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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>, R. S. Cruz<sup>7</sup> , Annuar Jain<sup>8</sup>, David Johnson<sup>9</sup> , Ully H. Kritzler<sup>9</sup>, Marianne Kuntz<sup>1</sup>, Noreen Majalap-Lee<sup>10</sup>, Nora Mielke<sup>1</sup>, Milenka X. Montoya Pilco<sup>1</sup>, Nicholas J. Ostle<sup>5,6</sup> , Yit Arn Teh<sup>1</sup> , Yadvinder Malhi<sup>2</sup>  and David F. R. P. Burslem<sup>1</sup> 

<sup>1</sup>Institute of Biological and Environmental Sciences, University of Aberdeen, 23 St Machar Drive, Aberdeen, AB24 3UU, UK; <sup>2</sup>Environmental and Rural Science, University of New England, Armidale 2351, NSW, Australia; <sup>3</sup>Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford, OX1 3QY, UK; <sup>4</sup>Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, SL5 7PY, UK; <sup>5</sup>Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster, LA1 4YQ, UK; <sup>6</sup>Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster, LA1 4AP, UK; <sup>7</sup>Instituto de Ciencias de la Naturaleza, Territorio y Energías Renovables, Pontificia Universidad Católica del Perú, Lima, Perú; <sup>8</sup>The South East Asia Rainforest Research Partnership (SEARRP), Danum Valley Field Centre, PO Box 60282, 91112 Lahad Datu, Sabah, Malaysia; <sup>9</sup>School of Earth and Environmental Sciences, The University of Manchester, Oxford Road, Manchester, M13 9PT, UK; <sup>10</sup>Forest Research Centre, Peti Surat 1407, 90715, Sandakan, Sabah, Malaysia

## Summary

Author for correspondence:  
Sabine Both  
Tel: +61 6773 4308  
Email: sboth@une.edu.au

Received: 20 April 2018  
Accepted: 12 August 2018

*New Phytologist* (2019) **221**: 1853–1865  
doi: 10.1111/nph.15444

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

- 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.
- We studied 32 physical, chemical and physiological traits from 284 tree species in eight 1 ha plots 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, nutrient pools, and pH.
- Our finding, that traits have dissimilar 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 facilitated by the measurement of many more functional traits than have been examined in previous studies.

## 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 characterizing the independent effects of human disturbance (McIntyre *et al.*, 1999; Mouillot *et al.*, 2013b; 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 in 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 nitrogen (N) and phosphorus (P) and specific leaf area (SLA) increase in response to gradients of both disturbance (Baraloto *et al.*, 2012; Carreño-Rocabado *et al.*, 2012, 2016) and soil nutrient availability (Fyllas *et al.*, 2009; Fortunel *et al.*, 2014a; Apaza-Quevedo *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, 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  $\delta^{15}\text{N}$  values (provides insight into sources and use of N). Our understanding about the links between trait sensitivity to anthropogenic disturbance, soil properties, and ecosystem processes in tropical forests therefore remains incomplete.

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

Tropical lowland forests in Southeast Asia are amongst the most species-rich communities worldwide, but are also those most threatened by logging and conversion to agriculture (Hansen *et al.*, 2013; Edwards *et al.*, 2014; Stibig *et al.*, 2014). The high density of commercially valuable species explains the high intensity of logging in Southeast Asian forests (Osman *et al.*, 2012; Gaveau *et al.*, 2014), which suffer rates of extraction that far exceed those in tropical forests elsewhere (see Asner *et al.*, 2005 for a discussion of the Brazilian Amazon; and Rutishauser *et al.*, 2015 for a discussion of various sites in the Amazon Basin). Logging creates a spatially patchy disturbance, with gaps and skid trails characterized by high light and temperature distributed among fragments of relatively unmodified forest (Johns, 1997). The selective removal of target species, logging-induced mortality and recruitment of pioneer species in disturbed areas affect tree species composition and the pools and fluxes of biomass and nutrients (Cannon *et al.*, 1998; Verburg & van Eijk-Bos, 2003; Pfeifer *et al.*, 2016; Riutta *et al.*, 2018). Although the magnitude of anthropogenic disturbance is much greater in forests in Southeast Asia than in South America, they have received far less attention regarding the modification of plant functional traits. Specifically, the potential for intense logging to override the

effects of environmental gradients, including soil properties, has not been investigated.

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

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

## Materials and Methods

### Study sites

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

All three areas are part of the Yayasan Sabah Forest Management Area, separated by *c.* 80 km, and belong to a formerly connected area of lowland dipterocarp rainforest characterized by high species richness and many tall, emergent trees. The

region has a moist tropical climate with an annual daily mean temperature of 26.7°C and annual precipitation of approximately 2600–2700 mm (Walsh & Newbery, 1999). Although the climate is aseasonal, there are occasional droughts and dry spells associated with supra-annual El Niño Southern Oscillation events (Walsh & Newbery, 1999; Newbery & Lingenfelder, 2009). The forest soils in Sabah are mostly orthic Acrisols or Ultisols (for more details see Marsh & Greer, 1992; Nainar *et al.*, 2015).

