounting for a larger proportion of plot basal area also make a

166   greater contribution to ecosystem functioning. Species were ranked based on their contribution to

167   total basal area at the most recent census for each plot (2011 to 2015), which ranged from 10.9–

168   41.8 m^2 ha^{-1}. All species that contributed to 70% of plot basal area (in decreasing order of species

169   basal area) were identified for sampling. In 57% of cases only one individual per species occurred;

170   otherwise, the individual with the greatest dbh within a species was sampled. This strategy

171   disproportionately sampled large-statured and abundant species. To ensure that smaller and

172   potentially rare species were also represented, we adopted a second strategy: stratified random and

173   taxon-independent sampling of all trees ≥ 10 cm dbh in three randomly selected 20 × 20 m subplots

174   within each 1 ha plot. As this strategy allowed for repeated samples of the same species, as well as

175   sampling from all height strata, it contained understory and shaded trees. This combination of

176   different sampling strategies provided a comprehensive representation of the tree community

177   (Paine *et al.* 2015) and resulted in an overall representation of > 90% of the total basal area per plot

178   (except one plot with 65%) and 51–71% of the species ≥ 10 cm dbh (Fig. S1).

179

180   *Soil properties*

181   We measured total nutrients and exchangeable nutrient pools to estimate both long-term nutrient

182   supply as well as plant-available forms. Two randomly located soil cores were taken per plot in 2014-

183   2015. Surface soil (0-10 cm) was analysed for pH, cation exchange capacity and total concentrations

184   of P, C, N, Mg, K and Ca using the protocols of Quesada *et al.* (2010, 2012). To assess availability of K,

185   Ca, Mg, P, NO_3^- and NH_4^+ we measured nutrient supply rates using in-situ ion exchange membranes

186   (PRSTM Probes, Western AG, Saskatoon, Canada). To account for spatial variability we installed four

187   probe pairs (each composed of one cation and anion probe) vertically at corners of three 50 × 50 cm

188   quadrats to 10 cm depth within each of the three subplots used in the stratified random sampling.

189   These were collected after two weeks, washed with distilled water and sent to the manufacturer for

190   analysis. They pooled the four probe pairs from each quadrat prior to elution with 0.5M HCl for 1 hr,

191   yielding 72 samples. NO_3^- and NH_4^+ were measured colorimetrically using automated flow injection

192   analysis (FIA). All other elements were analysed using Inductively Coupled Plasma Mass

193   Spectrometry (ICP-MS). Results are reported as supply rates over the burial period (micrograms/10

194   cm^2/14 days).

195

Trait measurements

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

216

Statistical analyses

218 Replicated leaf-level functional traits were averaged for sun and shade leaves for the few individuals
219 that possessed both to generate a tree-level dataset. Our results were identical for analyses using a
220 data-set comprising sun leaves alone, where available, or otherwise shade leaves, so henceforth we
221 use both sun and shade leaves together. Leaf chemical properties that are most relevant for
222 photosynthetic activity were expressed as mass-based as well as area-based values (chlorophyll a,
223 chlorophyll b, bulk carotenoids, N, and P). For all analyses, if necessary, leaf traits were log-
224 transformed to improve the normality of residuals. A CWM was calculated for each trait, weighted
225 by the abundance of each species in each plot (Pla *et al.* 2012). Values of dark respiration fluxes and
226 $\delta^{13}C$ were converted to positive values for ease of interpretation. To characterise soil properties in
227 relation to land use, we performed a principal component analysis (PCA) of soil chemical properties
228 across the eight plots with the measurements of total concentrations of P, C, N, Mg, K, Ca,

229   exchangeable Mg, K, Ca, NH_4^+ and NO_3^-, extractable P, pH and cation exchange capacity (CEC). To

230   visualise the distribution of CWM traits across forest types and test hypothesis 1, we conducted a

231   PCA using centred and standardised CWM trait values for each study plot.

232   In order to test hypothesis 2, site scores from the first two PCA axes of soil properties, along with

233   a binary variable representing logging history, were used as predictors in multiple regression models

234   to partition the variance in each CWM trait. The first two principal components from the soil PCA

235   were both statistically independent of logging history (linear model: $p \geq 0.48$). Nevertheless, because

236   the three predictors were weakly but non-significantly inter-correlated ($R^2 \leq 0.29$), we used the

237   hierarchical partitioning method of Chevan and Sutherland (1991), as implemented in the hier.part

238   library of R, to estimate the variance in functional traits explained by each. This technique calculates

239   the R^2 of every possible model, then averages over this set of models to allocate the variance

240   explained by each predictor variable. It thereby overcomes the effect of the order that inter-

241   correlated variables enter a model on the inferred variance explained by each variable (Chevan &

242   Sutherland 1991).

243   To address hypothesis 3, we computed plot-level values of functional diversity (FD) as Rao's

244   quadratic entropy (Rao's Q), which is the sum of the pairwise distances between species in

245   multidimensional trait space weighted by their relative abundance (Rao 1982) and compared forest

246   types with ANOVA.

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

248

249   **Results**

250   *Forest structure, species composition and soil properties of plots*

251   The study plots varied substantially in basal area (BA) and stem density, with BA varying fourfold

252   (10.9 m - 41.8 m^2 ha^{-1}, Table 1). Basal area was significantly lower in the SL plots but the range

253   among plots within each forest type was similar (means: SL 17.8 ± 12.7, OG 34.8 ± 14.9 m^2 ha^{-1};

254   ANOVA: $F_{1,6}$ = 15.26, p = 0.008). Stem density ranged from 331 to 565 ha^{-1}, peaking in plots with

255   intermediate BA but was not associated with logging ($F_{1,6}$ = 0.02, p = 0.90). Species richness was

256   similar in OG and SL plots, ranging from 124 to 211 tree species ha^{-1} ($F_{1,6}$ = 0.55, p = 0.49).

