# Logging increases the functional and phylogenetic dispersion of understorey plant communities in tropical lowland rain forest

Timm F. Döbert[1,2] (iD), Bruce L. Webber[1,2] (iD), John B. Sugau[3], Katharine J. M. Dickinson[4] and Raphael K. Didham*[1,2] (iD)

[1]School of Biological Sciences, The University of Western Australia, 35 Stirling Highway, Crawley WA 6009, Australia; [2]CSIRO Land and Water, Centre for Environment and Life Sciences, 147 Underwood Ave, Floreat WA 6014, Australia; [3]Forest Research Centre, Sabah Forestry Department, Sandakan, Sabah 90715, Malaysia; and [4]Department of Botany, University of Otago, PO Box 56, Dunedin 9054, New Zealand

## Summary

**1.** Logging is a major driver of tropical forest degradation, with severe impacts on plant richness and composition. Rarely have these effects been considered in terms of their impact on the functional and phylogenetic diversity of understorey plant communities, despite the direct relevance to community reassembly trajectories. Here, we test the effects of logging on functional traits and evolutionary relatedness, over and above effects that can be explained by changes in species richness alone. We hypothesised that strong environmental filtering will result in more clustered (underdispersed) functional and phylogenetic structures within communities as logging intensity increases.

**2.** We surveyed understorey plant communities at 180 locations across a logging intensity gradient from primary to repeatedly logged tropical lowland rain forest in Sabah, Malaysia. For the 691 recorded plant taxa, we generated a phylogeny to assess plot-level phylogenetic relatedness. We quantified 10 plant traits known to respond to disturbance and affect ecosystem functioning, and tested the influence of logging on functional and phylogenetic structure.

**3.** We found no significant effect of forest canopy loss or road configuration on species richness. By contrast, both functional dispersion and phylogenetic dispersion (net relatedness index) showed strong gradients from clustered towards more randomly assembled communities at higher logging intensity, independent of variation in species richness. Moreover, there was a significant nonlinear shift in the trait dispersion relationship above a logging intensity threshold of c. 65% canopy loss (±17% CL). All functional traits showed significant phylogenetic signals, suggesting broad concordance between functional and phylogenetic dispersion, at least below the logging intensity threshold.

**4.** *Synthesis.* We found a strong logging signal in the functional and phylogenetic structure of understorey plant communities, over and above species richness, but this effect was opposite to that predicted. Logging increased, rather than decreased, functional and phylogenetic dispersion in understorey plant communities. This effect was particularly pronounced for functional response traits, which directly link disturbance with plant community reassembly. Our study provides novel insights into the way logging affects understorey plant communities in tropical rain forest and highlights the importance of trait-based approaches to improve our understanding of the broad range of logging-associated impacts.

**Key-words:** above-ground biomass, Borneo, carbon storage, dipterocarp forest, disturbance gradient, land-use change, logging intensity, phylogenetic signal, plant functional traits, response diversity

## Introduction

The main driver of biodiversity loss in the tropics is conversion of tropical forests to agriculture (Gibbs *et al.* 2010).

However, degradation of habitat quality by logging and road construction also has severe impacts on biodiversity and ecosystem functioning (Edwards & Laurance 2013). Logging often precedes forest conversion to agricultural land uses, and the global extent of logged tropical forests exceeds the area of converted forests by an order of magnitude (Asner *et al.*

*Correspondence author. E-mail: raphael.didham@csiro.au

2009). As a result, the majority of remaining tropical forests have been logged at least once and an estimated one-third is considered heavily degraded (Gibson *et al.* 2011).

Habitat degradation due to logging poses serious challenges for biodiversity conservation (Laurance 2015). Logging alters the availability of resources and the configuration of remaining forest patches, driving compositional and structural shifts towards early-successional stages (Brown & Gurevitch 2004). The generally larger extent and higher intensity of anthropogenic logging impacts vs. natural gap-phase dynamics means that plant community reassembly trajectories likely differ from those that occur naturally, with potentially long-term consequences for forest regeneration (Denslow 1995). As such, logging may not only affect the capacity of forests to safeguard native biodiversity and store carbon (Bunker *et al.* 2005) but may also influence their resilience to other drivers of global environmental change, such as biotic invasions and climate change (Foley *et al.* 2005).

The impacts of logging on forest ecosystems are commonly assessed using measures of richness, diversity or species composition (Cannon, Peart & Leighton 1998). By contrast, quantitative variation in functional diversity (i.e. the variation in functional trait values among species in a community) and phylogenetic diversity (i.e. the extent of variation in ancestral relatedness) has rarely been considered in studies of logging disturbance (Grass *et al.* 2015). However, the use of functional and phylogenetic indices, over and above traditional taxonomic metrics, is finding increasing support in a growing number of studies quantifying community reassembly trajectories in the context of other forms of anthropogenic disturbances (Cadotte, Carscadden & Mirotchnick 2011).

Of particular relevance to applying trait-based approaches for quantifying ecosystem change is the distinction between 'response' and 'effect' traits to characterise two interrelated ways in which ecosystem disturbance might influence function (Lavorel & Garnier 2002). Response traits characterise how disturbance affects plant community composition and structure, and thus are crucial determinants of successional trajectories associated with environmental change (Suding *et al.* 2008). Such compositional and structural changes are then likely to influence ecosystem functioning, which reflects a community's degree of 'functional insurance' and can be determined using effect traits (Lavorel & Garnier 2002). As such, the distinction between these two types of functional classifications is linked to the concept of functional redundancy, where response diversity presents a first insurance against the loss of ecosystem functioning and a measure of ecosystem resilience (Laliberté *et al.* 2010). Hence, the relative independence of predominantly demographic traits associated with disturbance and mostly physiological traits relating to ecosystem functioning suggests a limited degree of convergence between response and effect traits (Lavorel & Garnier 2002). In situations where trait information is limited, the detection of phylogenetic signal (i.e. the degree to which phylogenetic similarity predicts functional trait similarity) has allowed phylogenetic diversity to serve as a proxy for functional diversity (Srivastava *et al.* 2012). Phylogenetic signal

can provide insight into how trait evolution affects community assembly (Weiher *et al.* 2011), based on the assumption that more closely related species will share similar trait attributes due to their longer common evolutionary history (Helmus *et al.* 2010).

