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

Sabine Both1, Terhi Riutta2,3, C. E. Timothy Paine4, Dafydd M. O. Elias5,6, Rudi Chino7, Annuar Jain8, David Johnson9, Ully H. Kritzler9, Marianne Kuntz1, Noreen Majalap-Lee10, Nora Mielke1, Milenka X. Montoya Pillco1, Nicholas J. Ostle5,6, Yit A. Teh1, Yadavinder Malhi2, David F. R. P. Burslem1

1 Institute of Biological and Environmental Sciences, University of Aberdeen, 23 St Machar Drive, Aberdeen, AB24 3UU, United Kingdom
2 Environmental Change Institute, School of Geography and the Environment, University of Oxford, South Parks Road, Oxford, OX1 3QY, United Kingdom
3 Imperial College London, Department of Life Sciences, Silwood Park Campus, Buckhurst Road, Ascot, SL5 7PY, United Kingdom
4 Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA, United Kingdom
5 Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster, LA1 4YQ, United Kingdom
6 Centre for Ecology & Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg, Lancaster, LA1 4AP, United Kingdom
7 Instituto de Ciencias de la Naturaleza, Territorio y Energías Renovables, Pontificia Universidad Católica del Perú, Lima, Perú
8 The South East Asia Rainforest Research Partnership (SEARRP), Danum Valley Field Centre, PO Box 60282, 91112, Lahad Datu, Sabah, Malaysia
9 School of Earth and Environmental Sciences, The University of Manchester, Oxford Road, Manchester, M13 9PT, United Kingdom
10 Forest Research Centre, Peti Surat 1407, 90715 Sandakan, Sabah, Malaysia

*Author for correspondence:
Sabine Both
Tel: +44 1224274257
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 (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 $\delta^{15}$N values (provides insight into sources and use of nitrogen). 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 due to 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 but additionally aim to determine the influence of soil properties including nutrient availability.

Tropical lowland forests in Southeast Asia are amongst the most species-rich communities worldwide, but are also the most threatened by intensive 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 (Asner et al. 2005). Logging creates a spatially patchy disturbance, with gaps and skid trails characterised 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 affects 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 significantly less attention regarding the modification of plant functional traits. Specifically, intense logging has the potential to override the effects of other environmental gradients including soil properties.

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 assess traits reflecting nutrient status, light capture and photosynthesis, and allocation to structure and defence to provide a whole-plant perspective and avoid overlooking traits that contribute to functional diversity. We tested the hypothesis that CWM values of functional traits and functional diversity shift in response to anthropogenic disturbance and soil properties. We used CWM traits to quantify average trait values, and a multi-trait index of functional diversity (FD) to quantify trait variation, which can occur independent of variation in CWM values of trait (Ricotta & Moretti 2011).
Specifically, we predict that (1) 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. Given the high logging intensity in Southeast Asia, we further hypothesise that (2) 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. Finally, due to the high overall tree species richness we predict that (3) functional diversity will remain high in response to disturbance, despite shifts in overall CWM traits.

Material 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 (MBCA, two plots) and the Danum Valley Conservation Area (DVCA, 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 to four times with the first round of logging in the mid-1970s and subsequent repeated logging during 1990-2008. Approximately 150–179 m$^3$ ha$^{-1}$ of timber was removed over this time period (Struebig et al. 2013), bracketing the mean extraction volume across Sabah (152 m$^3$ ha$^{-1}$, Fisher et al. 2011).