### Sampling design

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

### Soil properties

We measured total nutrients and exchangeable nutrient pools to estimate both long-term nutrient supply as well as plant-available forms. Two randomly located soil cores were taken per plot in 2014–2015. Surface soil (0–10 cm) was analysed for pH, cation exchange capacity and total concentrations of P, carbon (C), N, magnesium (Mg), potassium (K) and calcium (Ca) using the protocols of Quesada *et al.* (2010, 2012). To assess availability of K, Ca, Mg, P, NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>, we measured nutrient supply rates using *in situ* ion exchange membranes (PR<sup>S</sup>™ Probes; Western AG, Saskatoon, Canada). To account for spatial variability we installed four probe pairs (each composed of one cation and anion probe) vertically at corners of three 50 × 50 cm quadrats to 10-cm depth within each of the three subplots used in the

stratified random sampling. These were collected after 2 wk, washed with distilled water and sent to the manufacturer for analysis. They pooled the four probe pairs from each quadrat before elution with 0.5 M HCl for 1 h, yielding 72 samples. NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup> were measured colorimetrically using automated flow injection analysis. All other elements were analysed using inductively coupled plasma mass spectrometry. Results are reported as supply rates over the burial period ( $\mu\text{g } 10 \text{ cm}^{-2} 14 \text{ d}^{-1}$ ).

### Trait measurements

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

### Statistical analyses

To generate a tree-level dataset, replicated leaf-level functional traits were averaged over sun and shade leaves for the few individuals that possessed both. Our results were not significantly different for analyses on sun leaves alone, where available, or otherwise shade leaves, so we combined data from sun and shade leaves together. Leaf chemical properties that are most relevant for photosynthetic activity (Chl $a$ , Chl $b$ , bulk carotenoids, N, and P) were expressed as mass-based as well as area-based values. For 43% of species, multiple individuals were measured and trait values were averaged to generate species-level values. For all analyses, if necessary, species-level leaf traits were log-transformed to improve the normality of residuals. A CWM was calculated for

each trait, weighted by the number of individuals of each species in each plot (Pla *et al.*, 2012). Values of dark respiration fluxes and  $\delta^{13}\text{C}$  were converted to positive values for ease of interpretation. To characterize soil properties in relation to land use, we performed a principal component analysis (PCA) of soil chemical properties across the eight plots with the measurements of total concentrations of P, C, N, Mg, K, Ca, exchangeable Mg, K, Ca,  $\text{NH}_4^+$  and  $\text{NO}_3^-$ , extractable P, pH and cation exchange capacity (CEC). To visualize the distribution of CWM traits across forest types and test Hypothesis 1, we conducted a PCA using centred and standardized CWM trait values for each study plot.

In order to test Hypothesis 2, site scores from the first two PCA axes of soil properties, along with a binary variable representing logging history, were used as predictors in linear models to partition the variance in each CWM trait. The first two principal components (PC1, PC2) from the soil PCA were both statistically independent of logging history (linear model,  $P \geq 0.48$ ). Nevertheless, because the three predictors were weakly but non-significantly intercorrelated ( $R^2 \leq 0.29$ ), we used the hierarchical partitioning method of Chevan & Sutherland (1991), as implemented in the hier.part library of R, to estimate the variance in functional traits explained by each. This technique calculates the  $R^2$  of every possible model, then averages over this set of models to allocate the variance explained by each predictor variable. It thereby overcomes the effect of the order that intercorrelated variables enter a model on the inference of variance explained by each variable (Chevan & Sutherland, 1991). Tests of significance are less informative than partitioning the variance in CWM trait values in this analysis. Nevertheless, given that this analysis generated 99  $P$ -values (three tests on each of 32 functional traits, plus FD), we corrected the  $P$ -values using the false discovery rate (García, 2004).

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

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

## Results

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

The study plots varied substantially in basal area and stem density, with basal area varying fourfold ( $10.9\text{--}41.8\text{ m}^2\text{ ha}^{-1}$ ; Table 1). Basal area was significantly lower in the SL plots, but the range among 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,  $F_{1,6} = 15.26$ ,  $P = 0.008$ ). Stem density ranged from 331 to 565  $\text{ha}^{-1}$ , peaking in plots with intermediate basal area, but was not associated with logging ( $F_{1,6} = 0.02$ ,  $P = 0.90$ ). Species

**Table 1** Study plot description and soil properties ( $\pm$  SD)

Plot name	Location	Total basal area ( $\text{m}^2\text{ ha}^{-1}$ )	Stem density	Number of species	Carbon (C) (%)	Nitrogen (N) (%)	Total phosphorus (P) ( $\text{mg kg}^{-1}$ )	Total Ca ( $\text{mg kg}^{-1}$ )	Total potassium (K) ( $\text{mg kg}^{-1}$ )	Total magnesium (Mg) ( $\text{mg kg}^{-1}$ )	eCEC ( $\text{mmol} + \text{kg}^{-1}$ )	pH ( $\text{H}_2\text{O}$ )	$\text{NO}_3^-$ ( $\mu\text{g } 10\text{cm}^{-2} 14\text{d}^{-1}$ )	$\text{NH}_4^+$ ( $\mu\text{g } 10\text{cm}^{-2} 14\text{d}^{-1}$ )	Exchangeable Ca ( $\mu\text{g } 10\text{cm}^{-2} 14\text{d}^{-1}$ )	Exchangeable Mg ( $\mu\text{g } 10\text{cm}^{-2} 14\text{d}^{-1}$ )	Exchangeable K ( $\mu\text{g } 10\text{cm}^{-2} 14\text{d}^{-1}$ )	Exchangeable P ( $\mu\text{g } 10\text{cm}^{-2} 14\text{d}^{-1}$ )	
Old-growth forest (OG)																			
MLA-01	MBCA	41.8	396	141	1.67	0.14	163.01	50.06	101.03	39.67	36.44	3.95	$59.6 \pm 45.2$	$10.5 \pm 3.11$	$237 \pm 130$	$152 \pm 80.6$	$265 \pm 154$	$0.23 \pm 0.262$	
MLA-02	MBCA	37.3	484	170	2.00	0.17	266.44	194.68	80.62	99.41	43.18	4.25	$184 \pm 103$	$6.37 \pm 1.52$	$417 \pm 476$	$303 \pm 215$	$151 \pm 80.2$	$0.433 \pm 0.325$	
DAN-04	DVCA	30.8	456	128	1.80	0.18	557.21	603.28	16.12	389.63	63.88	5.81	$75.2 \pm 57.2$	$11.9 \pm 12.7$	$480 \pm 596$	$235 \pm 187$	$268 \pm 158$	$0.177 \pm 0.134$	
DAN-05	DVCA	29.1	413	144	1.84	0.17	255.59	140.50	77.03	180.37	44.90	4.46	$154 \pm 164$	$5 \pm 1.88$	$737 \pm 682$	$271 \pm 183$	$305 \pm 269$	$1.03 \pm 1.89$	
Selectively logged forest (SL)																			
SAF-03	SAFE	25.8	565	211	1.89	0.16	231.05	40.42	115.55	38.65	35.66	3.68	$83.8 \pm 63.7$	$26.4 \pm 44.9$	$392 \pm 265$	$318 \pm 201$	$332 \pm 308$	$8.51 \pm 12.4$	
SAF-04	SAFE	19.5	465	188	7.15	0.32	117.07	107.71	67.21	41.36	14.55	3.90	$83.4 \pm 60.5$	$2.68 \pm 4.32$	$1.35 \times 10^3 \pm 621$	$310 \pm 94.1$	$45.1 \pm 58$	$1.18 \pm 1.21$	
SAF-02	SAFE	14.8	416	124	1.51	0.12	137.33	160.50	105.86	41.80	49.38	4.04	$340 \pm 239$	$23.9 \pm 33.2$	$182 \pm 187$	$191 \pm 173$	$401 \pm 239$	$0.464 \pm 0.214$	
SAF-01	SAFE	10.9	331	129	3.08	0.28	375.15	887.03	96.37	266.36	70.76	4.66	$20 \pm 17.5$	$16.8 \pm 18.7$	$212 \pm 269$	$79 \pm 67.6$	$245 \pm 90.6$	$3.03 \pm 2.48$	