Recent conceptual advances in trait-based and phylogenetic approaches are improving our ability to investigate the mechanisms underlying plant community reassembly dynamics (Kraft, Valencia & Ackerly 2008). The view that increasing intensity of habitat modification should reduce functional diversity [in the sense of both functional richness (FRic) and dispersion] as well as phylogenetic diversity (Mouchet *et al.* 2010), is closely linked to the niche-based processes of environmental filtering and competitive exclusion. These ecological processes are thought to trade-off along ecological gradients, where environmental filtering dominates under more disturbed conditions and results in trait clustering, while competitive exclusion should be of greater importance in intact ecosystems and result in functional or phylogenetic overdispersion within communities (Kraft & Ackerly 2010).

The integration of functional and phylogenetic diversity measures into studies of plant community assembly in human-modified landscapes is crucial for effective conservation strategies (Mayfield *et al.* 2010). Anthropogenic disturbances are likely to have strong effects on functional and phylogenetic diversity in tropical lowland rain forests, yet these metrics have rarely been quantified even for canopy tree communities, let alone for understorey communities (Kraft & Ackerly 2010). This shortfall may be due, in part, to the difficulty of collecting trait data in highly diverse tropical forest communities (Verbeeck *et al.* 2014). Unfortunately, this difficulty constrains more effective conservation management, given that understorey vegetation dynamics, including plant invasion processes and native seedling recruitment, as well as plant–animal interactions are crucial determinants of community assembly trajectories (Devictor *et al.* 2010).

Here, we test whether the intensity of logging in tropical forests drives greater changes in trait diversity and evolutionary relatedness in understorey plant communities than can be explained by shifts in plant species richness alone. The tropical lowland rain forests on the island of Borneo are floristically among the most diverse systems on the planet (Myers *et al.* 2000), yet large-scale timber extraction and conversion to commercial tree plantations continue to drive their rapid degradation and loss (Gaveau *et al.* 2014). As is the case for the majority of tropical forests, the effects of logging on habitat quality in these forests have rarely been assessed, despite the critical implications for biodiversity conservation (Brown & Gurevitch 2004). Moreover, studies investigating the effects of logging on plant community dynamics across both tropical and temperate forest ecosystems have rarely focused on the understorey, despite its crucial relevance for successional trajectories (Roberts & Gilliam 2014). We hypothesised that (i) the functional and phylogenetic dispersion of understorey plant communities will decline with increasing logging intensity due to environmental filtering of traits associated with early-successional status and (ii) the influence of logging

on functional dispersion (FDis) will vary between response and effect traits due to their potentially differing roles in determining changes to plant community structure and ecosystem functioning following habitat modification.

## Materials and methods

### STUDY DESIGN AND VEGETATION SAMPLING

This study was conducted in the Kalabakan Forest Reserve (KFR; 4°70′ N, 117°58′ E), the Mount Louisa Forest Reserve (MLFR; 4°77′ N, 117°68′ E) and the Maliau Basin Conservation Area (MBCA; 4°75′ N, 116°96′ E) in Sabah, Malaysian Borneo (Appendix S1.1, Supporting Information). To investigate the legacy of past logging activities, we sampled understorey plant communities in 2 × 2 m plots distributed across eight spatial blocks under either logged or old-growth forest cover, each subdivided into three sub-blocks based on the broader framework of the Stability of Altered Forest Ecosystems (SAFE) project (Ewers *et al.* 2011; Fig. S1). Study plots reflected a gradient in historical logging intensity, ranging from areas of old-growth forest with no documented record of logging (i.e. in the MBCA) to selectively logged areas (i.e. in the MLFR) and salvage logged areas (i.e. in the KFR). The principal 10 000 ha SAFE study area in the KFR was first selectively logged in the late 1970s (i.e. no removal of trees below 60 cm DBH at 1·3 m above ground), followed by a round of salvage logging in the early 2000s (i.e. removal of trees above a 30 cm DBH limit). A total of 180 plots were sampled at random between December 2011 and March 2014, with 21–24 plots sampled per block (Appendix S1.2).

We recorded plant morphospecies identities and quantified their relative contribution to above-ground biomass (AGB) by harvesting all vegetative material up to a height of 2 m, excluding stems greater than 2 cm DBH. We included all plant material rooted outside but growing into the plot and excluded any parts that extended out of the plot from plants rooted within. All plant material was subsequently dried (c. 70 °C) for a minimum of 4 days (Appendix S1.3). A reference specimen of each morphospecies from each plot was identified, where possible, at the Sandakan Herbarium (SAN). Nomenclature follows the International Plant Names Index database (http://www.ip ni.org). Species were classified as native or exotic (*sensu* Webber & Scott 2012) and allocated to 1 of 10 plant growth forms following the APG III classification system: ferns, fern allies, forbs, graminoids, herbaceous climbers, herbaceous shrubs, tree saplings, woody climbers, woody shrubs or 'indeterminate'.

### DRIVERS OF LOGGING DISTURBANCE EFFECTS ON PLANT COMMUNITIES

For each plot, we recorded seven variables that reflected logging scale and intensity and thus might play a crucial role in plant community reassembly following anthropogenic disturbance (Brown & Gurevitch 2004): local-scale forest canopy loss (within a radius of 17·78 m, i.e. $10^{1·25}$ m), landscape-scale forest canopy loss (within a radius of 562·34 m, i.e. $10^{2·75}$ m), regional-scale density (km km$^{-2}$) of continuously maintained primary logging roads and occasionally used secondary logging roads (within a radius of 1778·28 m, i.e. $10^{3·25}$ m), and distance to nearest primary road, secondary road and river (Appendix S1.4). These local, landscape and regional scales were predefined in accordance with the $\log_{10}$-scale spatial sampling approach used for the broader SAFE project study design (Ewers *et al.* 2011).