257   A PCA of soil chemical properties explained 69.5% on the first two principal axes (Fig. 1). The

258   strongest gradient was defined by variation in total Mg, total P and CEC, whereas the second axis

259   represented a gradient of total C, total N and exchangeable Ca to exchangeable K and NH_4^+. Nutrient

260   concentrations varied markedly among plots, including 10-fold and 5-fold variation in total Mg and

261   total P concentrations along axis 1, and 9-fold and 10-fold variation in exchangeable K and NH_4^+

along axis 2 (Table 1). Soil properties differed among plots, but were independent of logging history,
indicated by the overlapping distribution of OG and SL plots in the PCA (Fig. 1).

Community-weighted mean traits

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

The second axis of functional trait space represented tissue nutrient concentrations and leaf area, but was independent of logging history (Fig. 2). This axis reflects covariation among CWM values of leaf area, leaf P_m, N_m, Mg_m and Ca_m concentrations, and a negative association of these traits with leaf C_m and tannin concentrations. Variability of these traits within both logged and unlogged forests was high, which suggests that the expression of these traits is driven by underlying soil properties rather than logging history.

Variance partitioning

We grouped the functional traits based on their main association with leaf nutrients, photosynthesis and structure. Partitioning the CWM response of traits to logging and the first two principal components of soil properties showed that these factors explained up to 90% of the variation in traits. Overall, the proportion of variance explained was on average 74.4%. (Fig. 3, Table S4). Variation in mass-based concentrations of leaf Ca_m, P_m, N_m and K_m and to a lesser extent Mg_m were associated with variation in soil properties. However, expressed on area basis, foliar P_a and N_a concentrations were mainly explained by logging. Variation in SLA and leaf thickness appears to underlie the contrasting response of mass and area based traits. Community-weighted mean values of C_m, P_m and Ca_m were most strongly and significantly explained by the first principal component of soil properties, reflecting the underlying gradients of soil total P and Ca concentrations along this

297 axis (Fig. 1). For leaf traits related to photosynthesis, 33.5–78.6% of variance was explained by

298 logging and a much smaller proportion by soil PC1 (1.5–21.8%) or soil PC2 (0.9–35.6%), see Table S4.

299 Structural traits were explained by a combination of both logging history and the independent

300 effects of soil properties. Logging explained on average 39.2% of variance in traits reflecting tissue

301 density and structural investment, such as specific force to punch and branch wood density, which

302 had consistently lower values in logged forest plots. Community-weighted mean LDMC was unusual

303 in that it was poorly explained by the predictor variables. In contrast, leaf size, expressed as CWM

304 leaf area and leaf mass, increased significantly with increasing values of soil PC1, which was linked to

305 plots with higher total N and exchangeable Ca concentrations (Fig. 1). There was a significant

306 increase in CWM tannin concentrations in logged forest plots and at higher values of soil PC1.

307

308 *Functional diversity*

309 Functional diversity, expressed as Rao's Q, was similar between forest types (Fig. 4; $F_{1,6} = 0.16$, p =

310 0.70), and neither logging nor soil properties explained a significant proportion of its variance (Fig.

311 3). Variance in FD was greater among SL than OG forests (Fig. 4), indicating the heterogeneous

312 conditions resulting from logging.

313

314 **Discussion**

315 Logging profoundly affected the expression of plant functional traits in Bornean tropical forests.

316 Logging was the primary driver of variation in CWM values of functional traits (Fig. 2), and explained

317 more variation than soil properties for 20 of 32 traits (Fig. 3). Similar impacts of logging on functional

318 trait expression have been demonstrated in Neotropical forests (Baraloto *et al.* 2012; Carreño-

319 Rocabado *et al.* 2012), although those studies did not analyse soil-related factors. Together, these

320 studies confirm that CWM traits are highly sensitive to land-use change in tropical forests, but

321 results from our study additionally highlight the context dependency of trait expression. Logging has

322 impacted over half of all tropical forests globally, and over 70% of forests in Sabah (Bryan *et al.* 2013;

323 Potapov *et al.* 2017). Therefore, the effect of logging on the expression of functional traits is likely to

324 pervade tropical forest landscapes and impact ecosystem processes. Effects on other trophic levels

325 are also likely. For example, herbivorous insects are sensitive to leaf traits such as LDMC and phenol

326 concentrations (Hevia *et al.* 2017). Moreover, logging-associated changes in forest structure and

327 CWM traits drive altered patterns of productivity in tropical forests (Pfeifer *et al.* 2016; Riutta *et al.*

328 2018).

329   In our study, the principal axis of functional trait space defined a clear gradient from values of

330 traits that maximise carbon capture and growth, which were predominantly expressed in selectively

331 logged forests, to greater allocation to tissue persistence and stability, which were predominantly
332 expressed in old-growth forests. This strong signal of anthropogenic disturbance is partly congruent
333 with the leaf economics spectrum, which differentiates species along a gradient based on leaf traits
334 contributing to resource acquisition and conservation (Wright *et al.* 2004; Díaz *et al.* 2016). Thus,
335 trees in logged forest communities expressed higher CWM values of area-based measures of N, P
336 and pigments, whereas old-growth forest communities expressed low CWM values of these traits
337 and higher values of traits conferring structural stability and resistance to herbivory, such as branch
338 wood density and leaf toughness. Supporting hypothesis 1, disturbance enhanced the recruitment of
339 species possessing traits that confer rapid carbon capture and investment in fast growth rates
340 (Baraloto *et al.* 2012; Carreño-Rocabado *et al.* 2012, 2016). We amplify previous results by
341 additionally demonstrating that logged forest communities expressed higher CWM values of $A_{sat,}$
342 A_{max} and R_d, whereas old-growth forest communities were characterised by higher values of traits
343 conferring structural stability of wood and leaves.