All three areas are part of the Yayasan Sabah Forest Management Area and belong to a formerly connected area of lowland dipterocarp rainforest characterised 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 ≥ 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 to 2015), which ranged from 10.9–
41.8 m² ha⁻¹. 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 ≥ 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 understory 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 ≥ 10 cm dbh (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, C, N, Mg, K and Ca using the protocols of Quesada et al. (2010, 2012). To assess availability of K,
Ca, Mg, P, NO₃⁻ and NH₄⁺ we measured nutrient supply rates using in-situ ion exchange membranes
(PRSTM 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 two weeks, washed with distilled water and sent to the manufacturer for
analysis. They pooled the four probe pairs from each quadrat prior to elution with 0.5M HCl for 1 hr,
yielding 72 samples. NO₃⁻ and NH₄⁺ were measured colorimetrically using automated flow injection
analysis (FIA). All other elements were analysed using Inductively Coupled Plasma Mass
Spectrometry (ICP-MS). Results are reported as supply rates over the burial period (micrograms/10
cm²/14 days).
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 m to 53 m. Branches were approximately 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 due to 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, $\delta^{13}$C and $\delta^{15}$N stable isotope composition, cellulose, hemicellulose and lignin concentrations. Analyses of pigments (chlorophyll a, chlorophyll 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 nitrogen. Herbarium voucher specimens were taken for identification of trees and were deposited in the herbarium at Danum Valley Field Centre. All trait measurements follow standardised protocols (Pérez-Harguindeguy et al. 2013), and detailed methods and an overview of sampling and replication are provided in Table S1.

Statistical analyses

Replicated leaf-level functional traits were averaged for sun and shade leaves for the few individuals that possessed both to generate a tree-level dataset. Our results were identical for analyses using a data-set comprising sun leaves alone, where available, or otherwise shade leaves, so henceforth we use both sun and shade leaves together. Leaf chemical properties that are most relevant for photosynthetic activity were expressed as mass-based as well as area-based values (chlorophyll a, chlorophyll b, bulk carotenoids, N, and P). For all analyses, if necessary, leaf traits were log-transformed to improve the normality of residuals. A CWM was calculated for each trait, weighted by the abundance of each species in each plot (Pla et al. 2012). Values of dark respiration fluxes and $\delta^{13}$C were converted to positive values for ease of interpretation. To characterise 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, NH$_4^+$ and NO$_3^-$, extractable P, pH and cation exchange capacity (CEC). To
visualise the distribution of CWM traits across forest types and test hypothesis 1, we conducted a
PCA using centred and standardised 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 multiple regression models
to partition the variance in each CWM trait. The first two principal components 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 inter-correlated ($R^2 \leq 0.29$), we used the
hierarchical partitioning method of Chevan and 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 inter-
correlated variables enter a model on the inferred variance explained by each variable (Chevan &
Sutherland 1991).

To address hypothesis 3, we computed plot-level values of functional diversity (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) and compared 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 (BA) and stem density, with BA varying fourfold
(10.9 m$^2$ - 41.8 m$^2$ 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 ± 12.7, OG 34.8 ± 14.9 m$^2$ ha$^{-1}$;
ANOVA: $F_{1,6} = 15.26, p = 0.008$). Stem density ranged from 331 to 565 ha$^{-1}$, peaking in plots with
intermediate BA but was not associated with logging ($F_{1,6} = 0.02, p = 0.90$). Species richness was
similar in OG and SL plots, ranging from 124 to 211 tree species 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 NH$_4^+$. Nutrient
concentrations varied markedly among plots, including 10-fold and 5-fold variation in total Mg and
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 $A_{\text{max}}$ and $A_{\text{sat}}$ 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
axis (Fig. 1). 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%), see 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 the predictor variables. In contrast, leaf size, expressed as CWM leaf area and leaf mass, increased significantly with increasing values of soil PC1, which was linked to plots with higher total N and exchangeable Ca concentrations (Fig. 1). There was a significant increase in CWM tannin concentrations in logged forest plots and at higher values of soil PC1.

**Functional diversity**

Functional diversity, expressed as Rao’s Q, was similar 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). Variance in FD was greater among SL than OG forests (Fig. 4), indicating 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. 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 context dependency of trait expression. 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. Effects on other trophic levels are also likely. For example, herbivorous insects are sensitive to leaf traits such as LDMC and phenol concentrations (Hevia et al. 2017). 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).

In our study, the principal axis of functional trait space defined a clear gradient from values of traits that maximise 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, trees 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 recruitment 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 $R_d$, whereas old-growth forest communities were characterised by higher values of traits conferring structural stability of wood and leaves.