Canopy loss (i.e. removal of the upper layer tree crown) was quantified by digitisation, manual classification and ground-truthing of high-resolution georeferenced aerial photographs collected in 1970/1971 vs. high-resolution Worldview 2 satellite imagery taken at the same locations between 2010 and 2014 (Appendix S1.4). At a ground sampling distance of 1·84 m, we were able to delineate mid-layer and upper layer tree crowns, thus allowing us to quantify the actual quantitative change in forest canopy cover (rather than using a proxy). All analyses were conducted in geographic information systems software (ArcGIS version 10.2.1; ESRI; Redlands, CA, USA).

As logging effects can covary with underlying environmental gradients, we also recorded the elevation of each plot, and variation in six soil biogeochemical variables (pH, humus depth, total nitrogen, available phosphorus, bulk density and moisture factor) combined into two orthogonal principal component analysis (PCA) variables reflecting a 'soil-compaction gradient' along PCA axis 1 and a 'soil-fertility gradient' along PCA axis 2 (Appendix S1.5, Table S1).

### PLANT FUNCTIONAL TRAITS AND PHYLOGENETIC STRUCTURE

For each plant taxon, we recorded 10 traits that capture plant resource allocation, dispersal, persistence and recruitment in response to disturbance, these being distinguished according to the response-effect trait framework (Table 1): six 'response traits' known to be sensitive to ecosystem disturbance (dispersal mode, fruit type, life-history mode, pollination syndrome, reproduction strategy and seed number) and four 'effect traits' known to influence ecosystem functioning [plant growth form, plant height, specific leaf area (SLA) and wood density; Appendix S2.1, Table S2; Lavorel & Garnier 2002; Laliberté *et al.* 2010]. Trait data were derived from different sources including compiled 'Floras' on Southeast Asian plants, published databases of specific traits, compilations of plant family and genus characteristics, and direct measurements of herbarium specimens or field-sampled plant material (Appendix S2.2).

To quantify changes in functional trait variation along the logging intensity gradient, we calculated plot-level community FRic and FDis using the Gower dissimilarity coefficient in the 'FD' package (Laliberté & Legendre 2010) in R 3.1.0 (R Core Team 2013). Functional richness describes the volume of niche trait space occupied by a community, whereas FDis describes the mean distance of species to the centroid of the whole community in multidimensional trait space (Laliberté & Legendre 2010). Functional dispersion was also calculated for response traits alone (FDisR) and for effect traits alone (FDisE). We compared observed FRic and FDis values to those expected under a null model of random community assembly (Mason *et al.* 2013), using biomass-weighted standardised effect sizes (SES) for each plot:

$$\text{SES} = -1 \times ((y_{\text{obs}} - \bar{y}_{\text{exp}})/\text{SD}_{\text{exp}})$$

where '$y_{\text{obs}}$' is the observed value, '$\bar{y}_{\text{exp}}$' is the mean value of the random draw and '$\text{SD}_{\text{exp}}$' is the standard deviation of the expected mean. Observed values that were significantly different than expected by chance alone indicate patterns of functional trait divergence (negative SES values) or convergence (positive SES values; Appendix S2.3, Table S3).

The effects of logging on phylogenetic structure of understorey plant communities were tested based on phylogenetic tree reconstruction using the Angiosperm Phylogeny Group III (2009) classification (supertree R20120829) in Phylomatic 4.1 (Webb & Donoghue 2005). The BLADJ (branch length adjustment) algorithm was used to estimate phylogenetic branch lengths (in millions of years) and assign

**Table 1.** Plant functional response (R) and effect (E) traits used in the analysis, with the total number of plant taxa (species or morphospecies) recorded for each trait. The trait attributes used for dispersal mode, fruit type and pollination syndrome were adapted from Mayfield, Ackerly & Daily (2006) with minor modifications. Categories for seed number were based on the threshold of <10 vs. >10 proposed in Dawson, Burslem & Hulme (2009) as well as the strong negative relationship between seed number and size and thus variation in plant life-history strategy (Coomes & Grubb 2003). The number of plant taxa (out of 691 taxa) as well as the proportion of the samples (in %; out of 2625 samples) for which respective trait data were available are indicated in brackets under plant functional traits; and number of plant taxa (out of the possible total for that trait) under attribute categories or range

| Plant functional traits | Data type | E/R | Attribute categories or range |
|---|---|---|---|
| Dispersal mode (555 taxa) (74·9% of samples) | Discrete | R | Animal (254), ant (7), ballistic (25), bat (4), bird (107), primate (22), water (10), wind (126) |
| Fruit type (611 taxa) (85·6% of samples) | Discrete | R | Achene (28), berry (135), berry-like (37), capsule (141), caryopsis (7), drupe (145), follicle (30), legume (36), nut (45), samara (5), and schizocarp (2) |
| Life history (632 taxa) (87·6% of samples) | Discrete | R | Annual (2), annual + biennial + perennial (4), annual + perennial (4), perennial (622) |
| Pollination syndrome (610 taxa) (81·6% of samples) | Discrete | R | Bat (1), bee (139), beetle (59), bird (12), butterfly (12), entomophilous.broad (201), entomophilous.narrow (76), fly (7), moth (8), passive (3), self (57), thrip (8), wasp (11), wind (16) |
| Reproduction strategy (685 taxa) (95·1% of samples) | Discrete | R | Seed (591), seed + vegetative (39), vegetative (55) |
| Seed number (560 taxa) (74·9% of samples) | Discrete | R | 1 (213), <4 (167), <10 (76), >10 (104) |
| Plant growth form (681 taxa) (95·4% of samples) | Discrete | E | Ferns (55), forbs (36), graminoids (15), herbaceous climbers (30), herbaceous shrubs (9), tree saplings (375), woody climbers (143), woody shrubs (18) |
| Plant height (380 taxa) (47·6% of samples) | Continuous | E | 0·5–80 m |
| Specific leaf area (691 taxa) (100% of samples) | Continuous | E | 46·8–957·9 $cm^2 g^{-1}$ |
| Wood density (398 taxa) (45·2% of samples) | Continuous | E | 0·21–0·91 $g cm^{-3}$ |

ages to known nodes in the tree using Phylocom 4.2 (Appendix S2.4, Table S4; Webb, Ackerly & Kembel 2008).