344 We observed lower CWM values of SLA in logged forests, in contrast to results from French
345 Guiana (Baraloto *et al.* 2012), and contrary to the expectation that SLA scales positively with A_{max}
346 and foliar N_a and P_a concentrations among species (Wright *et al.* 2004). The decoupling of SLA from
347 other leaf-economic traits may be explained by the abundance of pioneer species, which recruit
348 following disturbance and are adapted to resist the more exposed and potentially desiccating
349 conditions created by logging (Hardwick *et al.* 2015). A reduction in SLA may contribute to
350 photosynthetic water-use efficiency, especially when combined with enhanced investment in
351 photosynthetic enzymes, to ensure draw-down of internal CO_2 concentrations at a given stomatal
352 conductance (Reich *et al.* 2003). The greater enrichment of CWM $\delta^{13}C$ of logged forest tree
353 communities demonstrates lower discrimination for the heavier ^{13}C isotope and provides
354 independent evidence of enhanced integrated water-use efficiency for trees in this hotter and drier
355 environment (Farquhar *et al.* 1989; Rumman *et al.* 2018). The absence of a shift in SLA in response to
356 logging in French Guianan forests (Baraloto *et al.* 2012) suggests that logging imposes a more
357 extreme environmental contrast for trees growing in the less seasonal climate of Borneo than in
358 seasonal French Guiana. The impact of logging may be more severe in tree communities not adapted
359 to drought and emphasises the potential sensitivity of Bornean forests to future climatic change.

360 We show that trait expression responded independently to logging disturbance and soil
361 properties. Variation in soil properties can be attributed to interactions between underlying soil
362 texture and mineralogy, on one hand, and the impacts of logging disturbances including soil
363 inversion, removal, and compaction on the other (Pinard *et al.* 2000). However, soil properties did
364 not differ systematically between old-growth and selectively logged forests (Fig. 1), owing to

365   variation in underlying soil types and the heterogeneous nature of logging. This allowed us to assess

366   their independent effects on the expression of CWM functional traits. For most of the mass-based

367   nutrient concentrations, variation in soil properties explained more variation in CWM trait values

368   than did logging, whereas traits linked to photosynthesis and carbon capture were more sensitive to

369   logging than to variation in soil properties (Fig. 3). The mechanisms underlying these associations

370   deserve further study.

371   Moreover, we provide clear evidence that soil properties act on trait expression in two

372   independent ways; the first axis reflected total pools of nutrients, and the second reflected nutrient

373   availability (Fig. 1). Community-weighted mean values of leaf area, leaf dry mass and foliar

374   concentrations of P_m, P_a, N_m and Ca_m all increased significantly in response to the first axis of

375   variation in soil properties, whereas leaf C_m and tannin concentrations decreased along this gradient

376   (Fig. 3). The second component of soil variation also influenced some leaf traits, particularly $\delta^{13}C$, N_a

377   and P_a concentrations (Table 2, Table S4). Moreover, most traits were influenced either by the first

378   or second axis of variation in soil properties, but rarely both. This finding may reflect a trade-off in

379   how plants interact with local edaphic conditions, as suggested in other systems (Laliberte *et al*.

380   2015); a key future challenge will be to disentangle the mechanisms underpinning these contrasting

381   responses of functional traits to the soil environment. Our results highlight the need to consider the

382   context dependency of drivers of variation in functional traits. Landscape-level predictions of change

383   in functional trait expression in response to anthropogenic disturbance will need to account for the

384   additional effects of soil properties.

385   Despite the large variation in CWM traits, FD did not differ between logged and old-growth

386   forest, which is consistent with our third hypothesis and results from Neotropical forests (Fig. 4;

387   Baraloto *et al*. 2012; Carreño-Rocabado *et al*. 2012). This finding emphasises that forests can retain

388   species richness and trait variation, yielding similar FD, despite logging. In line with Mayfield *et al.*

389   (2010), logging did not result in loss of FD but in shifts of numerous CWM trait values, indicating a

390   lower sensitivity of multi-trait FD to these changes (Ricotta & Moretti 2011). FD was more variable

391   among logged forests than old-growth forests, probably owing to variation in logging history and

392   intensity, which affect forest structure (Cannon *et al.* 1994; Berry *et al.* 2008), microclimatic

393   conditions (Hardwick *et al.* 2015) and ecosystem functions (Mayfield *et al.* 2006; Both *et al.* 2017;

394   Riutta *et al.* 2018). The substantial variance in FD among the disturbed plots highlights the challenge

395   of predicting the impacts of anthropogenic modification on FD in environments where the outcomes

396   may be highly context-dependent (Costantini *et al.* 2016).

397   Assessments of functional composition and diversity at a community scale are critical as

398   human-modified landscapes become more extensive and exert an increasing role in the provision of

399 ecosystem services (Berry *et al.* 2010; Gibson *et al.* 2011). However, uncertainty remains over how
400 changes in community trait expression will affect ecosystem functioning and resilience after
401 selective logging and other forms of disturbance (Laliberté *et al.* 2010; Mayfield *et al.* 2010; Edwards
402 *et al.* 2014). Part of that uncertainty arises because rare tree species may contribute substantially to
403 resilience (Mouillot *et al.* 2013b), but tend to be under-represented in traditional sampling designs
404 adopted for measuring ecosystem functions. Our nested sampling design explicitly resolved this
405 issue by selecting both common and rare species across the full range of size classes. We therefore
406 advocate this approach in future assessments of trait expression at the community scale.

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

418

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612

613   **Figure captions**

614

615   Figure 1: Principal component analysis of plot-level soil properties. Notably, plots with similar logging

616   histories do not cluster together. The highest loadings on the first axis are CEC (12.6%), total Mg

617   (12.3%) and total P (12.2%). The highest loadings on the second axis are exchangeable K (12.0%),

618   total N (11.1%) and exchangeable Ca (11.1%). See Table S2 for all PCA loadings.

