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

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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, 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.

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

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

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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).

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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 $m^2 ha^{-1}$. 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, NO_3^- and NH_4^+ 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. NO_3^- and NH_4^+ 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 cm^2/14 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, δ^{13}C and δ^{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 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 (chlorophyll a, chlorophyll 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 result in 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 δ^{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 linear 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 inference of variance explained by each variable (Chevan & Sutherland 1991). Tests of significance are less important than partitioning the variance in CWM trait values in this analysis. Nevertheless, given that this analysis generated 99 p-values (3 tests on each of 32 functional traits, plus functional diversity), we corrected the p-values using the false discovery rate (García 2004).

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). 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 (BA) and stem density, with BA varying fourfold (10.9 m - 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, and 9-fold and 10-fold variation in exchangeable K and 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).

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Community-weighted mean traits

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

The second axis of functional trait space represented tissue nutrient concentrations and leaf area but was independent of logging history (Fig. 2). This axis reflects covariance 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

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). 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 cation exchange capacity (CEC) and total P, strongly affected the variance in leaf Ca_m, P_m, C_m. 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. 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 the predictor variables. In contrast, leaf size, expressed as CWM leaf area and leaf mass, incr eased 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, 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). The main proportion of variance was explained by soil PC2. The negative relationship with soil PC2 indicates xxx. Variability in FD was greater among SL than OG forests (Fig. 4), potentially 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 community-weighted mean (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 considerable relevance of the 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).

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, 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 add to previous results by additionally demonstrating that logged forest communities expressed higher CWM values of $A_{sat,}$ A_{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 specific leaf area (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 $A_{max,}$ foliar N_a, and foliar P_a concentrations among species (Wright *et al.* 2004). The lack of association between SLA and 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). Greater enrichment of CWM $\delta^{13}C$ of logged forest tree communities demonstrates reduced 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 occurring in the less seasonal climate of Borneo. Species that have evolved in a seasonal climate such as in French Guiana, may be better adapted to changes in microclimatic conditions, like those driven by logging (Blonder *et al.,* unpublished data). 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. Mean temperature for Borneo is predicted to rise by 0.9 – 3.2 °C, annual precipitation is predicted to become increasingly drier in central to western Borneo and wetter in northern and north-western Borneo (ICCP 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). 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 below-ground microbial diversity and ecosystem functions are largely unknown.

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 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 (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.

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Despite the large variation in CWM traits, functional diversity (FD) did not differ between logged and old-growth forest, which is consistent with our third hypothesis and with 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 (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 *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 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.

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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.

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Figure captions

Figure 1: Principal component analysis (PCA) of plot-level soil properties. 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: Principal component analysis (PCA) of plot-level community-weighted mean functional traits. Plots cluster by logging history, with increased values of traits that maximise carbon capture and growth in logged forest communities and greater allocation to tissue persistence and structural stability in old-growth forests. The highest loadings on the first axis are chlorophyll b_m (4.44%), N_a (4.37%), branch wood density (4.25%), A_{sat} (4.25%), A_{max} (4.21%) and SLA (4.17%). The highest loadings on second axis are P_m (7.45%), LA (7.02%), tannins (6.22%), C_m (5.88%) and leaf dry weight (5.75%). Mass-based nutrients are denoted by superscript “m” and area-based values by superscript “a”. See Table S3 for all PCA loadings.

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

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: $F_{1,6} = 0.16$, $p = 0.70$).