The phylogenetic dispersion of plant communities in each plot was calculated as the net relatedness index (NRI; Appendix S2.4, Table S3). The NRI is equivalent to the SES of the mean pairwise phylogenetic distance (MPD) for all individuals in each community (Webb 2000), and is based on the average branch length between each pair of taxa in a plot. Computation of MPD was conducted using the 'ape' (Paradis, Claude & Strimmer 2004) and 'picante' (Kembel *et al.* 2010) packages in R (Appendix S2.4).

As a sensitivity test of whether any observed relationship between logging and phylogenetic dispersion was driven solely by a shift from woody to non-woody vegetation, we also quantified NRI values based on independent phylogenies for tree saplings only, for the wider woody plant fraction (that also included woody shrubs and vines), and for the non-woody plant fraction only, following the methods described above.

To test whether closely related species resemble each other more in trait space than species drawn at random from the phylogenetic tree, we quantified the phylogenetic signal (Pagel 1999) using Blomberg's $K$ for continuous traits (Blomberg, Garland & Ives 2003) in the 'picante' (Kembel *et al.* 2010) and 'phytools' packages (Revell 2012) in R (R Core Team 2013). For discrete traits, we used the *fitDiscrete* function implemented in the R package 'geiger' (Harmon *et al.* 2008; Appendix S2.4).

### STATISTICAL ANALYSES

We tested the effects of logging intensity on taxonomic, functional and phylogenetic dispersion using generalised linear mixed effects models (GLMMs) in the 'lme4' (Bates *et al.* 2015) package in R. Fixed predictor variables were local-scale forest canopy loss, landscape-scale forest canopy loss, regional-scale density of secondary roads, distance to nearest primary road and their interaction effects. Plot elevation, soil PC1 and soil PC2 were included as covariates in all models (Table S5). Of the original predictor variables, we excluded 'density of primary roads' and 'distance to the nearest secondary road' due to strong collinearity with logging variables ($r > 0.65$), and 'shortest distance to river' due to moderate collinearity ($r > 0.4$) with elevation (Appendix S3.1). The distribution of some predictor variables was moderately skewed (Fig. S4), so we also conducted a PCA on all predictor variables to check that there were no outlier plots that might have undue leverage on the models (Fig. S5). No substantial outlier points were detected in the reduced ordination space (Fig. S5), therefore data from all 180 vegetation plots were retained in the GLMM analyses. Random intercepts were specified for 'block' (total eight blocks) and 'sub-block' nested within block (three sub-areas per block for a total of 24). For species richness, we specified a Poisson distribution (log-link function) and tested for overdispersion of model residuals. For functional and phylogenetic diversity metrics, we specified a Gaussian distribution (identity link function), and tested model residuals for normality and homogeneity of variances. All response variables met model assumptions.

Model simplification was performed using a multi-model inference approach (Burnham & Anderson 2002) and model averaging procedures based on the Akaike information criterion in the 'MuMIn' package (Bartoń 2015) in R (Appendix S3.1). Subsequently, we tested for potential confounding spatial autocorrelation of model residuals using the *spline.correlog* function in the 'ncf' package (Bjørnstad & Falck 2001). None of the GLMMs showed spatial autocorrelation of model residuals (Appendix S3.1).

Finally, for any significant relationships with logging, we tested whether there was evidence for a nonlinear 'threshold' effect of logging on understorey plant communities using a segmented mixed models approach (Muggeo *et al.* 2014). We applied the *segmented.lme* function (Muggeo *et al.* 2014) to quantify slope-

differences and changepoint estimates along the logging intensity gradient. Input to the *segmented.lme* function required a mixed model object returned by the function *lme* in the 'nlme' package (Pinheiro *et al.* 2015).

## Results

Across the 180 plots, we identified 691 plant taxa (species or morphospecies), 400 of which were identified to species level, from 289 known genera and 101 families. Plot-level variability in community attributes was high, ranging from 5 to 26 species and 20·8–1066·8 g m$^{-2}$ total AGB per plot. Seedlings of canopy-dominant Dipterocarpaceae were only recorded in 68 plots (38%), including at least 20 different known species, with biomass ranging from 0·2 to 348·8 g m$^{-2}$ per plot. Exotic plant taxa were more widely distributed, with 1–8 species found in 98 of 180 plots, and with moderately high AGB, ranging from 0·01 to 394·7 g m$^{-2}$. However, less than 15% of invaded plots had more than two exotic plant taxa, and there were only 20 exotic plant taxa identified across all plots, all of which were early-successional species (Table S6). The distribution of species in phylogenetic space indicated that exotic plants were randomly distributed in relation to native plants (Fig. S3).

Although understorey richness varied substantially between plots, this variability could not be explained by any of the measured logging predictor variables in the GLMM analyses (Table 2, Fig. 1a). Similarly, variation in FRic could not be explained by any of the measured predictor variables (Table S7, Fig. S6a). By contrast, the SES for FDis indicated strong variation along the logging intensity gradient, including evidence that the relationship was nonlinear (Table 2). A segmented mixed model test indicated significant evidence for a threshold nonlinearity at a moderately high level of logging intensity (back-transformed changepoint estimate = 65·3%, CI = 48·6–82·1%; slope difference U = 0·995, CI = 0·317–1·672; Table S8). While FDis was significantly higher than expected by chance alone (i.e. trait clustering) in the intact and low canopy-loss plots, there was a shift towards trait divergence at intermediate logging intensity, followed by a trend towards more randomly assembled communities in the most intensively logged areas (Table 2, Fig. 1b). The SES for FDisR indicated significantly higher trait clustering in plant communities in low canopy-loss areas, but more divergent traits among species in more heavily logged plots (Table S7, Fig. S6b). In contrast, none of the measured predictor variables had a significant effect on the SES for FDisE (Table S7,

