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## LETTER

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**Keywords:** woody debris, tropical humid forests, selective logging, Malaysia, Southeast Asia, Stability of Altered Forest Ecosystems Project, above-ground carbon

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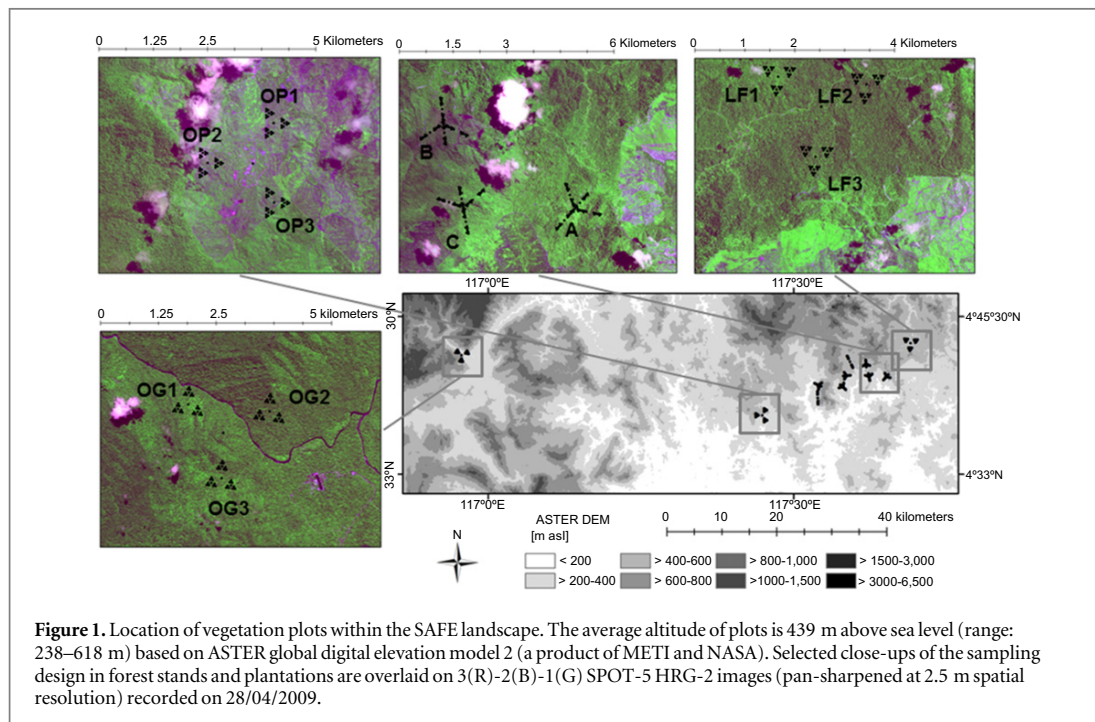
## Abstract

Despite a large increase in the area of selectively logged tropical forest worldwide, the carbon stored in deadwood across a tropical forest degradation gradient at the landscape scale remains poorly documented. Many carbon stock studies have either focused exclusively on live standing biomass or have been carried out in primary forests that are unaffected by logging, despite the fact that coarse woody debris (deadwood with  $\geq 10$  cm diameter) can contain significant portions of a forest's carbon stock. We used a field-based assessment to quantify how the relative contribution of deadwood to total above-ground carbon stock changes across a disturbance gradient, from unlogged old-growth forest to severely degraded twice-logged forest, to oil palm plantation. We measured in 193 vegetation plots ( $25 \times 25$  m), equating to a survey area of  $>12$  ha of tropical humid forest located within the Stability of Altered Forest Ecosystems Project area, in Sabah, Malaysia. Our results indicate that significant amounts of carbon are stored in deadwood across forest stands. Live tree carbon storage decreased exponentially with increasing forest degradation 7–10 years after logging while deadwood accounted for  $>50\%$  of above-ground carbon stocks in salvage-logged forest stands, more than twice the proportion commonly assumed in the literature. This carbon will be released as decomposition proceeds. Given the high rates of deforestation and degradation presently occurring in Southeast Asia, our findings have important implications for the calculation of current carbon stocks and sources as a result of human-modification of tropical forests. Assuming similar patterns are prevalent throughout the tropics, our data may indicate a significant global challenge to calculating global carbon fluxes, as selectively-logged forests now represent more than one third of all standing tropical humid forests worldwide.