619

620   Figure 2: PCA of plot-level community-weighted mean functional traits. Plots cluster by logging

621   history, with increased values of traits that maximise carbon capture and growth in logged forest

622   communities and greater allocation to tissue persistence and structural stability in old-growth

623   forests. The highest loadings on the first axis are chlorophyll b_m (4.44%), N_a (4.37%), branch wood

624   density (4.25%), A_{sat} (4.25%), A_{max} (4.21%) and SLA (4.17%). The highest loadings on second axis are

625   P_m (7.45%), LA (7.02%), tannins (6.22%), C_m (5.88%) and leaf dry weight (5.75%). Mass-based

626   nutrients are denoted by superscript "m" and area-based values by superscript "a". See Table S3 for

627   all PCA loadings.

628

629   Figure 3: Proportion of variance in community-weighted mean functional trait values explained by

630   forest type and the first two principal components of soil properties (Fig. 1). Functional traits are

631   grouped by the ecosystem function to which they most contribute. Statistical significance is derived

632   from linear regression models, asterisks indicate significance level, '+' and '-' indicate the direction of

633   the relationship. For forest type '+' indicates that trait values were greater in selectively logged than

634   old-growth forests (i.e. positive with first PC axis). For variance explained by soil, '+' indicates

635   positive relationship with the respective PC axis. See Table 2 and Table S4 for detailed results.

636

637   Figure 4: Box-and-whisker plots showing the median, upper and lower quartile of functional diversity

638   calculated as Rao's Q with no significant difference between forest type (ANOVA: $F_{1,6}$ = 0.16, p =

639   0.70).

640

Tables

Table 1: Study plot description and soil properties, plots are listed with decreasing basal area. Basal area, stem density and number of tree species refers to all tree individuals ≥ 10 cm dbh.

Plot name	Location	Total basal area [m² ha⁻¹]	Stem density	Number of species	C [%]	N [%]	Total P [mg kg⁻¹]	Total Ca [mg kg⁻¹]	Total K [mg kg⁻¹]	Total Mg [mg kg⁻¹]	eCEC [mmol⁺ kg⁻¹]	pH (H₂O)	NO₃⁻ [µg 10 cm² 14 days⁻¹]	NH₄⁺ [µg 10 cm² 14 days⁻¹]	Exchangable Ca [µg 10 cm² 14 days⁻¹]	Exchangable Mg [µg 10 cm² 14 days⁻¹]	Exchangable K [µg 10 cm² 14 days⁻¹]	Extractable P [µg 10 cm² 14 days⁻¹]
Old-growth forest																		
MLA-01	MBCA	41.8	396	141	1.67	0.14	163.01	50.06	101.03	39.67	36.44	3.95	59.6 ± 45.2	10.5 ± 3.11	237 ± 130	152 ± 80.6	265 ± 154	0.23 ± 0.262
MLA-02	MBCA	37.3	484	170	2.00	0.17	266.44	194.68	80.62	99.41	43.18	4.25	184 ± 103	6.37 ± 1.52	417 ± 476	303 ± 215	151 ± 80.2	0.433 ± 0.325
DAN-04	DVCA	30.8	456	128	1.80	0.18	557.21	603.28	16.12	389.63	63.88	5.81	75.2 ± 57.2	11.9 ± 12.7	480 ± 596	235 ± 187	268 ± 158	0.177 ± 0.134
DAN-05	DVCA	29.1	413	144	1.84	0.17	255.59	140.50	77.03	180.37	44.90	4.46	154 ± 164	5 ± 1.88	737 ± 682	271 ± 183	305 ± 269	1.03 ± 1.89
Selectively logged forest																		
SAF-03	SAFE project	25.8	565	211	1.89	0.16	231.05	40.42	115.55	38.65	35.66	3.68	83.8 ± 63.7	26.4 ± 44.9	392 ± 265	318 ± 201	332 ± 308	8.51 ± 12.4
SAF-04	SAFE project	19.5	465	188	7.15	0.32	117.07	107.71	67.21	41.36	14.55	3.90	83.4 ± 60.5	2.68 ± 4.32	1.35*10³ ± 621	310 ± 94.1	45.1 ± 58	1.18 ± 1.21
SAF-02	SAFE project	14.8	416	124	1.51	0.12	137.33	160.50	105.86	41.80	49.38	4.04	340 ± 239	23.9 ± 33.2	182 ± 187	191 ± 173	401 ± 239	0.464 ± 0.214
SAF-01	SAFE project	10.9	331	129	3.08	0.28	375.15	887.03	96.37	266.36	70.76	4.66	20 ± 17.5	16.8 ± 18.7	212 ± 269	79 ± 67.6	245 ± 90.6	3.03 ± 2.48

646 Table 2: Results from linear regression models from which the explained variance was generated,

647 factors are the categorical 'forest type' (OG – old-growth, SL – selectively logged), and continuous

648 'soil PC1' and 'soil PC2'. For analyses values of dark respiration R_d fluxes and $\delta^{13}C$ were converted to

649 positive values for ease of interpretation, here untransformed values are shown. For abbreviations

650 and description of the functional traits, see table S1.