**Table 2.** Results of mixed-effect modelling of the effects of local- and landscape-scale logging intensity on species richness, functional dispersion (FDis) and phylogenetic dispersion (NRI)

| Response variable | Species richness | | FDis | | NRI | |
|---|---|---|---|---|---|---|
| | Null model | Full model | Null model | Full model | Null model | Full model |
| Fixed effects | $b$ ($\pm 1$ SE) | $b$ ($\pm 1$ SE) | $b$ ($\pm 1$ SE) | $b$ ($\pm 1$ SE) | $b$ ($\pm 1$ SE) | $b$ ($\pm 1$ SE) |
| Intercept | 13·652 (0·570) | **2·615 (0·043)** | 0·381 (0·145) | 0·131 (0·110) | 0·1232 (0·102) | 0·213 (0·092) |
| Elevation | – | 0·006 (0·018) | – | – | – | – |
| Soil PC1 | – | 0·002 (0·012) | – | – | – | – |
| Soil PC2 | – | −0·013 (0·022) | – | – | – | – |
| Local-scale forest canopy loss (linear term) | – | 0·001 (0·008) | – | **−0·564 (0·084)** | – | **−0·220 (0·061)** |
| Local-scale forest canopy loss (quadratic term) | – | – | – | **0·248 (0·074)** | – | – |
| Landscape-scale forest canopy loss | – | 0·001 (0·019) | – | – | – | – |
| Density secondary roads | – | −0·004 (0·030) | – | – | – | – |
| Nearest primary road | – | 0·002 (0·013) | – | – | – | – |
| Landscape-scale forest canopy loss: dens. sec. roads. | – | −0·021 (0·047) | – | – | – | – |
| VC for random effects | VC | VC | VC | VC | VC | VC |
| Block | 1·09 | 0·051 | 0·383 | 0·181 | 0·236 | 0·212 |
| Sub-block | 1·46 | 0·110 | – | – | 0·161 | 0·100 |
| VC for fixed effects | – | 0·002 | – | 0·18 | – | 0·050 |
| PCV$_{(Block)}$ | – | 95·33% | – | 52·68% | – | 10·27% |
| PCV$_{(Sub-block)}$ | – | 92·45% | – | – | – | 37·78% |
| $R^2_{GLMM(m)}$ | – | 1·77% | – | 28·42% | – | 9·50% |
| $R^2_{GLMM(c)}$ | – | 16·88% | – | 33·60% | – | 20·40% |
| AIC | 1030·07 | 1017·47 | 411·06 | 382·98 | 381·80 | 375·26 |

AIC = Akaike information criterion; dens. sec. roads = density of secondary roads; PCV = per cent change in variance between the null and full models; VC = variance components. Model parameters were calculated using restricted maximum likelihood (REML) estimation, and a weighted model averaging approach. Marginal $R^2$ (variance explained by just the fixed effects) and conditional $R^2$ (variance explained by both fixed and random effects) were calculated for the top models after Nakagawa & Schielzeth (2013). Note that these approximations are not currently available for the recently developed segmented mixed models approach (Muggeo *et al.* 2014), and we provide an indicative fit of a continuous nonlinear relationship (a second-order polynomial) that was the best-fit GLMM model for these data. To account for model selection uncertainty, we report unconditional SE. Bolded coefficients are significantly different from zero ($P < 0.05$).
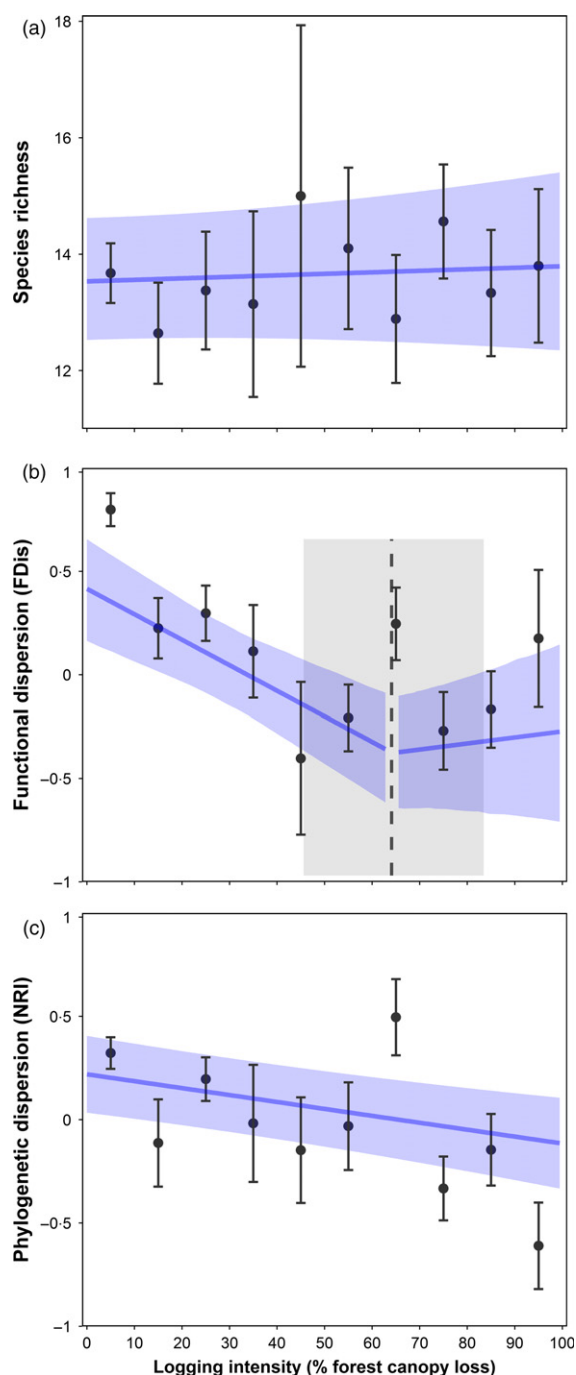
**Fig. 1.** GLMM model-predicted relationships between logging intensity and (a) species richness, (b) functional dispersion (FDis; ±1 SE) and (c) phylogenetic dispersion (NRI; ±1 SE). The mean fitted relationships in (a) and (c) were generated using the *predict* function with shaded areas indicating the 95% confidence interval (CI) around estimates. In (b), no *predict* function is yet available for segmented mixed models, so model predictions were generated using resampling of model estimates (with 1000 random draws), with the shaded area indicating the 95% CI of the bootstrap replicate estimates (for illustrative purposes). Symbols represent the raw means (±1 SE). Logging intensity represents forest canopy loss from 1970 to 2010 at a local scale (i.e. 17·78 m radius buffer). Functional dispersion values are biomass-weighted standardised effect sizes (SES) and analogous to the net related index (NRI). [Colour figure can be viewed at wileyonlinelibrary.com]