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 $A_{\text{max}}$ and foliar N and P concentrations among species (Wright et al. 2004). The decoupling of SLA from other leaf-economic traits may be explained by the abundance of pioneer species, which recruit following disturbance and are adapted to resist the more exposed and potentially desiccating conditions created by logging (Hardwick et al. 2015). 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 CO$_2$ concentrations at a given stomatal conductance (Reich et al. 2003). The greater enrichment of CWM $\delta^{13}$C of logged forest tree communities demonstrates lower discrimination for the heavier $^{13}$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 growing in the less seasonal climate of Borneo than in seasonal French Guiana. The impact of logging may be more severe in tree communities not adapted to drought and emphasises the potential sensitivity of Bornean forests to future climatic change.

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.

Moreover, 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). Community-weighted mean values of leaf area, leaf dry mass and foliar
concentrations of P_m, P_a, N_m and Ca_m all increased significantly 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
δ^{13}C, N_a and P_a concentrations (Table 2, Table S4). Moreover, most traits were influenced either by the first
or second axis of variation in soil properties, but rarely both. This finding may reflect a trade-off in
how plants interact with local edaphic conditions, as suggested in other systems (Laliberte 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.

Despite the large variation in CWM traits, FD did not differ between logged and old-growth
forest, which is consistent with our third hypothesis and results from Neotropical forests (Fig. 4;
Baraloto et al. 2012; Carreño-Rocabado et al. 2012). This finding emphasises 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 multi-trait FD to these changes (Ricotta & Moretti 2011). FD was more variable
among logged forests than old-growth forests, 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 exert 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 et al. 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. 2013b), but tend to be under-represented in traditional sampling designs adopted for measuring ecosystem functions. Our nested sampling design explicitly resolved this issue by selecting both common and rare 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 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

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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, DB and YM designed the study with input from DJ, NO and YAT. SB, DE, TR, UHK, RC and MMP collected field data, SB, RC, DE, AJ, UHK, MK, NML, NM and MMP conducted laboratory analyses. SB and CETP analysed the data. SB led the writing of the manuscript with contributions from all co-authors. YAT, DB, DJ, YM and NO secured the funding. All authors declare no conflict of interest.
References


For Peer Review


Figure captions

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<sub>m</sub> (4.44%), N<sub>a</sub> (4.37%), branch wood density (4.25%), A<sub>sat</sub> (4.25%), A<sub>max</sub> (4.21%) and SLA (4.17%). The highest loadings on second axis are P<sub>m</sub> (7.45%), LA (7.02%), tannins (6.22%), C<sub>m</sub> (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<sub>1,6</sub> = 0.16, p = 0.70).
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.