## 1. Introduction

Coarse woody debris (CWD), comprising standing dead trees and fallen trunks and branches, is important for various ecological functions in tropical forest ecosystems. Dead wood provides a habitat for wildlife such as wood-feeding termites (Eggleton *et al* 1995),

cavity-nesting birds (Gibbs *et al* 1993), saproxylic beetles (Grove 2002) and bats (Giles 2012). It facilitates tree regeneration by providing 'nurse logs' (Fukasawa 2012), interacts with disturbance regimes such as fire (Pyle *et al* 2009), and acts as a significant carbon and nutrient reservoir (Chambers *et al* 2000). CWD may account for roughly 10% of total carbon



storage across tropical forests (Pregitzer and Euskirchen 2004), and may store as much as 33% of tropical forests' above-ground biomass (Clark *et al* 2002, Rice *et al* 2004). Yet, the relative contribution of CWD to carbon stocks in logged tropical forests remains poorly documented (Clark *et al* 2002, Baker *et al* 2007).

Carbon stored in the dead wood of a forest stand is one of the five carbon pools identified by the Intergovernmental Panel on Climate Change that should be measured and monitored for carbon book-keeping (Watson *et al* 2000). Accurate accounting of these pools is essential for mitigation, e.g. via REDD+ (reducing emissions from deforestation and degradation + enhancing forest carbon stocks) (Mertz *et al* 2012). Decomposition of dead wood contributes to carbon emissions originating from forests, and the magnitude of this contribution will depend on the variation in CWD stocks due to forest type and age (Pregitzer and Euskirchen 2004, Kissing and Powers 2010), mortality pulses (Rice *et al* 2004), topography affecting tree mortality (Gale 2000), chemical composition of the debris and hence the forest's tree species composition (Baker *et al* 2007), and the land use history and management of an area (Eaton and Lawrence 2006, Kauffman *et al* 2009).

Selective logging, which can cut deep into forest interiors, is a major land use change process with short-term and long-term impacts on emissions of carbon dioxide (Feldpausch *et al* 2005). The International Timber Trade Organisation (ITTO) estimates that 350 million ha of humid tropical forests contributed to timber production in 2005 (ITTO 2006); approximately 31% of the total humid tropical forest

area based on remotely sensed forest cover estimates for the same year (Hansen *et al* 2010). Since then, the practice of selective logging, either legal or illegal, has been on the rise in many of the ITTO's 33 member countries, reaching 403 million ha in 2010 (Blaser *et al* 2011). Timber harvesting focuses on high-value species and removes large, high-biomass trees from a forest stand. Logging infrastructure and residual canopy damage can dominate carbon emissions in logged forests (Pearson *et al* 2014). Logging events additionally accelerate the formation of CWD, from which carbon is released as decomposition progresses (Feldpausch *et al* 2005, Houghton 2005).

The majority of studies investigating causes of spatial variation in biomass and carbon stocks of tropical forests remain focussed on living trees (Malhi *et al* 2006, Saatchi *et al* 2007, Houghton *et al* 2009), with the assumption that these represent the largest fraction of total above-ground biomass (Nascimento and Laurance 2002). Meanwhile, the decrease of live tree biomass in response to selective logging combined with the extent of tropical forest area under logging may well mean that the importance of CWD stocks is increasing. Here, we analyse, whether (1) CWD stocks and their relative contribution to overall above-ground carbon increase with increasing forest disturbance, and whether (2) any variation in CWD stocks can be linked to forest attributes such as micro-topographic and structural traits. We address these questions by focussing on the forest degradation landscape of the Stability of Altered Forest Ecosystems (SAFE) Project in Sabah, Malaysia (Ewers *et al* 2011).