Fig. S6b). The final model fit indicated that the explanatory power of the fixed predictor variables was 28·4% for a nonlinear (second-order polynomial) FDis model and 36·5% for FDisR (Tables 2 and S7). The random effects in the models (block and sub-block) only minimally increased the total variation explained for either FDis or FDisR (Tables 2 and S7).

Local-scale forest canopy loss due to logging was also the only significant predictor of variation in phylogenetic dispersion (NRI; Table 2, Fig. 1c). Similar to FDis, plant species in the intact and low canopy-loss plots tended to be phylogenetically more closely related than expected under random assembly, whereas communities at higher levels of logging disturbance appeared randomly assembled (Fig. 1c). Unlike FDis, we found no support for a nonlinear threshold effect of logging on phylogenetic dispersion of understorey plant communities (slope difference U = −1·105, CI = −2·429–0·220; Table S9). A sensitivity test showed that the negative effect of logging on NRI was not driven solely by a shift from woody to non-woody vegetation, as logging intensity was still a significant negative predictor of NRI for a re-analysis of the tree sapling component alone (logging coefficient, $b = -0.247 \pm 0.094$, $P = 0.008$) and the broader woody plant component alone (logging coefficient, $b = -0.160 \pm 0.070$, $P = 0.023$). However, these logging effects were significant at landscape scales (562 m) rather than at the more local scale (17 m) found for the understorey community as a whole. There was no significant relationship between logging and phylogenetic dispersion for the non-woody vegetation component considered separately (intercept-only model, $b = -0.119 \pm 0.096$, n.s.).

The similar direction of effect for logging influence on both functional and phylogenetic dispersion suggested a strong phylogenetic signal in trait responses. This was confirmed in the analyses of phylogenetic signal for the three continuous traits (i.e. plant height, SLA and wood density), with Blomberg's $K$ values that were significantly lower than 1 (ranging from 0·40 to 0·62, Table 3). Likewise, the seven discrete traits (i.e. dispersal mode, fruit type, life-history mode, pollination syndrome, reproduction strategy, seed number and plant growth form) all showed strong phylogenetic signal, with Pagel's $\lambda$ values ranging from 0·85 to 1·00 (mean = 0·96, Table 3). More closely related species were significantly more similar in trait responses than would be expected by chance alone.

## Discussion

Functional trait and phylogenetic relationships are increasingly used as descriptive metrics of habitat quality change (Kraft, Valencia & Ackerly 2008). In combination, they provide a more detailed insight into the ecological processes that govern plant community reassembly than can be obtained from traditional taxonomic metrics alone (Cadotte, Carscadden & Mirotchnick 2011). In the present study, we did not detect significant forest canopy loss or road effects on the species richness of understorey plant communities despite a wide gradient in logging intensity from zero to nearly 100%

**Table 3.** Phylogenetic signal of 10 plant functional traits (see Table 1) based on Blomberg's $K$ for continuous traits and Pagel's $\lambda$ for discrete traits. Significance was estimated by using 999 randomisations; $n$ = the number of taxa included (out of 691)

| Plant functional trait | $n$ | $K$ | $P$ | $\lambda$ | $P$ |
|---|---|---|---|---|---|
| Dispersal mode | 555 | – | – | 1·00 | <0·001 |
| Fruit type | 611 | – | – | 1·00 | <0·001 |
| Life-history mode | 632 | – | – | 0·85 | <0·001 |
| Pollination syndrome | 610 | – | – | 1·00 | <0·001 |
| Reproduction strategy | 685 | – | – | 0·96 | <0·001 |
| Seed number | 560 | – | – | 1·00 | <0·001 |
| Plant growth form | 681 | – | – | 1·00 | <0·001 |
| Plant height | 380 | 0·62 | <0·01 | – | – |
| Specific leaf area | 691 | 0·41 | <0·001 | – | – |
| Wood density | 398 | 0·40 | <0·001 | – | – |

of the canopy removed. Logging operations, unlike localised treefall gaps, can cause severe damage to understorey plant communities and soil, and also directly facilitate the introduction of invasive plants, as has been shown for both tropical and temperate forest ecosystems (Pinard, Barker & Tai 2000; Roberts & Gilliam 2014). As such, logging not only results in large-scale transition of old-growth forest into an early-successional stage but may also increase the propagule pressure from plant invaders and drive changes in plant–animal interactions due to the scale of disturbance (Ewers *et al.* 2015; Piponiot *et al.* 2016). Surprisingly, in this study, the net result of these processes was that overall species richness remained remarkably consistent in both intact and logged forests. The absence of a logging signal on species richness has also been found outside the tropics, such as in a recent meta-analysis of 96 studies showing no clear effect of logging on temperate forest understorey plant species richness (Duguid & Ashton 2013). Hence, our study supports the growing notion that taxonomic metrics alone have limited power to robustly quantify mechanistic aspects of the effect of logging on community reassembly (Baraloto *et al.* 2012).