Plots are listed by decreasing basal area. Basal area, stem density and number of tree species refers to all tree individuals  $\geq 10$  cm diameter at breast height (dbh). Plot locations are Maliau Basin Conservation Area (MBCA), Danum Valley conservation Area (DVCA) and the Stability of Altered Forest Ecosystem (SAFE) project site. eCEC, effective cation exchange capacity.

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

A PCA of soil chemical properties explained 69.5% on the first two principal axes (Fig. 1). The strongest gradient was defined by variation in total Mg, total P and CEC, whereas the second axis represented a gradient of total C, total N and exchangeable Ca to exchangeable K and  $\text{NH}_4^+$ . Nutrient concentrations varied markedly among plots, including 10-fold and five-fold variation in total Mg and total P concentrations, and nine-fold and 10-fold variation in exchangeable K and  $\text{NH}_4^+$  (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

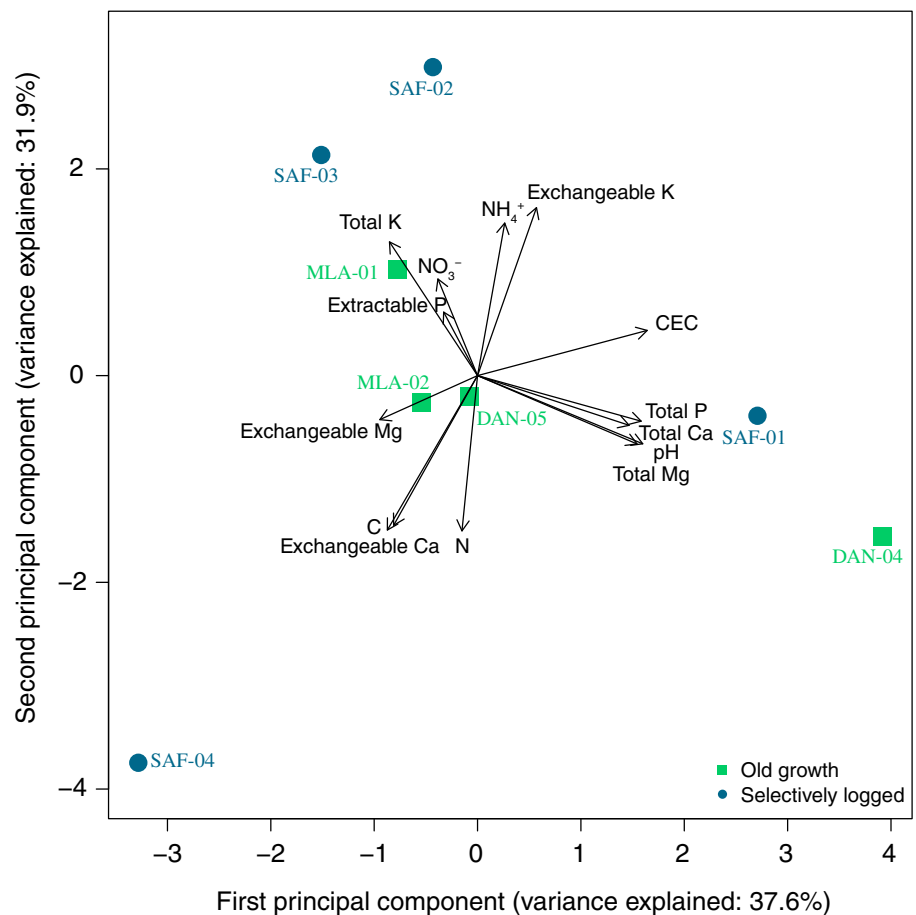
Major gradients in CWM trait expression were visualized by PCA, with the first two axes explaining 77.7% of the variance in functional traits (Fig. 2). There was a clear differentiation of functional composition between OG and SL plots along the first principal component, indicated by a distinct clustering of the study plots. Tree communities in OG plots were characterized 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 maximum photosynthetic rate, light-saturated photosynthetic rate, and dark respiration ( $A_{\text{max}}$ ,  $A_{\text{sat}}$  and  $R_{\text{d}}$ , respectively). These higher rates of gas exchange were supported by the expression of higher CWM area-based pigment concentrations in SL communities and higher  $N_{\text{a}}$ ,  $N_{\text{m}}$  and  $P_{\text{a}}$  concentrations. Tree communities in SL were enriched in  $^{13}\text{C}$  compared with OG communities, indicating greater water-use efficiency.