| Functional trait | CWM trait value (and 95% confidence intervals) | | Forest type | | soil PC1 | | soil PC2 | |
	OG	SL	F-value	p-value	F-value	p-value	F-value	p-value
Rao's Q	0.791 (0.735 - 0.847)	0.789 (0.736 - 0.842)	0.197	0.680 ns	0.119	0.748 ns	3.060	0.155 ns
$\delta^{15}N$ [‰]	1.64 (0.966 - 2.32)	0.846 (0.204 - 1.49)	5.032	0.088 ns	0.185	0.689 ns	0.527	0.508 ns
Ca_m [mg g^{-1}]	7.09 (6.12 - 8.2)	6.6 (5.75 - 7.59)	6.114	0.069 ns	17.555	0.014 *	1.578	0.278 ns
Mg_m [mg g^{-1}]	2.57 (2.06 - 3.2)	2.41 (1.96 - 2.97)	0.724	0.443 ns	1.275	0.322 ns	0.490	0.523 ns
K_m [mg g^{-1}]	9.99 (8.4 - 11.9)	10.8 (9.13 - 12.7)	0.923	0.391 ns	0.321	0.601 ns	2.758	0.172 ns
N_m [%]	1.83 (1.74 - 1.91)	1.97 (1.89 - 2.05)	9.191	0.039 *	7.746	0.050 *	4.523	0.101 ns
P_m [mg g^{-1}]	0.998 (0.912 - 1.09)	0.99 (0.909 - 1.08)	1.484	0.290 ns	13.219	0.022 *	0.444	0.542 ns
C_m [%]	44.6 (44.3 - 44.9)	44.7 (44.4 - 45)	12.266	0.025 *	89.717	0.001 ***	0.240	0.650 ns
$\delta^{13}C$ [‰]	-32.4 (-32.1 - (-32.8))	-31.4 (-31.1 - (-31.8))	28.775	0.006 **	8.747	0.042 *	11.356	0.028 *
P_a [mg mm^{-2}]	$6.62{*}10^{-5}$ ($6.21{*}10^{-5}$ - $7.06{*}10^{-5}$)	$8.04{*}10^{-5}$ ($7.57{*}10^{-5}$ - $8.54{*}10^{-5}$)	33.208	0.005 **	12.267	0.025 *	10.391	0.032 *
N_a [mg mm^{-2}]	0.128 (0.12 - 0.136)	0.166 (0.158 - 0.174)	97.699	0.001 ***	0.520	0.511 ns	19.704	0.011 *
R_d [µmol CO_2 m^{-2} s^{-1}]	-1.03 (-0.871 - (-1.19))	-1.25 (-1.09 - (-1.4))	7.708	0.050 ns	1.546	0.282 ns	5.759	0.074 ns
A_{max} [µmol CO_2 m^{-2} s^{-1}]	11.7 (8.94 - 14.5)	18 (15.4 - 20.6)	23.237	0.009 **	0.878	0.402 ns	4.268	0.108 ns
A_{sat} [µmol CO_2 m^{-2} s^{-1}]	4.08 (2.66 - 5.5)	7.03 (5.69 - 8.38)	20.267	0.011 *	0.284	0.622 ns	4.495	0.101 ns
Carotenoids$_a$ [mg mm^{-2}]	$4.74{*}10^{-5}$ ($4.47{*}10^{-5}$ - $5.02{*}10^{-5}$)	$5.54{*}10^{-5}$ ($5.28{*}10^{-5}$ - $5.79{*}10^{-5}$)	47.726	0.002 **	1.707	0.261 ns	7.957	0.048 *
Carotenoids$_m$ [mg g^{-1}]	0.687 (0.667 - 0.708)	0.667 (0.647 - 0.687)	6.353	0.065 ns	1.555	0.281 ns	0.264	0.635 ns
Chl b$_a$ [mg mm^{-2}]	$7.42{*}10^{-5}$ ($6.79{*}10^{-5}$ - $8.04{*}10^{-5}$)	$7.95{*}10^{-5}$ ($7.36{*}10^{-5}$ - $8.55{*}10^{-5}$)	5.552	0.078 ns	1.678	0.265 ns	1.333	0.313 ns
Chl b$_m$ [mg g^{-1}]	1.09 (1.05 - 1.13)	0.97 (0.931 - 1.01)	40.379	0.003 **	0.005	0.945 ns	2.605	0.182 ns
Chl a$_a$ [mg mm^{-2}]	$1.8{*}10^{-4}$ ($1.69{*}10^{-4}$ - $1.92{*}10^{-4}$)	$2.06{*}10^{-4}$ ($1.95{*}10^{-4}$ - $2.17{*}10^{-4}$)	29.141	0.006 **	1.457	0.294 ns	7.060	0.057 ns
Chl a$_m$ [mg g^{-1}]	2.62 (2.54 - 2.71)	2.49 (2.41 - 2.57)	13.853	0.020 *	0.967	0.381 ns	0.020	0.894 ns
SLA [mm^2 mg^{-1}]	16.3 (15.3 - 17.4)	13.2 (12.2 - 14.1)	52.069	0.002 **	3.036	0.156 ns	5.338	0.082 ns
LA [mm^2]	$1.37{*}10^4$ ($1.13{*}10^4$ - $1.65{*}10^4$)	$1.31{*}10^4$ ($1.1{*}10^4$ - $1.57{*}10^4$)	1.678	0.265 ns	11.116	0.029 *	1.898	0.240 ns
Leaf dry weight [mg]	922 (784 - $1.08{*}10^3$)	$1.08{*}10^3$ (930 - $1.27{*}10^3$)	2.077	0.223 ns	10.600	0.031 *	6.120	0.069 ns
Leaf thickness [mm]	0.221 (0.209 - 0.233)	0.236 (0.224 - 0.249)	7.196	0.055 ns	0.213	0.668 ns	2.319	0.203 ns
Specific force to punch [N mm^{-2}]	1.23 (1.03 - 1.47)	0.889 (0.751 - 1.05)	13.209	0.022 *	0.431	0.547 ns	0.013	0.915 ns
Force to punch [N mm^{-1}]	0.266 (0.227 - 0.311)	0.212 (0.183 - 0.247)	7.611	0.051 ns	0.300	0.613 ns	0.260	0.637 ns
LDMC [mg g^{-1}]	416 (391 - 440)	410 (387 - 433)	0.143	0.725 ns	0.332	0.595 ns	0.079	0.793 ns
Branch density [g cm^{-3}]	0.564 (0.528 - 0.599)	0.493 (0.46 - 0.526)	15.309	0.017 *	2.442	0.193 ns	1.522	0.285 ns
Phenol$_m$ [mg g^{-1}]	36.4 (33.7 - 39.1)	42.7 (40.2 - 45.3)	29.960	0.005 **	5.004	0.089 ns	2.762	0.172 ns
Tannin$_m$ [mg g^{-1}]	8.56 (7.7 - 9.41)	9.41 (8.6 - 10.2)	8.888	0.041 *	8.069	0.047 *	0.004	0.951 ns
Lignin & recalcitrants [%]	19.4 (17.3 - 21.4)	17.3 (15.3 - 19.2)	2.707	0.175 ns	3.333	0.142 ns	0.080	0.791 ns
Cellulose [%]	22.5 (20.9 - 24)	20.9 (19.4 - 22.4)	3.343	0.142 ns	0.313	0.606 ns	0.995	0.375 ns
Hemicellulose [%]	12.3 (11.4 - 13.1)	11.8 (11 - 12.6)	1.728	0.259 ns	0.767	0.431 ns	0.270	0.631 ns