Tables

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

Plot name	Location	Total basal area [m^2 ha^{-1}]	Stem density	Number of species	C [%]	N [%]	Total P [mg kg^{-1}]	Total Ca [mg kg^{-1}]	Total K [mg kg^{-1}]	Total Mg [mg kg^{-1}]	eCEC [$mmol^+$ kg^{-1}]	pH (H_2O)	NO_3^- [μg 10 cm^2 14 $days^{-1}$]	NH_4^+ [μg 10 cm^2 14 $days^{-1}$]	Exchangable Ca [μg 10 cm^2 14 $days^{-1}$]	Exchangable Mg [μg 10 cm^2 14 $days^{-1}$]	Exchangable K [μg 10 cm^2 14 $days^{-1}$]	Extractable [μg 10 cm^2 14
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 ± 45.2	10.5 ± 3.11	237 ± 130	152 ± 80.6	265 ± 154	0.23 ± 0.2
MLA-02	MBCA	37.3	484	170	2.00	0.17	266.44	194.68	80.62	99.41	43.18	4.25	184 ± 103	6.37 ± 1.52	417 ± 476	303 ± 215	151 ± 80.2	0.433 ± 0.3
DAN-04	DVCA	30.8	456	128	1.80	0.18	557.21	603.28	16.12	389.63	63.88	5.81	75.2 ± 57.2	11.9 ± 12.7	480 ± 596	235 ± 187	268 ± 158	0.177 ± 0.1
DAN-05	DVCA	29.1	413	144	1.84	0.17	255.59	140.50	77.03	180.37	44.90	4.46	154 ± 164	5 ± 1.88	737 ± 682	271 ± 183	305 ± 269	1.03 ± 1.8
Selectively logged forest (SL)																		
SAF-03	SAFE project	25.8	565	211	1.89	0.16	231.05	40.42	115.55	38.65	35.66	3.68	83.8 ± 63.7	26.4 ± 44.9	392 ± 265	318 ± 201	332 ± 308	8.51 ± 12
SAF-04	SAFE project	19.5	465	188	7.15	0.32	117.07	107.71	67.21	41.36	14.55	3.90	83.4 ± 60.5	2.68 ± 4.32	$1.35*10^3$ ± 621	310 ± 94.1	45.1 ± 58	1.18 ± 1.2
SAF-02	SAFE project	14.8	416	124	1.51	0.12	137.33	160.50	105.86	41.80	49.38	4.04	340 ± 239	23.9 ± 33.2	182 ± 187	191 ± 173	401 ± 239	0.464 ± 0.2
SAF-01	SAFE project	10.9	331	129	3.08	0.28	375.15	887.03	96.37	266.36	70.76	4.66	20 ± 17.5	16.8 ± 18.7	212 ± 269	79 ± 67.6	245 ± 90.6	3.03 ± 2.4

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.