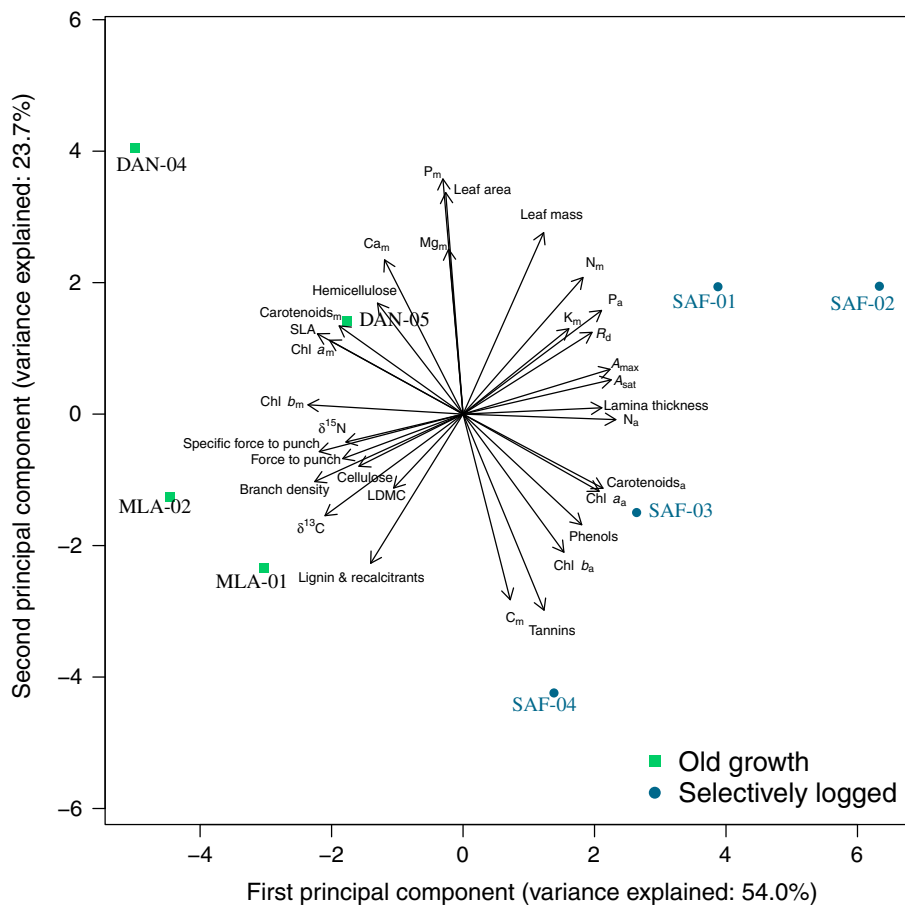
The second axis of functional trait space represented tissue nutrient concentrations and leaf area, but was independent of logging history (Fig. 2). This axis reflects covariation among CWM values of leaf area, leaf  $P_{\text{m}}$ ,  $N_{\text{m}}$ ,  $Mg_{\text{m}}$  and  $Ca_{\text{m}}$  concentrations, and a negative association of these traits with leaf  $C_{\text{m}}$  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 by logging history.

### Variance partitioning

Partitioning the community-level response of traits to logging and the first two principal components of soil properties showed



**Fig. 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 magnesium (Mg) (12.3%) and total phosphorus (P) (12.2%). The highest loadings on the second axis are exchangeable potassium (K) (12.0%), total nitrogen (N) (11.1%) and exchangeable calcium (Ca) (11.1%). See Supporting Information Table S2 for all PCA loadings.



**Fig. 2** Principal component analysis (PCA) of plot-level community-weighted mean functional traits. Plots cluster by logging history, with increased values of traits that maximize 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  $Chl_{b_m}$  (4.44%),  $N_a$  (4.37%), branch wood density (4.25%),  $A_{sat}$  (4.25%),  $A_{max}$  (4.21%) and specific leaf area (SLA; 4.17%). The highest loadings on second axis are  $P_m$  (7.45%), leaf area (7.02%), tannins (6.22%),  $C_m$  (5.88%) and leaf dry weight (5.75%). Mass-based nutrients are denoted by subscript 'm' and area-based values by subscript 'a'. See Supporting Information Table S3 for all PCA loadings.  $R_d$ , dark respiration; LDMC, leaf dry matter content.

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). To present these results, we group the functional traits based on their main association with leaf nutrients, photosynthesis or structure. 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, both with soil PC1 and 2. Particularly soil PC1, enveloping a gradient from exchangeable  $Mg$  to CEC and total P, strongly affected the variance in leaf  $Ca_m$ ,  $P_m$  and  $C_m$ . However, expressed on an 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. For leaf traits related to photosynthesis, 33.5–78.6% of variance was explained by logging and a much smaller proportion by soil PC1 (1.5–21.8%) or soil PC2 (0.9–35.6%; Table S4). Structural traits were explained by a combination of both logging history and the independent effects of soil properties. Logging explained, on average, 39.2% of variance in traits reflecting tissue density and structural investment, such as specific force to punch and branch wood density, which had consistently lower values in logged forest plots. Community-weighted mean LDMC was unusual in that it was poorly explained by all the predictor variables. By contrast, leaf size, expressed as CWM leaf area and leaf mass, increased with increasing values of soil PC1, which was linked to plots with higher total N and exchangeable Ca concentrations

(Fig. 1). There was an increase in CWM tannin concentrations in logged forest plots and at higher values of soil PC1. The CWM values of  $C_m$  and  $N_a$  were significantly explained by the first principal component of soil properties, and forest type, respectively, whereas other traits were statistically independent of the predictors (Fig. 3).