<table>
<thead>
<tr>
<th>Plot name</th>
<th>Location</th>
<th>Total basal area [m² ha⁻¹]</th>
<th>Stem density of species [stem ha⁻¹]</th>
<th>Number of species</th>
<th>C [%]</th>
<th>N [%]</th>
<th>Total P [µg 10 cm⁻² 14 days⁻¹]</th>
<th>Total Ca [mg kg⁻¹]</th>
<th>Total Mg [mg kg⁻¹]</th>
<th>Total K [mg kg⁻¹]</th>
<th>eCEC [mmol kg⁻¹]</th>
<th>pH (H₂O)</th>
<th>NO₃⁻ [µg 10 cm⁻² 14 days⁻¹]</th>
<th>NH₄⁺ [µg 10 cm⁻² 14 days⁻¹]</th>
<th>Exchangable Ca [µg 10 cm⁻² 14 days⁻¹]</th>
<th>Exchangable Mg [µg 10 cm⁻² 14 days⁻¹]</th>
<th>Exchangable K [µg 10 cm⁻² 14 days⁻¹]</th>
<th>Extractable P [µg 10 cm⁻² 14 days⁻¹]</th>
</tr>
</thead>
<tbody>
<tr>
<td>MLA-01</td>
<td>MBCA</td>
<td>41.8</td>
<td>396</td>
<td>141</td>
<td>1.67</td>
<td>0.14</td>
<td>163.01</td>
<td>50.06</td>
<td>101.03</td>
<td>39.67</td>
<td>36.44</td>
<td>3.95</td>
<td>59.6 ± 45.2</td>
<td>10.5 ± 3.11</td>
<td>237 ± 130</td>
<td>152 ± 80.6</td>
<td>265 ± 154</td>
<td>0.23 ± 0.262</td>
</tr>
<tr>
<td>MLA-02</td>
<td>MBCA</td>
<td>37.3</td>
<td>484</td>
<td>170</td>
<td>2.00</td>
<td>0.17</td>
<td>266.44</td>
<td>194.68</td>
<td>60.62</td>
<td>99.41</td>
<td>43.18</td>
<td>4.25</td>
<td>184 ± 103</td>
<td>6.37 ± 1.52</td>
<td>417 ± 476</td>
<td>303 ± 215</td>
<td>151 ± 80.2</td>
<td>0.43 ± 0.325</td>
</tr>
<tr>
<td>DAN-04</td>
<td>DVCA</td>
<td>30.8</td>
<td>456</td>
<td>128</td>
<td>1.80</td>
<td>0.18</td>
<td>557.21</td>
<td>603.28</td>
<td>16.12</td>
<td>389.63</td>
<td>63.88</td>
<td>5.81</td>
<td>75.2 ± 57.2</td>
<td>11.9 ± 12.7</td>
<td>480 ± 596</td>
<td>235 ± 187</td>
<td>268 ± 158</td>
<td>0.17 ± 0.134</td>
</tr>
<tr>
<td>DAN-05</td>
<td>DVCA</td>
<td>29.1</td>
<td>413</td>
<td>144</td>
<td>1.84</td>
<td>0.17</td>
<td>255.59</td>
<td>140.50</td>
<td>77.03</td>
<td>180.37</td>
<td>44.90</td>
<td>4.46</td>
<td>154 ± 164</td>
<td>5 ± 1.88</td>
<td>737 ± 682</td>
<td>271 ± 183</td>
<td>305 ± 269</td>
<td>1.03 ± 1.89</td>
</tr>
<tr>
<td>SAF-03</td>
<td>SAFE project</td>
<td>25.8</td>
<td>565</td>
<td>211</td>
<td>1.89</td>
<td>0.16</td>
<td>231.05</td>
<td>40.42</td>
<td>115.55</td>
<td>38.65</td>
<td>35.66</td>
<td>3.68</td>
<td>83.8 ± 63.7</td>
<td>26.4 ± 44.9</td>
<td>392 ± 265</td>
<td>318 ± 201</td>
<td>332 ± 308</td>
<td>8.51 ± 12.4</td>
</tr>
<tr>
<td>SAF-04</td>
<td>SAFE project</td>
<td>19.5</td>
<td>465</td>
<td>188</td>
<td>7.15</td>
<td>0.32</td>
<td>117.07</td>
<td>107.71</td>
<td>67.21</td>
<td>41.36</td>
<td>14.55</td>
<td>3.90</td>
<td>83.4 ± 60.5</td>
<td>2.68 ± 4.32</td>
<td>1.35 ± 10³ ± 621</td>
<td>310 ± 94.1</td>
<td>45.1 ± 58</td>
<td>1.18 ± 1.21</td>
</tr>
<tr>
<td>SAF-02</td>
<td>SAFE project</td>
<td>14.8</td>
<td>416</td>
<td>124</td>
<td>1.51</td>
<td>0.12</td>
<td>137.33</td>
<td>160.50</td>
<td>105.86</td>
<td>41.80</td>
<td>49.38</td>
<td>4.04</td>
<td>340 ± 239</td>
<td>23.9 ± 33.2</td>
<td>182 ± 187</td>
<td>191 ± 173</td>
<td>401 ± 239</td>
<td>0.464 ± 0.214</td>
</tr>
<tr>
<td>SAF-01</td>
<td>SAFE project</td>
<td>10.9</td>
<td>331</td>
<td>129</td>
<td>3.08</td>
<td>0.28</td>
<td>375.15</td>
<td>887.03</td>
<td>96.37</td>
<td>266.36</td>
<td>70.76</td>
<td>4.66</td>
<td>20 ± 17.5</td>
<td>16.8 ± 18.7</td>
<td>212 ± 269</td>
<td>79 ± 67.6</td>
<td>245 ± 90.6</td>
<td>3.03 ± 2.48</td>
</tr>
</tbody>
</table>
Table 2: Results from linear regression models from which the explained variance was generated, factors are the categorical ‘forest type’ (OG – old-growth, SL – selectively logged), and continuous ‘soil PC1’ and ‘soil PC2’. For analyses values of dark respiration $R_d$ fluxes and $\delta^{13}C$ were converted to positive values for ease of interpretation, here untransformed values are shown. For abbreviations and description of the functional traits, see table S1.