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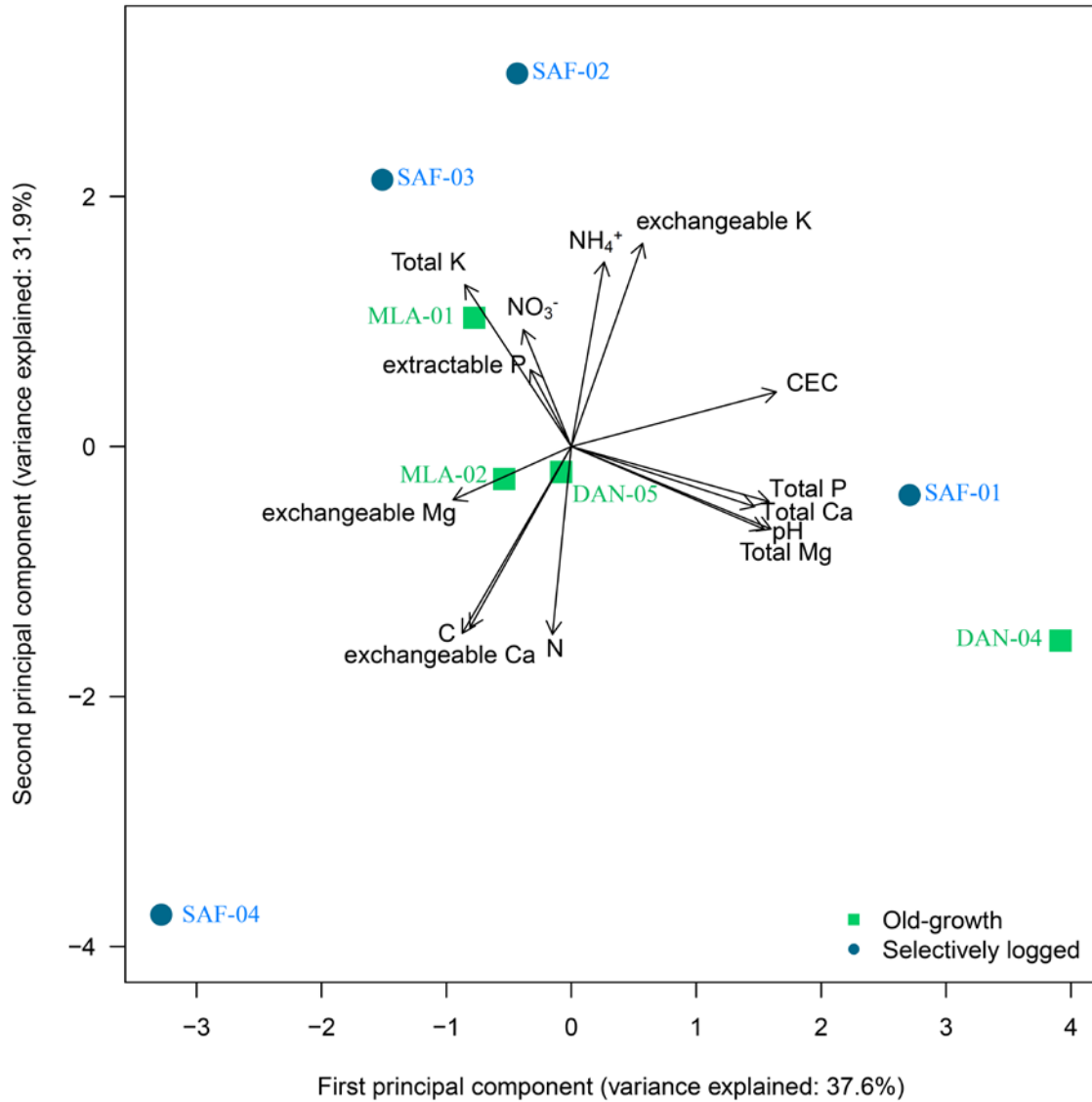
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Figure 1: Principal component analysis of plot-level soil properties. Notably, plots with similar logging histories do not cluster together. The highest loadings on the first axis are CEC (12.6%), total Mg (12.3%) and total P (12.2%). The highest loadings 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.
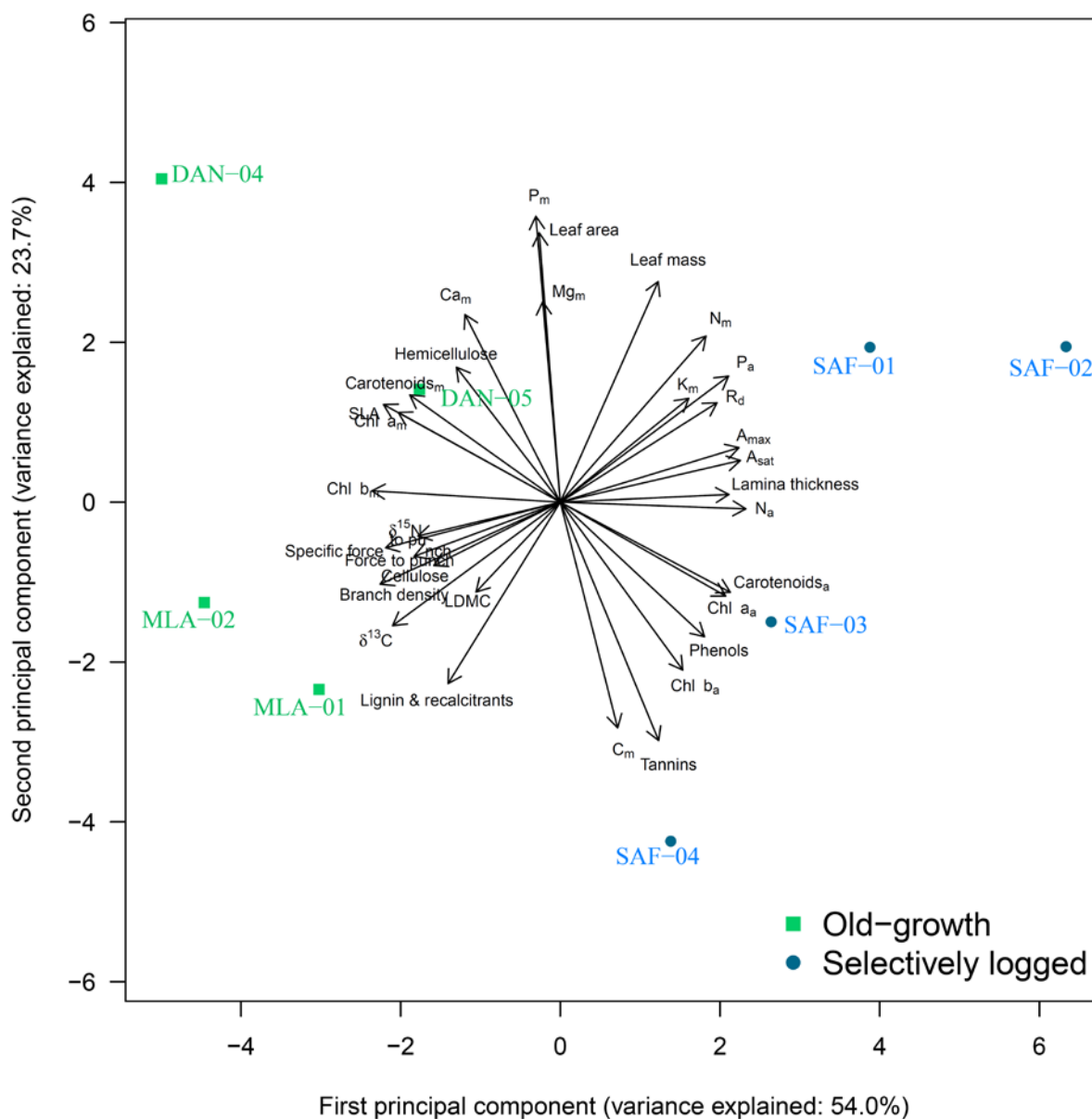