## FUNCTIONAL DISPERSION ACROSS A LOGGING INTENSITY GRADIENT

In spite of the lack of change in species richness, we found a strong effect of logging intensity on the FDis of understorey plant communities. At the local scale, co-occurring species under intact or largely closed-canopy forest were more similar in trait space than predicted by chance alone, whereas communities exhibited random trait assembly in heavily logged areas. Moreover, there was a significant nonlinear threshold in logging intensity at c. 65% (±17% CL), above which there was a notable shift in functional responses of understorey plant communities to logging. Overall, these findings are opposite to our initial expectation that logging would cause a decline in trait dispersion, and that strongly disturbance-structured communities would exhibit significant trait underdispersion. Instead, the observed trait clustering under closed-canopy conditions may be due to environmental filtering where low-light conditions of the tropical rain forest

understorey provide a narrow spectrum of regeneration niches. Alternatively, there may be just a few clades that are superior in competitive ability and outcompete all other distantly related species. Interestingly, a similar pattern of functional clustering in understorey tree communities under intact forest canopy was also reported for a tropical rain forest in China (Yang *et al.* 2014).

The distinction between response and effect traits accounts for differences in dispersal strategies and resource use in plants (Lavorel & Garnier 2002). We therefore expected that the FDisR and FDisE would show different patterns in trait distribution due to logging. In our study, the intensity of logging in localised forest patches had a particularly strong effect on response trait dispersion. Understorey communities at intact or largely closed forest canopy sites revealed clustering in FDisR, whereas co-occurring species in heavily logged forest stands were more divergent in FDis than would be expected by chance. Overdispersion in response traits (i.e. dispersal mode, fruit type, life-history mode, pollination syndrome, reproduction strategy and seed number) at high forest canopy loss might suggest that at the time of sampling, there potentially existed a broader spectrum in regeneration niches that allowed for diverse adaptation strategies. This finding possibly suggests that the plant community might have been sampled during a transitional period between the succession initiation phase and later successional stages, in which the predominantly herbaceous early-stage pioneer species were joined by subsequent colonisation of woody community components (Chazdon 2008). In one of the few other studies to account for the different ecological roles of response and effect traits, Ding *et al.* (2012) found that after 55 years of regeneration following shifting cultivation practices, plant communities in a tropical rain forest in China were overdispersed in response traits.

In contrast, we found no significant effect of forest canopy loss and road metrics on effect traits (i.e. plant growth form, plant height, SLA and wood density; Table 3) which may support the assumption that disturbance does not lead to differentiation in traits associated with forest productivity and biogeochemical processes (Grime 2006). On the other hand, it is important to note that our analysis of effect traits is based on a multi-trait-based FDis index that reflects complementarity among multiple traits rather than directional shifts in trait mean values of individual effect traits. For instance, in a tropical forest in Bolivia, Carreño-Rocabado *et al.* (2012) found that moderate levels of logging disturbance had little influence on average species richness or functional trait diversity, despite a significant directional decrease in community-weighted mean wood density and increase in community-weighted mean SLA at high logging intensity. However, the expression of individual trait responses is more sensitive to the sampling scheme and the character of the disturbance, providing a possible explanation for the contrasting findings reported from a regenerating tropical rain forest in Mexico, where there was no shift in wood density and a decrease in SLA following disturbance (Lohbeck *et al.* 2013). Overall, we find strong support for the notion that delineation of

response and effect traits allows for the parallel exploration of responses to disturbance and changes in ecosystem functioning (Laliberté *et al.* 2010). In that, we gain a better understanding of how logging affects plant community reassembly and whether plant communities are resilient to changing environmental conditions.

### PHYLOGENETIC DISPERSION ACROSS A LOGGING INTENSITY GRADIENT

To our knowledge, we present the first study to link phylogenetic and FDis for the entire understorey of a tropical forest community. The few comparable studies exploring plant reassembly dynamics in the context of anthropogenic disturbance restricted their sampling to woody species (and the order Zingiberales; Letcher 2010). In our study, the NRI for phylogenetic dispersion in understorey plant communities only partly reflected the patterns observed for FDis. Understorey communities at intact or largely closed forest canopy sites showed evidence of phylogenetic clustering, with co-occurring species significantly more closely related than would be expected by chance. In contrast, random assembly processes dominated in heavily logged forest stands. However, in contrast to FDis, there was no evidence for a threshold effect of logging on phylogenetic dispersion of understorey plant communities, suggesting that at high levels of logging intensity there is a breakdown in the strong positive covariance between functional and phylogenetic dispersion. Comparative evidence for the impact of anthropogenic disturbance on phylogenetic relatedness of tropical forest understorey communities is rare and often contrasting. For example, in two studies conducted in primary tropical rain forest in south-western China, Yang *et al.* (2014) found phylogenetic clustering in understorey tree communities (<5 cm DBH), whereas Mo *et al.* (2013) indicated that communities were phylogenetically overdispersed. Meanwhile, patterns of phylogenetic overdispersion in angiosperm understorey plant communities (<5 cm DBH) were also reported by Letcher (2010) for old-growth tropical rain forest in Costa Rica. Those studies that also included sites in secondary forests have found conflicting results, from random assembly (Mo *et al.* 2013) to overdispersion (Letcher 2010) or clustering (Ding *et al.* 2012) in patterns of phylogenetic structuring in understorey plant communities.

The lack of congruence across these studies suggests that not only environmental conditions but potentially also sampling design might influence the outcome of phylogenetic diversity analyses (Swenson *et al.* 2007). Phylogenetic structure varies with tree size class, such that results for understorey communities can vary substantially from those that focus on adult trees at the same sites (Swenson 2013). For example, the canopy layer of a tropical rain forest in French Guiana revealed greater phylogenetic diversity than the respective seedling layer (Gonzalez *et al.* 2010), reflecting a common pattern of increasing phylogenetic dispersion with the size class analysed (Swenson 2013). Moreover, several studies have shown that the distribution of phylogenetic

structure can vary strongly depending on the extent of the sampling area (Swenson *et al.* 2007). For example, Ding *et al.* (2012) found that phylogenetic evenness increased with increasing spatial scale. Finally, the type and intensity of disturbance as well as the time since disturbance may explain conflicting trends (Chazdon 2008). For example, there are marked differences in the ecological and environmental conditions of secondary forest growing on abandoned pasture compared with secondary forest recovering from logging disturbance (Swenson 2013). Hence, several crucial factors obscure generalisations of plant community reassembly trajectories in tropical forests.