**Table 1.** Density of CWD was measured across five decay classes following protocols modified from Chao *et al* (2008) and Keller *et al* (2004). In 2014, we randomly sampled deadwood pieces, extracted samples as drill plugs, cubes or powder bags depending on decay status, and analysed those samples in the field lab. We averaged across samples to obtain wood density per piece and then averaged across all pieces ( $n$ : number of pieces) to obtain mean wood density (wd,  $\text{g cm}^{-3}$ ) for each decay class (dc).

dc	Description from Harmon <i>et al</i> (1995)	wd	$n$
1	Little decay, bark cover extensive, leaves and fine twigs present	$0.40 \pm 0.03$	18
2	No leaves and fine twigs, bark starting to fall off, logs relatively undecayed	$0.58 \pm 0.08$	24
3	No bark and few branch stubs (not moving when pulled), sapwood decaying	$0.37 \pm 0.03$	40
4	No branches and bark, outer wood case hardened, inner wood decomposing	$0.26 \pm 0.02$	33
5	Wood often scattered across the soil surface, logs elliptical in cross-section	$0.16 \pm 0.06$	4

## 2. Methods

### 2.1. The SAFE degradation landscape

The SAFE Project (4 38' N to 4 46' N, 116 57' to 117 42' E; figure 1) features a gradient of forest disturbance from unlogged primary forest through to severely degraded forest and oil palm plantation (Ewers *et al* 2011). There were 193 vegetation plots ( $25 \times 25$  m) established at SAFE in 2010 (Marsh and Ewers 2013) and distributed among 17 sampling blocks (table 1): three oil palm plantation blocks (OP1 and OP2 planted in 2006 and OP3 planted in 2000), two primary forest blocks (OG1 and OG2), two lightly or illegally logged forest blocks (OG3 and VJR), four twice-logged forest blocks (LFE, LF1–LF3) and six salvage-logged forest blocks that are currently being converted into a fragmented agricultural landscape (A–F) (Ewers *et al* 2011). In the latter two categories, sites were selectively logged once during the 1970s and again in the late 1990s to the early 2000s, removing medium hardwoods (*Drybalanops* and *Dipterocarpus*) and lighter hardwoods (*Shorea* and *Parashorea*). The logging rotations at lightly-logged and salvage-logged blocks were implemented under a modified uniform system, removing an estimated  $113 \text{ m}^3 \text{ ha}^{-1}$  extraction during the first rotation followed by an estimated  $37 \text{ m}^3 \text{ ha}^{-1}$  extraction during the second rotation. In the salvage-logged forest, timber restrictions were lifted during the second rotation and the forest was re-logged three times with an estimated cumulative extraction rate of  $66 \text{ m}^3 \text{ ha}^{-1}$  (Struebig *et al* 2013). Selective rounds of logging resulted in heavily degraded stands, with a high density of roads and skid trails, a paucity of commercial timber species, few emergent trees, and the dominance of pioneer and invasive vegetation.

Vegetation plots were established across the forest degradation landscape according to a hierarchical sampling design as an objective procedure to assess regional stores (Ewers *et al* 2011). The design was chosen to ensure unbiased decisions as to where to establish vegetation monitoring plots in the field (Ewers *et al* 2011). Plots were located at roughly equal altitude and oriented to minimize potentially confounding factors such as slope, latitude, longitude and distance to forest edges (prior to controlled forest-to-oil palm

conversion currently being carried out at SAFE) (Ewers *et al* 2011).