### Functional diversity

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

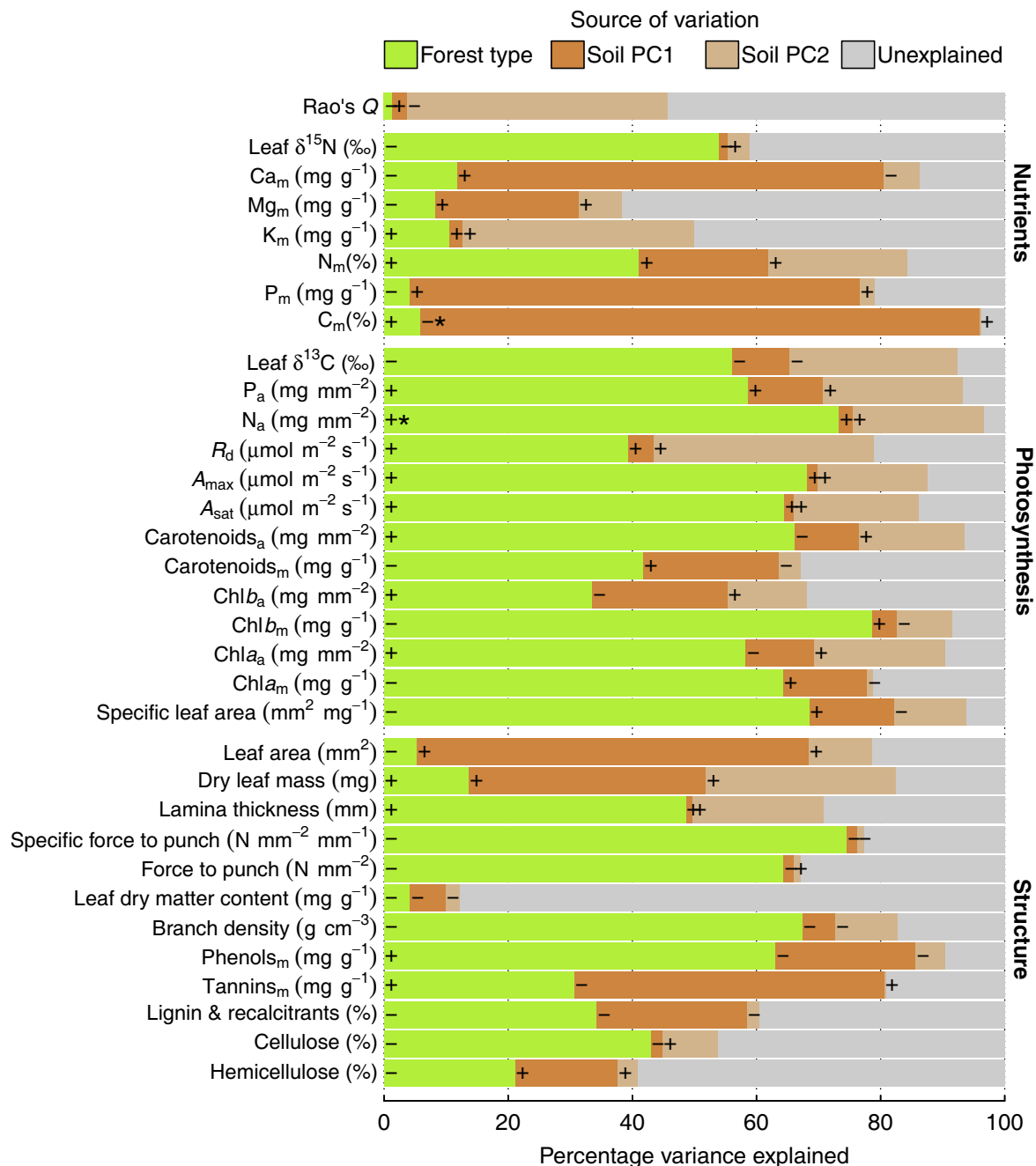
### Discussion

Logging profoundly affected the expression of plant functional traits in Bornean tropical forests. Logging was the primary driver of variation in CWM values of functional traits (Fig. 2), and explained more variation than soil properties for 20 of 32 traits (Fig. 3). Similar impacts of logging on functional trait expression have been demonstrated in Neotropical forests (Baraloto *et al.*,

**Table 2** Results from linear regression models from which the explained variance was generated; factors are the categorical 'forest type' (old growth (OG), selectively logged (SL)), and continuous 'soil PC1' and 'soil PC2'.