Nevertheless, according to the tropical forest succession model proposed by Chazdon (2008), plant communities typically pass through three phases of forest succession: stand initiation, stem exclusion and understorey reinitiation. Initially, environmental filtering selects for species that share functional traits associated with rapid colonisation and which are less closely related than would be expected by chance alone (Chazdon 2008). Over time, the predominant mechanism for community reassembly shifts towards biotic interactions resulting in an increase in phylogenetic overdispersion at later successional stages (Mo *et al.* 2013). For example, Whitfeld *et al.* (2012) found that in a tropical lowland rain forest in New Guinea, plant communities shifted from phylogenetic clustering to overdispersion over the course of succession. This finding indicated that closely related early-successional individuals were replaced by late-successional individuals from a broader diversity of lineages (Norden *et al.* 2012). Our evidence for non-clustered understorey plant communities at intensively logged sites therefore lends support to the idea that communities are in a transitional phase, and the forest is recovering its floristic and structural complexity (Letcher 2010). This gradual increase in phylogenetic dispersion is expected, as community assembly is increasingly influenced by the establishment of shade-adapted late-successional species (Muscarella *et al.* 2015).

### PHYLOGENETIC SIGNAL OF FUNCTIONAL TRAITS

There was significant phylogenetic signal in all 10 plant functional traits measured, suggesting that phylogenetic dispersion is strongly indicative of the FDis of plant communities. Indeed, our results showed a strong, albeit not perfect, concordance between functional and phylogenetic dispersion (at least up to a threshold in logging influence on FDis), suggesting that closely related species have similar trait values and that the selected traits capture the spectrum of variation (i.e. unmeasured traits hold no additional information; Swenson 2013). Similar findings of significant phylogenetic signal in the functional traits of tropical rain forest plants and respective concordance between functional and phylogenetic community structure have also been reported in a few other tropical forest systems (e.g. Chazdon *et al.* 2003; Swenson & Enquist 2009; Kraft & Ackerly 2010; Yang *et al.* 2014; Muscarella *et al.* 2015). However, our study is the first to suggest that there might be a potential breakdown in this relationship

in highly disturbed forests. As such, our study broadly supports the assumption that ancestral relatedness represents a pragmatic proxy for estimating the ecological similarity of species, which is particularly relevant in the context of tropical forests due to the logistical constraint of generating comprehensive morphological and physiological trait databases for the majority of tree species in such rich communities (Swenson 2013). But further research is needed to confirm whether the phylogenetic signal in plant functional traits varies at different levels of logging disturbance.

### COMMUNITY REASSEMBLY IN LOGGED FORESTS

The unexpected functional and phylogenetic clustering observed in intact and low canopy-loss areas in this study highlights the complexity of the processes involved in determining species coexistence and community assembly (Mayfield & Levine 2010). Generally, biotic interactions are considered to be the predominant mechanism shaping community assembly in highly diverse tropical rain forests, including competition for sparse and spatiotemporally heterogeneous resources (Webb 2000). These processes would be expected to result in phylogenetically overdispersed communities in intact understories, as competition is typically most intense between closely related species with similar resource requirements (Mo *et al.* 2013). On the other hand, coexistence theory also suggests that competition dynamics can generate clustered patterns (Chesson 2000) when a few clades are superior in competitive ability and outcompete all other distantly related species (Mayfield & Levine 2010). At the opposite extreme, ecosystem disturbance is generally thought to result in resource homogenisation and strong environmental filtering, leading to a narrower spectrum of trait expression, and this can also cause a shift towards plant communities dominated by a few closely related plant taxa (Lebrija-Trejos *et al.* 2010). These contrasting findings underscore the challenges in drawing generalisable predictions about understorey plant community responses to logging disturbances. This situation may be due in part to the nature of the disturbance, the sampling design or a strong site-specific signal in the trajectory of tropical forest regeneration following anthropogenic disturbance. After all, broad generalisations are even difficult to make for temperate ecosystems, which are much better studied and less complex than their tropical counterparts (Roberts & Gilliam 2014). Nevertheless, it will be important to expand the currently sparse literature on logging effects on understorey plant communities in the tropics to better understand the processes that govern reassembly dynamics following anthropogenic disturbances.

In addition, further research on the effects of logging-induced changes in the spatial and temporal dynamics of animal behaviour, including shifts in plant selection by herbivores, as well as availability of pollinators and dispersers, will be crucial to better understand plant community reassembly dynamics. Finally, it will be critical to explore whether the observed functional and phylogenetic trait shifts constitute a permanent (potentially 'threshold') phase transition into an alternate forest state that will become increasingly dominated by invasive plant species, or whether it is a transient stage on the successional trajectory towards reassembly of intact tropical rain forests.

## Authors' contributions

T.F.D., B.L.W., K.J.M.D. and R.K.D. conceived the ideas and designed methodology; T.F.D. and J.B.S. collected the data; T.F.D., B.L.W. and R.K.D. analysed the data; T.F.D. and R.K.D. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## Data accessibility

Data can be accessed through the Dryad Digital Repository https://doi.org/10.5061/dryad.f77p7 (Döbert *et al.* 2017).

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## Supporting Information

Details of electronic Supporting Information are provided below.

**Appendix S1.** Supplementary methods describing site selection, vegetation sampling and measurement of predictor variables.

**Appendix S2.** Supplementary methods describing the measurement of functional traits and phylogenetic structure.

**Appendix S3.** Supplementary methods and results for statistical analyses.