### 2.2. Quantifying forest attributes within vegetation plots

We measured all 193 permanent vegetation plots for above-ground biomass and deadwood in 2010 and 2011, equating to a total survey area of  $>12$  ha. We set out each  $25 \times 25$  m plot with North–South orientation (using a slope correction factor to account for topography) and tagged each tree that had more than 50% of its visible roots located inside the plot (Marthews *et al* 2012). Each tree was measured for DBH (in cm) using a diameter tape and a subset of trees was fitted with a dendrometer to allow re-measurements in the coming years. We measured height (in m) of trees ‘by eye’. For validation of our height measurements, we compared height estimates in the field to height estimated based on region-environment-structure models describing height-DBH allometric relationships in Asian forests:  $H_{\text{mod}} = \exp(0.2797 + 0.5736 \ln(\text{DBH}) + 0.0120 \cdot A + 0.0034 \cdot \text{PV} - 0.0449 \cdot \text{SD} + 0.0191 \cdot \text{TA})$  (Feldpausch *et al* 2011). For subsequent analyses, to account for potential errors in height estimates, we binned estimated tree heights into equal classes of 5 m length each (e.g. 0–5, 5–10, 10–15 m). Climatic parameters for the SAFE landscape (mean annual temperature  $\text{TA} = 24.8^\circ\text{C}$ , dry season length  $\text{SD} = \text{zero months}$  with rainfall  $<100$  mm, annual precipitation coefficient of variation  $\text{PV} = 10.27\%$ ) for inclusion in the allometric model were extracted from the WORD-CLIM datasets (Hijmans *et al* 2005). Basal area  $A$  ( $\text{m}^2 \text{ ha}^{-1}$ ) was derived from tree DBH measurements for each plot and averaged within forest stands.

Above-ground biomass ( $\text{AGB}_{\text{live}}$ ) was derived for each tree from tree size, using an improved pan-tropical algorithm (Chave *et al* 2014) and, additionally, using two global and three regional algorithms (see table S1 in the electronic supplementary material). Here, we restrict ourselves to reporting results based on Chave *et al*'s (2014) model (developed in 2005 and improved in 2014) as a recent study showed that it provided better biomass estimates than regional algorithms when applied to destructive samples from East Kalimantan (Rutishauser *et al* 2013). We used our pan-tropical model with a mean oven-dry wood specific



gravity of  $0.64 \text{ g cm}^{-3}$ , estimated for species in the nearby Lambir Hills National Park (King *et al* 2006). Oil palms have a fundamentally different physical structure to forest trees, so we estimated  $\text{AGB}_{\text{live}}$  in oil palm plantations separately. We computed dry mass in Mg for each palm tree from its height (in m) using  $\text{AGB}_{\text{palm}} = \frac{0.3747 * \text{height} * 100 + 3.6334}{1000}$  (Thenkabail *et al* 2004).

Wood-specific gravity is an important predictor of above-ground biomass and decreases, averaged at plot level, with increasing level of disturbance as the species composition of the forest changes (Slik *et al* 2008). To investigate the possible scale of the bias between our conservative approach and an approach using wood specific gravity values reflecting different disturbance level of forest stands, we used Slik *et al*'s (2008) estimates derived for forest plots in Eastern Borneo. For each tree, we computed  $\text{AGB}_{\text{sim}}$  as above but using wood specific gravity estimates drawn randomly ( $N=100$ ) from a normal distribution of wood specific gravity values. This distribution was defined by maximum and standard deviation and depended on the tree's location: primary forests ( $0.64 \pm 0.18$ ) (King *et al* 2006), and lightly logged forests ( $0.57 \pm 0.02$ ), twice logged forests ( $0.54 \pm 0.03$ ), and salvage logged forests ( $0.41 \pm 0.05$ ) (Slik *et al* 2008).

In each plot, we counted woody debris items, distinguishing between standing dead wood, fallen dead wood (including fallen branches) and hanging dead wood. We classified each individual piece of CWD into one of five decay classes (Baker *et al* 2007). We excluded fine woody debris  $<10$  cm diameter from the dataset. For standing dead wood, diameter was measured at one end ( $D_1$ ) as DBH or above the root buttress as appropriate, and height was estimated visually. Diameter at the upper end ( $D_{\text{upper}} = D_2$ ) was estimated using the taper function (Chambers *et al* 2000). Major branches over 10 cm are recorded in a similar way. In practice, we rarely encountered standing dead trees with big branches as they fall off quite quickly and so branches were generally measured on the ground. For fallen woody debris, we measured the length and diameter at both ends ( $D_1, D_2$ ) using a tape measure and during later density assessments the Leica Disto D2 laser distance measure. We made a note if they were a branch.