Figure 2: PCA of plot-level community-weighted mean functional traits. Plots cluster by logging history, with increased values of traits that maximise carbon capture and growth in logged forest communities and greater allocation to tissue persistence and structural stability in old-growth forests. The highest loadings on the first axis are chlorophyll b_m (4.44%), N_a (4.37%), branch wood density (4.25%), A_{sat} (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.
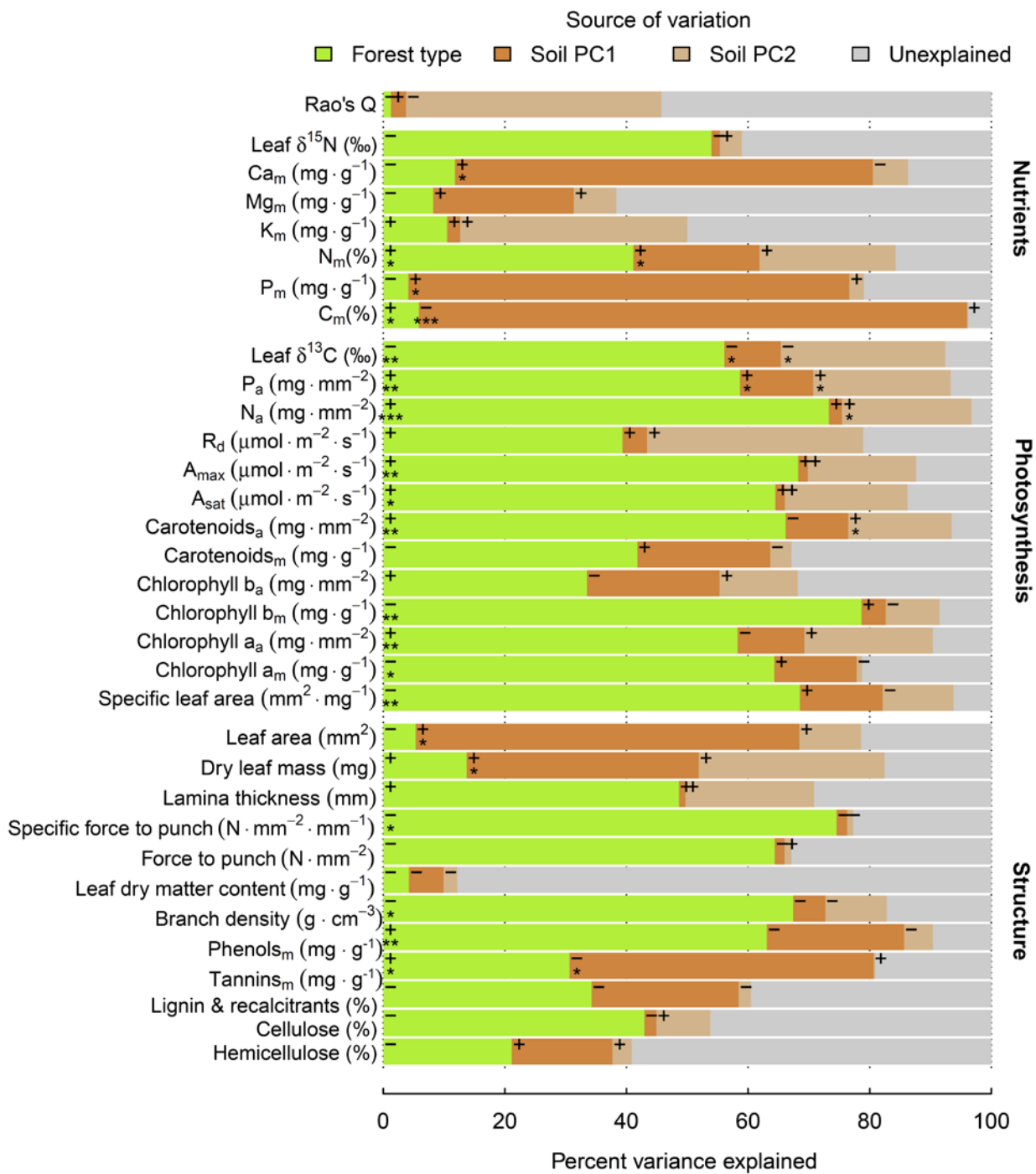
Figure 3: Proportion of variance in community-weighted mean functional trait values explained by forest type and the