<table>
<thead>
<tr>
<th>Functional trait</th>
<th>CWM trait value (and 95% confidence intervals)</th>
<th>Forest type</th>
<th>soil PC1</th>
<th>soil PC2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>OG (1.69<em>10^{-5} - 1.1</em>10^{-5})</td>
<td>SL (7.95<em>10^{-5} - 8.55</em>10^{-5})</td>
<td>F-value</td>
<td>p-value</td>
</tr>
<tr>
<td>Rao’s Q</td>
<td>0.791 (0.735 - 0.847)</td>
<td>0.789 (0.736 - 0.842)</td>
<td>0.197</td>
<td>0.680 ns</td>
</tr>
<tr>
<td>$\delta^{15}N$ [%]</td>
<td>6.62<em>10^{-5} (6.21</em>10^{-5} - 7.06*10^{-5})</td>
<td>8.04<em>10^{-5} (7.57</em>10^{-5} - 8.54*10^{-5})</td>
<td>33.208</td>
<td>0.005 **</td>
</tr>
<tr>
<td>$N_a$ [%]</td>
<td>0.128 (0.12 - 0.136)</td>
<td>0.166 (0.158 - 0.174)</td>
<td>97.699</td>
<td>0.001 ***</td>
</tr>
<tr>
<td>$R_o$ [μmol CO$_2$ m$^{-2}$ s$^{-1}$]</td>
<td>4.08 (2.66 - 5.5)</td>
<td>7.03 (5.69 - 8.38)</td>
<td>20.267</td>
<td>0.011 *</td>
</tr>
<tr>
<td>Carotenoids$_a$ [mg mm$^{-2}$]</td>
<td>5.44<em>10^{-5} (5.28</em>10^{-5} - 5.79*10^{-5})</td>
<td>5.72<em>10^{-5} (5.54</em>10^{-5} - 5.92*10^{-5})</td>
<td>47.726</td>
<td>0.002 **</td>
</tr>
<tr>
<td>Carotenoids$_b$ [mg mm$^{-2}$]</td>
<td>0.687 (0.667 - 0.708)</td>
<td>0.667 (0.647 - 0.678)</td>
<td>6.353</td>
<td>0.065 ns</td>
</tr>
<tr>
<td>Chlorophyll a$_b$ [mg mm$^{-2}$]</td>
<td>7.42<em>10^{-5} (7.69</em>10^{-5} - 8.04*10^{-5})</td>
<td>7.95<em>10^{-5} (7.36</em>10^{-5} - 8.55*10^{-5})</td>
<td>5.552</td>
<td>0.078 ns</td>
</tr>
<tr>
<td>Chlorophyll b$_b$ [mg mm$^{-2}$]</td>
<td>1.09 (1.05 - 1.13)</td>
<td>0.97 (0.931 - 1.01)</td>
<td>40.379</td>
<td>0.003 **</td>
</tr>
<tr>
<td>Chlorophyll a$_a$ [mg mm$^{-2}$]</td>
<td>1.8<em>10^{-5} (1.69</em>10^{-5} - 1.92*10^{-5})</td>
<td>2.06<em>10^{-5} (1.95</em>10^{-5} - 2.17*10^{-5})</td>
<td>29.141</td>
<td>0.006 **</td>
</tr>
<tr>
<td>Chlorophyll a$_b$ [mg mm$^{-2}$]</td>
<td>2.62 (2.54 - 2.71)</td>
<td>2.49 (2.41 - 2.57)</td>
<td>13.853</td>
<td>0.020 *</td>
</tr>
<tr>
<td>SLA [mm$^2$ mg$^{-1}$]</td>
<td>16.3 (15.6 - 17.4)</td>
<td>13.2 (12.2 - 14.1)</td>