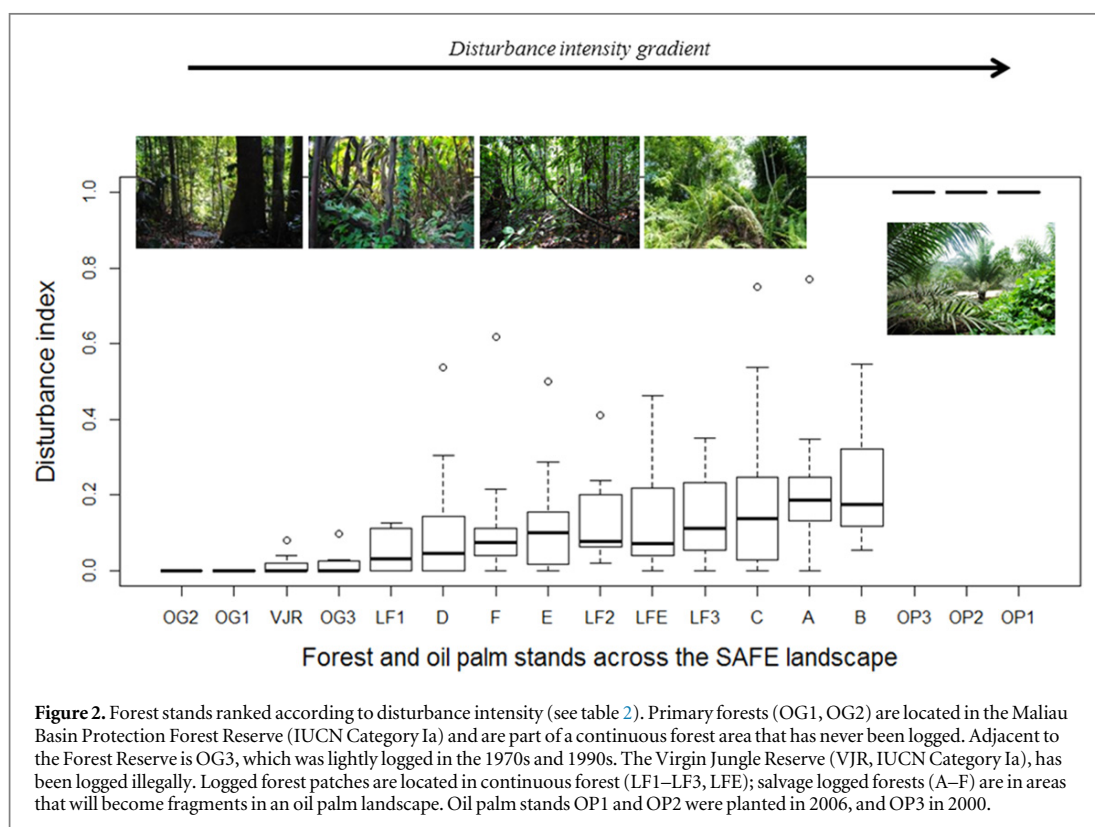
Volume of each piece of CWD was calculated using the 'frustum of a cone' formula (Baker *et al* 2007) and summed within plots. We assume that the state of decomposition of CWD is correlated with its density (Keller *et al* 2004). We measured density of deadwood pieces across five decay classes sampled randomly across the SAFE landscape (table 1). We subsequently computed CWD mass as the product of volume per decay class and wood density for that class. We note that like Keller *et al* (2004), we found that material in decay class 1 was, on average, less dense than material in decay class 2. Our lower sample size

may have introduced a sampling error and the distribution in decay class 1 pieces varied strongly across forest disturbance types. There may also be a species-dependent effect; a European study found irregular patterns of CWD density across decay classes for fir, larch and pine species, where the decline with increasing decay was only apparent from decay class 3 (Paletto and Tosi 2010).

For tree material, we converted CWD mass to CWD carbon stock  $C_{\text{dead}}$  at 47.4% (Martin and Thomas 2011). We estimated above-ground live carbon mass  $C_{\text{live}}$  (Mg) from  $\text{AGB}_{\text{live}}$  assuming that dry-stem biomass of trees has a carbon content of 47.4% (Martin and Thomas 2011). Similarly, we accounted for disturbance effects on plot-level averages of wood-specific gravity by computing live carbon mass  $C_{\text{sim}}$  (Mg) from  $\text{AGB}_{\text{sim}}$ . We used 41.3% to convert biomass in oil palms to carbon content, based on findings from oil palm plantations of Sumatra and East Kalimantan, Indonesia (Vlek *et al* 2004). All,  $C_{\text{live}}$  and  $\text{AGB}_{\text{live}}$  as well as  $C_{\text{sim}}$  and  $\text{AGB}_{\text{sim}}$  were summed across trees within vegetation plots.