first two principal components of soil properties (Fig. 1). Functional traits are grouped by the ecosystem function to which they most contribute. Statistical significance is derived from linear regression models, asterisks indicate significance level, '+' 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.
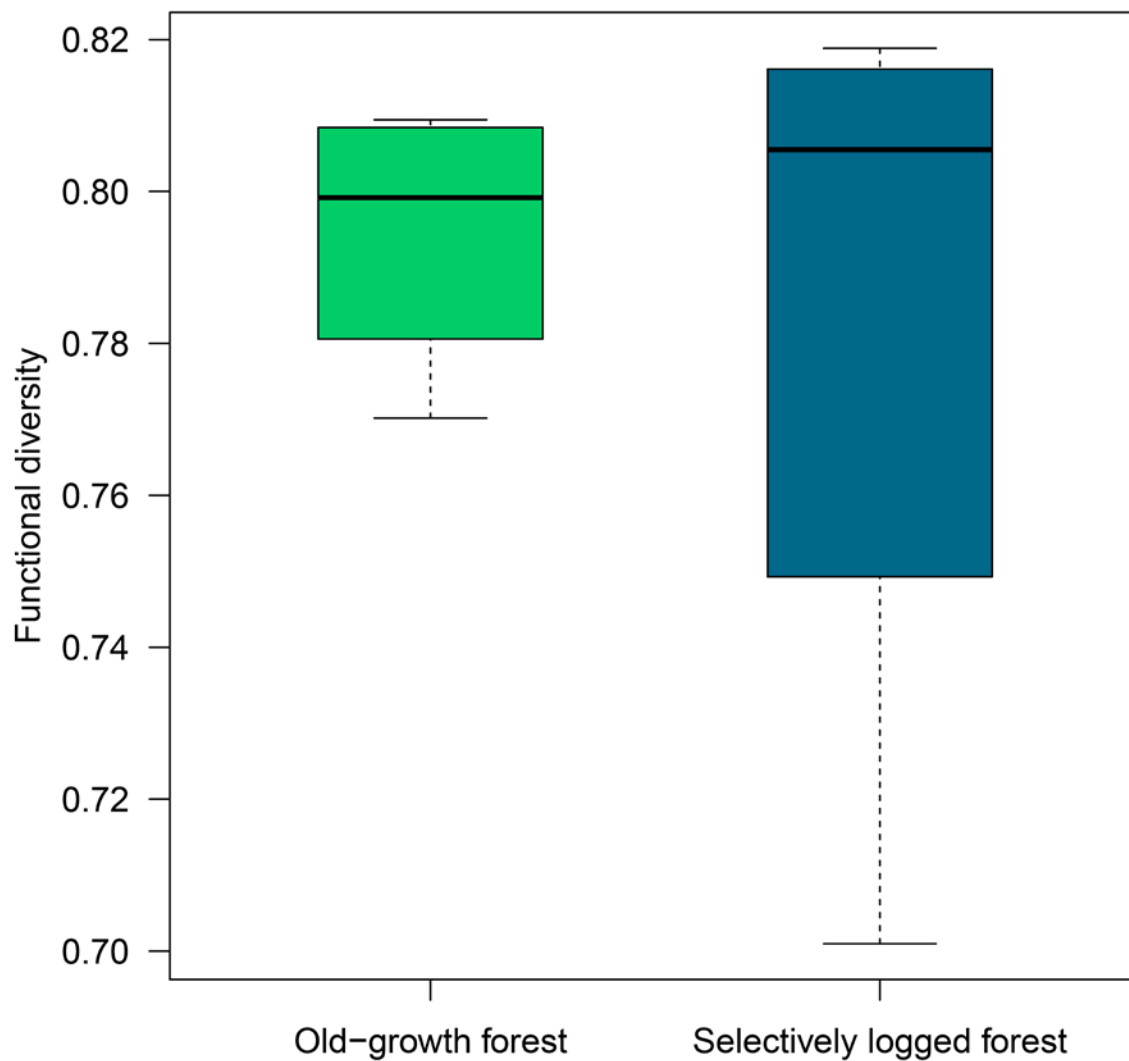
Figure 4: Box-and-whisker plots showing the median, upper and lower quartile of functional diversity calculated as Rao's Q with no significant difference between forest type (ANOVA: $F_{1,6} = 0.16$, p = 0.70).