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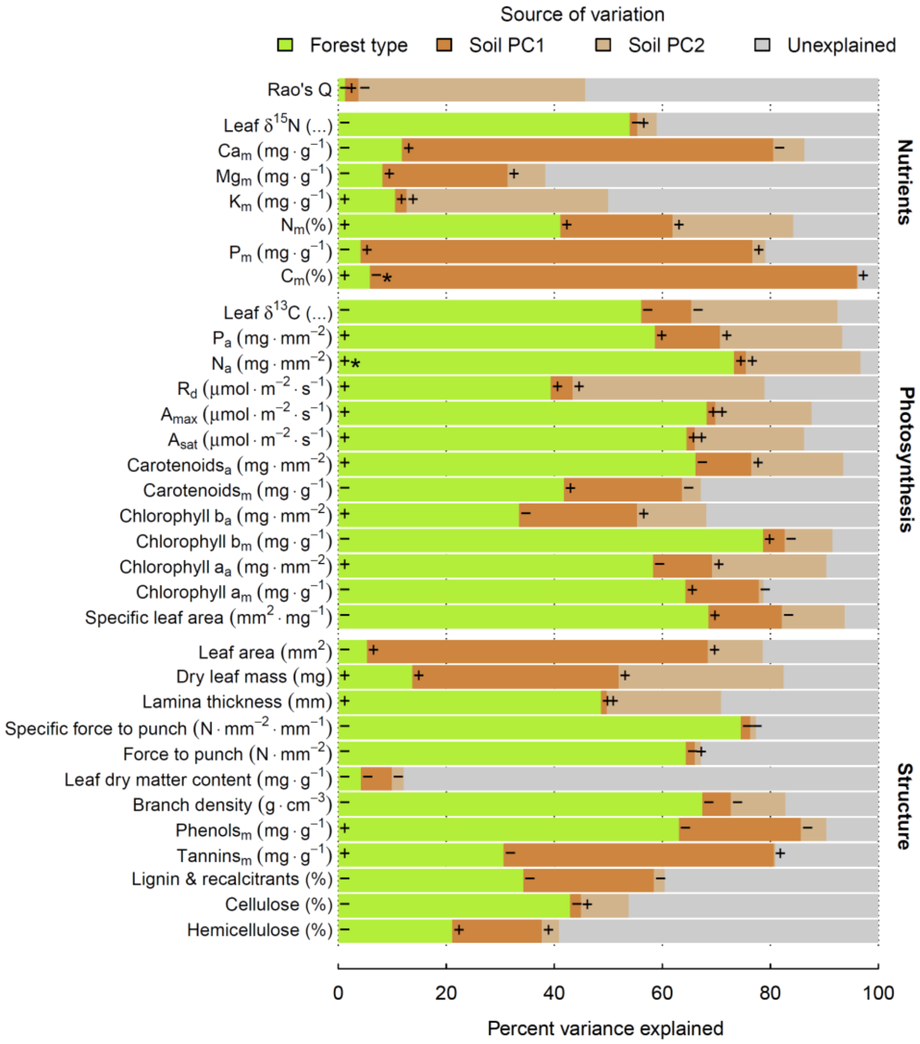
	CWM trait value (95% confindence intervals)		Forest type			Soil PC1			Soil PC2		
Functional trait	OG	SL	F value	p-value		F value	p-value		F value	p-value	
hemicellulose_perc	12.3 (11.4 - 13.1)	11.8 (11 - 12.6)	1.7284	0.4371	ns	0.7672	0.5839	ns	0.27	0.725	ns
cellulose_perc	22.5 (20.9 - 24)	20.9 (19.4 - 22.4)	3.3431	0.3055	ns	0.3132	0.725	ns	0.995	0.538	ns
lignin_recalcitrants_perc	19.4 (17.3 - 21.4)	17.3 (15.3 - 19.2)	2.7065	0.3403	ns	3.333	0.3055	ns	0.0803	0.8265	ns
Total_tannin_mg_gDW	8.56 (7.7 - 9.41)	9.41 (8.6 - 10.2)	8.8879	0.1586	ns	8.0687	0.1626	ns	0.0043	0.9508	ns
Total_phenol_mg_gDW	36.4 (33.7 - 39.1)	42.7 (40.2 - 45.3)	29.9599	0.0641	ns	5.0043	0.2147	ns	2.762	0.3403	ns
WD_B	0.564 (0.528 - 0.599)	0.493 (0.46 - 0.526)	15.3085	0.1227	ns	2.4421	0.3608	ns	1.5223	0.4406	ns
LDMC_mg_g_mean	416 (391 - 440)	410 (387 - 433)	0.1426	0.78	ns	0.3322	0.725	ns	0.0786	0.8265	ns
Fp_N_mm_mean	0.266 (0.227 - 0.311)	0.212 (0.183 - 0.247)	7.611	0.1626	ns	0.2997	0.725	ns	0.2597	0.725	ns
specific_Fp_mean	1.23 (1.03 - 1.47)	0.889 (0.751 - 1.05)	13.209	0.1285	ns	0.4308	0.686	ns	0.013	0.9337	ns
leaf_thickness_mm_mean	0.221 (0.209 - 0.233)	0.236 (0.224 - 0.249)	7.1956	0.1697	ns	0.2132	0.7434	ns	2.3189	0.3712	ns
dry_weight_mg_mean	922 (784 - 1.08e+03)	1.08e+03 (930 - 1.27e+03)	2.0771	0.4013	ns	10.6002	0.1385	ns	6.1195	0.1891	ns
LA_mm2_mean	1.37e+04 (1.13e+04 - 1.65e+04)	1.31e+04 (1.1e+04 - 1.57e+04)	1.6779	0.4371	ns	11.1158	0.1367	ns	1.8983	0.4249	ns
SLA_mm2_mg_mean	16.3 (15.3 - 17.4)	13.2 (12.2 - 14.1)	52.0691	0.057	ns	3.0363	0.3225	ns	5.338	0.2081	ns
chla_mg.g	2.62 (2.54 - 2.71)	2.49 (2.41 - 2.57)	13.8526	0.1285	ns	0.967	0.539	ns	0.0201	0.922	ns
chla_mg.mm2	0.00018 (0.000169 - 0.000192)	0.000206 (0.000195 - 0.000217)	29.1407	0.0641	ns	1.4573	0.4408	ns	7.0602	0.1697	ns
chlb_mg.g	1.09 (1.05 - 1.13)	0.97 (0.931 - 1.01)	40.3793	0.0622	ns	0.0054	0.9508	ns	2.6047	0.3462	ns
chlb_mg.mm2	7.42e-05 (6.79e-05 - 8.04e-05)	7.95e-05 (7.36e-05 - 8.55e-05)	5.5521	0.2032	ns	1.6784	0.4371	ns	1.3329	0.4618	ns
carot_mg.g	0.687 (0.667 - 0.708)	0.667 (0.647 - 0.687)	6.3526	0.1891	ns	1.5548	0.4406	ns	0.2638	0.725	ns
carot_mg.mm2	4.74e-05 (4.47e-05 - 5.02e-05)	5.54e-05 (5.28e-05 - 5.79e-05)	47.7257	0.057	ns	1.7074	0.4371	ns	7.9565	0.1626	ns
Asat_mean	4.08 (2.66 - 5.5)	7.03 (5.69 - 8.38)	20.2667	0.0936	ns	0.2841	0.725	ns	4.4952	0.2333	ns
Amax_mean	11.7 (8.94 - 14.5)	18 (15.4 - 20.6)	23.2366	0.0844	ns	0.8777	0.5526	ns	4.2675	0.2424	ns
DR_mean	1.03 (0.871 - 1.19)	1.25 (1.09 - 1.4)	7.7079	0.1626	ns	1.546	0.4406	ns	5.7587	0.199	ns
N_mg.mm2	0.128 (0.12 - 0.136)	0.166 (0.158 - 0.174)	97.6994	0.0343	*	0.5198	0.6654	ns	19.7036	0.0936	ns
total_P_mg.mm2	6.62e-05 (6.21e-05 - 7.06e-05)	8.04e-05 (7.57e-05 - 8.54e-05)	33.2076	0.0641	ns	12.2667	0.1294	ns	10.3913	0.1385	ns
X13C	32.4 (32.1 - 32.8)	31.4 (31.1 - 31.8)	28.7751	0.0641	ns	8.7471	0.1586	ns	11.3558	0.1367	ns
C_perc	44.6 (44.3 - 44.9)	44.7 (44.4 - 45)	12.2663	0.1294	ns	89.7169	0.0343	*	0.2403	0.7309	ns
total_P_mg.g	0.998 (0.912 - 1.09)	0.99 (0.909 - 1.08)	1.4839	0.4408	ns	13.2189	0.1285	ns	0.444	0.686	ns
N_perc	1.83 (1.74 - 1.91)	1.97 (1.89 - 2.05)	9.1914	0.1586	ns	7.7457	0.1626	ns	4.523	0.2333	ns
total_K_mg.g	9.99 (8.4 - 11.9)	10.8 (9.13 - 12.7)	0.9229	0.5454	ns	0.3208	0.725	ns	2.7576	0.3403	ns
total_Mg_mg.g	2.57 (2.06 - 3.2)	2.41 (1.96 - 2.97)	0.7237	0.5925	ns	1.2751	0.4687	ns	0.4897	0.672	ns
total_Ca_mg.g	7.09 (6.12 - 8.2)	6.6 (5.75 - 7.59)	6.1143	0.1891	ns	17.5554	0.1051	ns	1.5777	0.4406	ns
X15N	1.64 (0.966 - 2.32)	0.846 (0.204 - 1.49)	5.032	0.2147	ns	0.1854	0.7495	ns	0.5269	0.6654	ns
RaoQ	0.791 (0.735 - 0.847)	0.789 (0.736 - 0.842)	0.1971	0.748	ns	0.1187	0.7961	ns	3.0601	0.3225	ns