Functional trait	Community-weighted mean (CWM) trait value (and 95% CI)				Forest type		Soil PC1		Soil PC2				
	Old growth		Selectively logged		F-value	P-value	F-value	P-value	F-value	P-value			
	Mean	95% CI	Mean	95% CI									
Rao's Q	0.791 (0.735–0.847)		0.789 (0.736–0.842)		0.197	0.748	ns	0.119	0.796	ns	3.060	0.323	ns
$\delta^{15}\text{N}$ (‰)	1.64 (0.966–2.32)		0.846 (0.204–1.49)		5.032	0.215	ns	0.185	0.750	ns	0.527	0.665	ns
$\text{Ca}_m$ (mg g <sup>-1</sup> )	7.09 (6.12–8.2)		6.6 (5.75–7.59)		6.114	0.189	ns	17.555	0.105	ns	1.578	0.441	ns
$\text{Mg}_m$ (mg g <sup>-1</sup> )	2.57 (2.06–3.2)		2.41 (1.96–2.97)		0.724	0.593	ns	1.275	0.469	ns	0.490	0.672	ns
$\text{K}_m$ (mg g <sup>-1</sup> )	9.99 (8.4–11.9)		10.8 (9.13–12.7)		0.923	0.545	ns	0.321	0.725	ns	2.758	0.340	ns
$\text{N}_m$ (%)	1.83 (1.74–1.91)		1.97 (1.89–2.05)		9.191	0.159	ns	7.746	0.163	ns	4.523	0.233	ns
$\text{P}_m$ (mg g <sup>-1</sup> )	0.998 (0.912–1.09)		0.99 (0.909–1.08)		1.484	0.441	ns	13.219	0.129	ns	0.444	0.686	ns
$\text{C}_m$ (%)	44.6 (44.3–44.9)		44.7 (44.4–45)		12.266	0.129	ns	89.717	0.034	*	0.240	0.731	ns
$\delta^{13}\text{C}$ (‰)	-32.4 (-32.1 to -32.8)		-31.4 (-31.1 to -31.8)		28.775	0.064	ns	8.747	0.159	ns	11.356	0.137	ns
$\text{P}_a$ (mg mm <sup>-2</sup> )	6.62 × 10 <sup>-5</sup> (6.21 × 10 <sup>-5</sup> –7.06 × 10 <sup>-5</sup> )		8.04 × 10 <sup>-5</sup> (7.57 × 10 <sup>-5</sup> –8.54 × 10 <sup>-5</sup> )		33.208	0.064	ns	12.267	0.129	ns	10.391	0.139	ns
$\text{N}_a$ (mg mm <sup>-2</sup> )	0.128 (0.12–0.136)		0.166 (0.158–0.174)		97.699	0.034	*	0.520	0.665	ns	19.704	0.094	ns
$R_d$ (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	-1.03 (-0.871 to -1.19)		-1.25 (-1.09 to -1.4)		7.708	0.163	ns	1.546	0.441	ns	5.759	0.199	ns
$A_{\text{max}}$ (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	11.7 (8.94–14.5)		18 (15.4–20.6)		23.237	0.084	ns	0.878	0.553	ns	4.268	0.242	ns
$A_{\text{sat}}$ (μmol CO <sub>2</sub> m <sup>-2</sup> s <sup>-1</sup> )	4.08 (2.66–5.5)		7.03 (5.69–8.38)		20.267	0.094	ns	0.284	0.725	ns	4.495	0.233	ns
Carotenoids <sub>a</sub> (mg mm <sup>-2</sup> )	4.74 × 10 <sup>-5</sup> (4.47 × 10 <sup>-5</sup> –5.02 × 10 <sup>-5</sup> )		5.54 × 10 <sup>-5</sup> (5.28 × 10 <sup>-5</sup> –5.79 × 10 <sup>-5</sup> )		47.726	0.057	ns	1.707	0.437	ns	7.957	0.163	ns
Carotenoids <sub>m</sub> (mg g <sup>-1</sup> )	0.687 (0.667–0.708)		0.667 (0.647–0.687)		6.353	0.189	ns	1.555	0.441	ns	0.264	0.725	ns
Chl <sub>a</sub> (mg mm <sup>-2</sup> )	7.42 × 10 <sup>-5</sup> (6.79 × 10 <sup>-5</sup> –8.04 × 10 <sup>-5</sup> )		7.95 × 10 <sup>-5</sup> (7.36 × 10 <sup>-5</sup> –8.55 × 10 <sup>-5</sup> )		5.552	0.203	ns	1.678	0.437	ns	1.333	0.462	ns
Chl <sub>b</sub> (mg g <sup>-1</sup> )	1.09 (1.05–1.13)		0.97 (0.931–1.01)		40.379	0.062	ns	0.005	0.951	ns	2.605	0.346	ns
Chl <sub>a</sub> (mg mm <sup>-2</sup> )	1.8 × 10 <sup>-4</sup> (1.69 × 10 <sup>-4</sup> –1.92 × 10 <sup>-4</sup> )		2.06 × 10 <sup>-4</sup> (1.95 × 10 <sup>-4</sup> –2.17 × 10 <sup>-4</sup> )		29.141	0.064	ns	1.457	0.441	ns	7.060	0.170	ns
Chl <sub>m</sub> (mg g <sup>-1</sup> )	2.62 (2.54–2.71)		2.49 (2.41–2.57)		13.853	0.129	ns	0.967	0.539	ns	0.020	0.922	ns
Specific leaf area (mm <sup>2</sup> mg <sup>-1</sup> )	16.3 (15.3–17.4)		13.2 (12.2–14.1)		52.069	0.057	ns	3.036	0.323	ns	5.338	0.208	ns
Leaf area (mm <sup>2</sup> )	1.37 × 10 <sup>4</sup> (1.13 × 10 <sup>4</sup> –1.65 × 10 <sup>4</sup> )		1.31 × 10 <sup>4</sup> (1.1 × 10 <sup>4</sup> –1.57 × 10 <sup>4</sup> )		1.678	0.437	ns	11.116	0.137	ns	1.898	0.425	ns
Leaf DW (mg)	922 (784–1.08 × 10 <sup>3</sup> )		1.08 × 10 <sup>3</sup> (930–1.27 × 10 <sup>3</sup> )		2.077	0.401	ns	10.600	0.139	ns	6.120	0.189	ns
Leaf thickness (mm)	0.221 (0.209–0.233)		0.236 (0.224–0.249)		7.196	0.170	ns	0.213	0.743	ns	2.319	0.371	ns
Specific force to punch (N mm <sup>-2</sup> )	1.23 (1.03–1.47)		0.889 (0.751–1.05)		13.209	0.129	ns	0.431	0.686	ns	0.013	0.934	ns
Force to punch (N mm <sup>-1</sup> )	0.266 (0.227–0.311)		0.212 (0.183–0.247)		7.611	0.163	ns	0.300	0.725	ns	0.260	0.725	ns
LDMC (mg g <sup>-1</sup> )	416 (391–440)		410 (387–433)		0.143	0.780	ns	0.332	0.725	ns	0.079	0.827	ns
Branch density (g cm <sup>-3</sup> )	0.564 (0.528–0.599)		0.493 (0.46–0.526)		15.309	0.123	ns	2.442	0.361	ns	1.522	0.441	ns
Phenol <sub>m</sub> (mg g <sup>-1</sup> )	36.4 (33.7–39.1)		42.7 (40.2–45.3)		29.960	0.064	ns	5.004	0.215	ns	2.762	0.340	ns
Tannin <sub>m</sub> (mg g <sup>-1</sup> )	8.56 (7.7–9.41)		9.41 (8.6–10.2)		8.888	0.159	ns	8.069	0.163	ns	0.004	0.951	ns
Lignin and recalcitrants (%)	19.4 (17.3–21.4)		17.3 (15.3–19.2)		2.707	0.340	ns	3.333	0.306	ns	0.080	0.827	ns
Cellulose (%)	22.5 (20.9–24)		20.9 (19.4–22.4)		3.343	0.306	ns	0.313	0.725	ns	0.995	0.538	ns
Hemicellulose (%)	12.3 (11.4–13.1)		11.8 (11–12.6)		1.728	0.437	ns	0.767	0.584	ns	0.270	0.725	ns