CWD in oil palm plantations often consists of palm fronds, which are commonly cut and discarded in piles within the plantation to facilitate nutrient recycling and soil conservation. We measured the base width and length of each leaf frond in the plot. To establish the mass of these fronds, we collected the top frond from each pile in each plot, air-dried them for  $>1$  month and then weighed them. Mass of fronds (Mg) was modelled as a function of frond base width and frond length. We used the resulting relationship to estimate the mass of each frond within the vegetation plot ( $\text{Mass} = \left( 220.08 + 0.32 * \frac{\text{Width}_{\text{Frondbase}} * \text{Length}_{\text{Frond}}}{2} \right) / 1000 \text{ 000}$ ) ( $R^2_{\text{adj}} = 0.69, P < 0.00 \text{ 01}$ ). Mass of dead trunks was estimated following the approach described above. We summed the mass of dead fronds and trunks within each plot, and converted oil palm mass to  $C_{\text{dead}}$  at 41.7% (Vlek *et al* 2004). Across the plots, we could therefore partition carbon into that stored in living trees ( $C_{\text{live}}$  or  $C_{\text{sim}}$ ) and that in CWD ( $C_{\text{dead}}$ ). From these values we calculated the importance of deadwood carbon as  $C_{\text{dead-imp}} = C_{\text{dead}} / (C_{\text{dead}} + C_{\text{live}})$  or  $C_{\text{sim-imp}} = C_{\text{dead}} / (C_{\text{dead}} + C_{\text{sim}})$ .

For each plot, we also recorded canopy closure (*sensu* fractional vegetation cover), the presence/absence of significant old logging trails that were still clearly visible in the field, terrain slope and the presence/absence of riverine gullies within plot boundaries. Mean slope was derived from 12 slope measurements within plots, from the centre towards the North, South, East and West and along the N-NW, N-NE, W-NW, W-SW, S-SW, S-SE, E-NE and E-SE axes. Based on these slopes, we also determined whether the plot within the landscape was located on a ridge, on a slope, or at the bottom of a riverine gully ('gulliness'). Fractional vegetation cover (in % per plot) was estimated from 12 to 13 hemispherical



upward-facing photographs acquired 1 m above ground level per plot following in house-algorithms (Pfeifer *et al* 2014) and using CAN-EYE V6.3.8 (Weiss and Baret 2010).

### 2.3. Quantifying the continuous disturbance gradient

We quantified disturbance as the number of logged trees relative to the number of trees that would be standing in each plot if the forest had been left undisturbed. We used our data for OG1 and OG2 in Maliau Basin Conservation Area as the undisturbed baseline data. During vegetation assessments, we recorded the cause of death for woody debris pieces wherever possible, distinguishing between natural causes (i.e. tree was killed by a liana, a strangler fig or lightning) and anthropogenic causes (i.e. tree was cut or burnt). We summed the number of standing and logged tree stumps in each plot as well as the number of live trees with DBH  $\geq 10$  cm. We subsequently calculated the disturbance index for each plot as  $\text{DISTURBANCE} = \text{number of logged stumps} / (\text{number logged stumps} + \text{number of live trees})$ . Note that oil palms were not counted as live trees as they are explicitly individuals that did not survive the logging and deforestation processes. Thus our disturbance index scales from zero in primary forest to a maximum of one in oil palm plantations. We compared this quantitative measure of disturbance to canopy closure estimates (averaged across plots within stands) and to qualitative assessments of forest quality, scored on a

scale between 1 and 5 (1: 'no trees and open canopy with ginger/vines or low scrub', 2: open with occasional small trees over ginger/vine layer, 3: small trees fairly abundant/canopy at least partially closed, 4: lots of trees, some large, canopy closed, 5: 'no evidence of logging at all, closed canopy with large trees').