Source of variation
Forest type
Soil PC1
Soil PC2
Unexplained
Rao's Q
Leaf δ^{15}N (...)
Ca$_m$ (mg · g^{-1})
Mg$_m$ (mg · g^{-1})
K$_m$ (mg · g^{-1})
N$_m$(%)
P$_m$ (mg · g^{-1})
C$_m$(%)
Leaf δ^{13}C (...)
P$_a$ (mg · mm^{-2})
N$_a$ (mg · mm^{-2})
R$_d$ (µmol · m^{-2} · s^{-1})
A$_{max}$ (µmol · m^{-2} · s^{-1})
A$_{sat}$ (µmol · m^{-2} · s^{-1})
Carotenoids$_a$ (mg · mm^{-2})
Carotenoids$_m$ (mg · g^{-1})
Chlorophyll b$_a$ (mg · mm^{-2})
Chlorophyll b$_m$ (mg · g^{-1})
Chlorophyll a$_a$ (mg · mm^{-2})
Chlorophyll a$_m$ (mg · g^{-1})
Specific leaf area (mm^2 · mg^{-1})
Leaf area (mm^2)
Dry leaf mass (mg)
Lamina thickness (mm)
Specific force to punch (N · mm^{-2} · mm^{-1})
Force to punch (N · mm^{-2})
Leaf dry matter content (mg · g^{-1})
Branch density (g · cm^{-3})
Phenols$_m$ (mg · g^{-1})
Tannins$_m$ (mg · g^{-1})
Lignin & recalcitrants (%)
Cellulose (%)
Hemicellulose (%)
Nutrients
Photosynthesis
Structure
0
20
40
60
80
100
Percent variance explained