For analyses, values of dark respiration  $R_d$  fluxes and  $\delta^{13}\text{C}$  were converted to positive values for ease of interpretation; untransformed values are shown here. For abbreviations and description of the functional traits, see Supporting Information Table S1. ns, not significant; LDMC, leaf dry matter content.

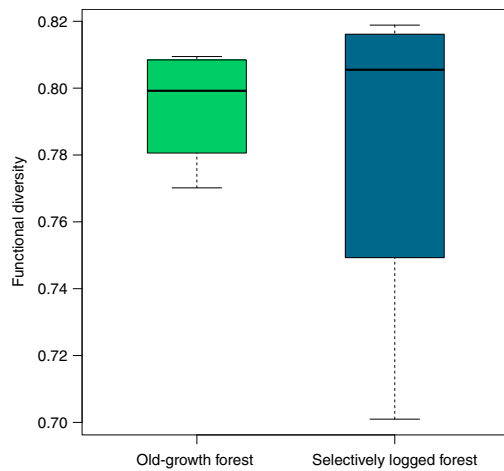


**Fig. 3** Proportion of variance in community-weighted mean functional trait values explained by forest type and the first two principal components (PC) of soil properties (Fig. 1). Functional traits are grouped by the ecosystem function to which they most contribute. Statistical significance is derived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

2012; Carreño-Rocabado *et al.*, 2012), although those studies did not analyse soil-related factors. Together, these studies confirm that CWM traits are highly sensitive to land-use change in tropical forests, but results from our study additionally highlight the relevance of environmental context for trait expression. This is an important outcome in the light of the fact that logging has impacted over half of all tropical forests globally, and over 70%

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





**Fig. 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:  $F_{1,6} = 0.16$ ,  $P = 0.70$ ).

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

We observed lower CWM values of SLA in logged forests, in contrast to results from French Guiana (Baraloto *et al.*, 2012), and contrary to the expectation that SLA scales positively with  $A_{\text{max}}$ , foliar  $N_{\text{a}}$ , and foliar  $P_{\text{a}}$  concentrations among species (Wright *et al.*, 2004). The lack of association

between SLA and other leaf-economic traits is surprising and deserves further study. Microclimatic changes resulting from logging (Hardwick *et al.*, 2015) may filter for species that can resist the potentially desiccating conditions created by logging gaps and decreased canopy height. A reduction in SLA may contribute to photosynthetic water-use efficiency, especially when combined with enhanced investment in photosynthetic enzymes, to ensure draw-down of internal  $\text{CO}_2$  concentrations at a given stomatal conductance (Reich *et al.*, 2003). The greater enrichment of CWM  $\delta^{13}\text{C}$  of logged forest tree communities demonstrates lower discrimination for the heavier  $^{13}\text{C}$  isotope and provides independent evidence of enhanced integrated water-use efficiency for trees in this hotter and drier environment (Farquhar *et al.*, 1989; Rumman *et al.*, 2018). The absence of a shift in SLA in response to logging in French Guianan forests (Baraloto *et al.*, 2012) suggests that logging imposes a more extreme environmental contrast for trees in the less seasonal climate of Borneo. Species that have evolved in a seasonal climate such as that in French Guiana might be better adapted to changes in microclimatic conditions, such as those driven by logging (B. Blonder *et al.*, unpublished). The impact of logging may be more severe in tree communities not adapted to drought and emphasizes the potential sensitivity of Bornean forests to future climatic change. The mean temperature in Borneo is predicted to rise by 0.9–3.2°C, while the annual precipitation in central to western Borneo is predicted to decrease, even as precipitation in northern and north-western Borneo is predicted to increase (i.e. wetter; IPCC, 2013; Scriven *et al.*, 2015).