### 2.4. Modelling variation in above-ground carbon stocks

Plot disturbance was aggregated to the level of the 17 sampling blocks (A–F, LF1–LF3 and LFE, VJR and OG3, OG1 and OG2, OP1–OP3) by averaging across plots within blocks (figure 2). We modelled the continuous relationships between disturbance and five response variables representing above-ground carbon stocks (i.e.  $C_{\text{live}}$  and  $C_{\text{sim}}$ ,  $C_{\text{dead}}$ ,  $C_{\text{dead-imp}}$  and  $C_{\text{sim-imp}}$ ) using nonlinear and general linear models (family='Gaussian', link='identity') as implemented in the R 'stats' package (R Development Core T 2013). We used one-way ANOVA with posthoc Tukey HSD tests for pairwise comparisons to detect general differences between plots with logging trails or rivers compared to plots without logging trails or rivers. We employed linear mixed effects models to predict dead-wood carbon stocks from plot attributes (i.e. terrain steepness, presence of rivers and trails, gulliness, canopy closure) and their interactions, with forest stand included in the model as a random effect. We fitted models using maximum likelihood criterion implemented with the 'lmer' command within the R package 'lme4' (Bates, Maechler and Bolker 2012). We

**Table 2.** Distribution of above-ground carbon stocks (mean and standard error) in live biomass ( $C_{\text{sim}}$ , Mg/plot) and coarse woody debris mass ( $C_{\text{dead}}$ , Mg/plot) across SAFE's forest stands. Estimates of  $C_{\text{sim}}$  and importance of deadwood carbon versus live tree carbon ( $C_{\text{sim\_imp}}$ ) accounted for changes in wood specific gravity with increasing level of disturbance when computing live tree aboveground biomass (for details see text). Stands were ranked from low disturbance to high disturbance (i.e. number of logged trees relative to the number of trees that would be standing in each plot if the forest had been left undisturbed) (see also figure 2). Forest quality (quality) was also estimated from qualitative criteria (scored from 1: very disturbed to 5: not disturbed) for each plot ( $n$ : number of plots) and then averaged within forest stands. The relative contribution of coarse woody debris carbon to above-ground carbon stocks ( $C_{\text{sim\_imp}}$ ) increases with disturbance of the forests. Fractional vegetation cover (FCover) does not show consistent trends with disturbance.

Stand	$n$	$C_{\text{sim}}$		$C_{\text{dead}}$		$C_{\text{sim\_imp}}$ (%)		FCover (%)		Quality
		mean	se	mean	se	mean	se	mean	se	
OG2	9	14.33	2.61	0.64	0.22	5.44	2.19	80.1	3.2	5.0 ± 0.0
OG1	9	11.89	2.45	1.69	0.51	14.65	4.63	77.8	3.0	4.7 ± 0.2
VJR	8	3.80	0.54	1.14	0.39	21.89	5.96	76.8	2.5	3.4 ± 0.2
OG3	9	12.84	1.71	1.24	0.33	9.86	2.62	71.1	1.0	4.2 ± 0.2
LF1	9	2.30	0.34	2.10	1.28	32.28	8.43	85.2	2.3	3.0 ± 0.2
D	16	1.13	0.21	1.03	0.39	37.81	8.72	70.9	3.6	2.2 ± 0.1
F	16	2.31	0.32	1.73	0.62	36.64	6.64	72.7	2.3	2.9 ± 0.2
E	16	0.98	0.22	0.80	0.17	50.02	6.47	69.9	2.9	2.1 ± 0.3
LF2	9	4.33	0.34	1.39	0.39	22.10	4.21	79.7	3.0	3.1 ± 0.1
LFE	8	4.07	0.97	0.93	0.30	23.75	7.81	82.5	2.5	3.3 ± 0.3
LF3	9	3.98	0.33	1.13	0.15	23.03	3.75	80.2	2.1	2.9 ± 0.1
C	16	1.28	0.30	1.07	0.28	47.60	5.77	72.6	3.6	2.2 ± 0.2
A	16	1.36	0.33	2.31	0.60	63.91	6.70	71.0	4.4	2.4 ± 0.3
B	16	1.64	0.29	1.75	0.49	48.58	5.02	75.5	3.1	2.7 ± 0.2
OP3	9	0.28	0.12	0.16	0.04	50.85	12.15	60.2	6.5	—
OP2	9	0.37	0.20	2.18	1.15	70.76	9.80	36.6	6.2	—
OP1	8	0.11	0.03	0.42	0.07	76.53	4.73	44.1	7.3	—