<td>52.069</td>
<td>0.002 **</td>
</tr>
<tr>
<td>LA [mm$^2$]</td>
<td>1.37<em>10^{-5} (1.13</em>10^{-5} - 1.65*10^{-5})</td>
<td>1.31<em>10^{-5} (1.11</em>10^{-5} - 1.57*10^{-5})</td>
<td>1.678</td>
<td>0.265 ns</td>
</tr>
<tr>
<td>Leaf dry weight [mg]</td>
<td>922 (784 - 1.08*10^{-5})</td>
<td>1.08<em>10^{-5} (930 - 1.27</em>10^{-5})</td>
<td>2.077</td>
<td>0.223 ns</td>
</tr>
<tr>
<td>Leaf thickness [mm]</td>
<td>0.221 (0.209 - 0.233)</td>
<td>0.236 (0.224 - 0.249)</td>
<td>7.196</td>
<td>0.055 ns</td>
</tr>
<tr>
<td>Specific force to punch [N mm$^{-2}$]</td>
<td>1.23 (1.03 - 1.47)</td>
<td>0.889 (0.751 - 1.05)</td>
<td>13.209</td>
<td>0.022 *</td>
</tr>
<tr>
<td>Force to punch [N mm$^{-2}$]</td>
<td>0.266 (0.227 - 0.311)</td>
<td>0.212 (0.183 - 0.247)</td>
<td>7.611</td>
<td>0.051 ns</td>
</tr>
<tr>
<td>LDMC [mg g$^{-1}$]</td>
<td>416 (391 - 440)</td>
<td>410 (387 - 433)</td>
<td>0.143</td>
<td>0.725 ns</td>
</tr>
<tr>
<td>Branch density [g cm$^{-3}$]</td>
<td>0.564 (0.528 - 0.599)</td>
<td>0.493 (0.46 - 0.526)</td>
<td>15.309</td>
<td>0.017 *</td>
</tr>
<tr>
<td>Phenol$_a$ [mg g$^{-1}$]</td>
<td>36.4 (33.7 - 39.1)</td>
<td>42.7 (40.2 - 45.3)</td>
<td>29.960</td>
<td>0.005 **</td>
</tr>
<tr>
<td>Tannins$_a$ [mg g$^{-1}$]</td>
<td>8.56 (7.7 - 9.41)</td>
<td>9.41 (8.6 - 10.2)</td>
<td>8.888</td>
<td>0.041 *</td>
</tr>
<tr>
<td>Lignin &amp; recalcitrants [%]</td>
<td>19.4 (17.3 - 21.4)</td>
<td>17.5 (15.3 - 19.2)</td>
<td>2.707</td>
<td>0.175 ns</td>
</tr>
<tr>
<td>Cellulose [%]</td>
<td>22.5 (20.9 - 24)</td>
<td>20.9 (19.4 - 22.4)</td>
<td>3.343</td>
<td>0.142 ns</td>
</tr>
<tr>
<td>Hemicellulose [%]</td>
<td>12.3 (11.4 - 13.1)</td>
<td>11.8 (11.2 - 12.6)</td>
<td>1.728</td>
<td>0.259 ns</td>
</tr>
</tbody>
</table>
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.
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Figure 4: Box-and-whisker plots showing the median, upper and lower quartile of functional diversity calculated as Rao’s Q with no significant difference between forest type (ANOVA: $F_{1,6} = 0.16$, $p = 0.70$).