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

We provide clear evidence that soil properties act on trait expression in two independent ways: the first axis reflected total pools of nutrients, and the second reflected nutrient availability

(Fig. 1). CWM values of leaf area, leaf dry mass and foliar concentrations of  $P_m$ ,  $P_a$ ,  $N_m$  and  $Ca_m$  all increased in response to the first axis of variation in soil properties, whereas leaf  $C_m$  and tannin concentrations decreased along this gradient (Fig. 3). The second component of soil variation also influenced some leaf traits, particularly  $\delta^{13}C$ ,  $N_a$  and  $P_a$  concentrations (Tables 2, S4). Moreover, most traits were influenced by either the first or second axis of variation in soil properties, but rarely both. This finding may reflect a tradeoff in how plants interact with local edaphic conditions, as suggested in other systems (Laliberté *et al.*, 2015); a key future challenge will be to disentangle the mechanisms underpinning these contrasting responses of functional traits to the soil environment. Our results highlight the need to consider the context dependency of drivers of variation in functional traits. Landscape-level predictions of change in functional trait expression in response to anthropogenic disturbance will need to account for the additional effects of soil properties. Our work therefore provides valuable data to the modelling community and will help to address recent calls to integrate empirical data into biogeochemical cycling models (Baker *et al.*, 2017). Recently, it was shown that plant trait diversity permits forests in the Amazon to adapt to new climatic conditions (Sakschewski *et al.*, 2016), and a new trait-based model has explored the influence of climate and soil nutrient availability on primary production and carbon-use efficiency of trees (Fyllas *et al.*, 2014). Our data offer the potential to extend the scope of these models to other critical regions and explore the effects of land use change on key ecosystem functions.

Despite the large variation in CWM traits, FD did not differ between selectively logged and old-growth forest, which is consistent with Hypothesis 3 and with results from Neotropical forests (Fig. 4; Baraloto *et al.*, 2012; Carreño-Rocabado *et al.*, 2012). This finding emphasizes that forests can retain species richness and trait variation, yielding similar FD, despite logging. In line with Mayfield *et al.* (2010), logging did not result in loss of FD but in shifts of numerous CWM trait values, indicating a lower sensitivity of multitrait FD to these changes (Ricotta & Moretti, 2011). FD was more variable among logged forests than among old-growth forests (Fig. 4), probably owing to variation in logging history and intensity, which affect forest structure (Cannon *et al.*, 1994; Berry *et al.*, 2008), microclimatic conditions (Hardwick *et al.*, 2015) and ecosystem functions (Mayfield *et al.*, 2006; Both *et al.*, 2017; Riutta *et al.*, 2018). The substantial variance in FD among the disturbed plots highlights the challenge of predicting the impacts of anthropogenic modification on FD in environments where the outcomes may be highly context-dependent (Costantini *et al.*, 2016).

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

of that uncertainty arises because rare tree species may contribute substantially to resilience (Mouillot *et al.*, 2013a), but tend to be underrepresented in traditional sampling designs adopted for measuring ecosystem functions. Our nested sampling design explicitly resolved this issue by selecting both common and rare, big and small tree species across the full range of size classes. We therefore advocate this approach in future assessments of trait expression at the community scale.

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

## Acknowledgements










We acknowledge financial support by the UK Natural Environment Research Council (NE/K016253/1), with additional support through an ERC Advanced Investigator Award to YM (GEM-TRAIT; 321131). We are indebted to the Sabah Biodiversity Council, Yayasan Sabah, the Maliau Basin and Danum Valley Management Committees, the Institute for Tropical Biology and Conservation at the University of Malaysia, Sabah, and the Sabah Forest Research Centre at Sepilok. We thank Glen Reynolds and the South East Asia Rainforest Research Partnership (SEARRP). This study was supported by funding from the Sime Darby Foundation to the SAFE Project. This project would not have been possible without the indispensable support from dozens of research assistants in Sabah. The support from Laura Kruitbos, Unding Jami, Lisa P. Bentley, Benjamin Blonder, Puikiat Hoo, Palasiah Jotan, Alexander Shenkin and Chun Xing Wong is gratefully acknowledged. We thank Bernadus Bala Ola, Bill McDonald, Alexander Karolus and MinSheng Khoo for species identification. This publication is a contribution from the UK NERC-funded Biodiversity And Land-use Impacts on Tropical Ecosystem Function (BALI) consortium (<http://bali.hmtf.info>) through its Human Modified Tropical Forests thematic programme.

## Author contributions

SB, DFRPB and YM designed the study with input from DJ, NJO and YAT. SB, DMOE, TR, UHK, RC and MXMP collected field data; SB, RC, DMOE, AJ, UHK, MK, NM-L, NM

and MXMP conducted laboratory analyses. SB and CETP analysed the data. SB led the writing of the manuscript with contributions from all co-authors. YAT, DFRPB, DJ, YM and NJO secured the funding. All authors declare no conflict of interest.

## ORCID

Yit Arn Teh  <http://orcid.org/0000-0001-7976-6794>  
 Sabine Both  <http://orcid.org/0000-0003-4437-5106>  
 David F. R. P. Burslem  <http://orcid.org/0000-0001-6033-0990>  
 R. S. Cruz  <http://orcid.org/0000-0003-1463-8278>  
 David Johnson  <http://orcid.org/0000-0003-2299-2525>  
 Yadvinder Malhi  <http://orcid.org/0000-0002-3503-4783>  
 Nicholas J. Ostle  <http://orcid.org/0000-0003-3263-3702>  
 C. E. Timothy Paine  <http://orcid.org/0000-0001-8705-3719>  
 Terhi Riutta  <http://orcid.org/0000-0002-8308-5307>

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

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

**Methods S1** Detailed description of the trait measurements.

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

**Table S2** Loadings of the soil environmental variables in the principal component analysis.

**Table S3** Loadings of the community-weighted mean traits in the principal component analysis.

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

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