computed single predictor models and multiple predictor models. The final model was chosen using the step function in lmerTest. We choose the anova function implemented in lmerTest to estimate  $P$  values for parameters based on Satterthwaite's approximations (Kuznetsova *et al* 2014).

### 3. Results

#### 3.1. Above-ground carbon stocks in deadwood and live trees

Above-ground carbon stocks in CWD of forest stands ranged from  $C_{\text{dead}} = 0.64$  ( $\pm 0.22$ ) Mg/plot ( $\sim 10.22$  Mg ha $^{-1}$ , in primary forest stand OG2) to  $2.31$  ( $\pm 0.60$ ) Mg/plot ( $\sim 36.93$  Mg ha $^{-1}$ , in salvage logged forest stand A). Above-ground carbon stocks in live trees ranged from  $C_{\text{sim}} = 0.98$  ( $\pm 0.22$ ) Mg/plot ( $\sim 15.71$  Mg ha $^{-1}$ , in salvage logged forest stand E) to  $14.34$  ( $\pm 2.61$ ) Mg/plot ( $\sim 229.37$  Mg ha $^{-1}$ , in the primary forest stand OG2) (table 2). The proportion of carbon stored in deadwood varied from  $5.4$  ( $\pm 2.2$ ) % in primary forest stand OG2 to  $63.9$  ( $\pm 6.7$ ) % in salvage logged forest stand A (table 2).

Above-ground carbon stored in live trees (with wood gravity adjusted to be a function of disturbance) decreased significantly and exponentially with increasing disturbance, a pattern that holds true at both plot and stand level (figure 3). Carbon stored in CWD varied considerably among and within forest stands, showing only weak trends with disturbance. As expected, the importance of carbon stored in deadwood increased with increasing disturbance following a

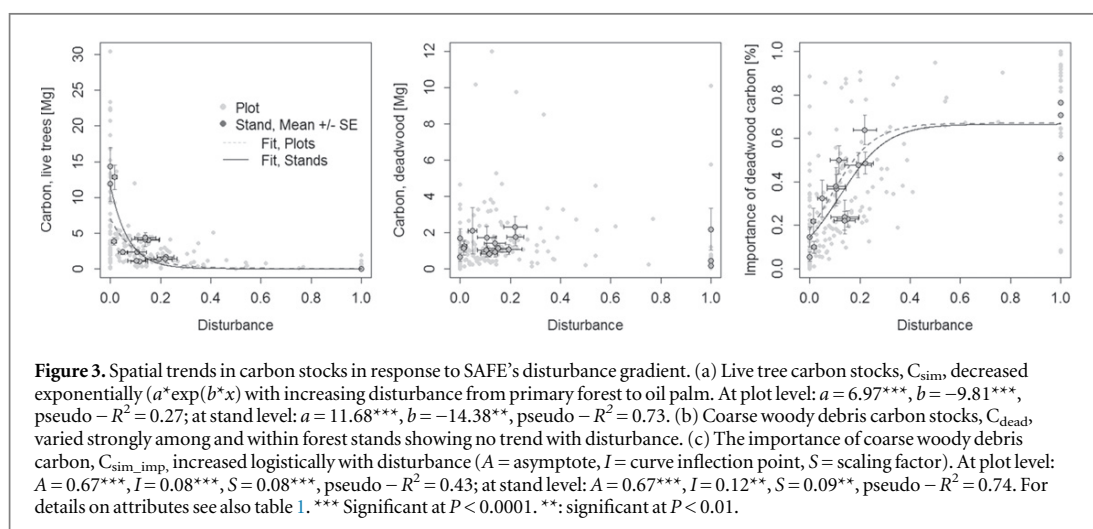
logistic model (figure 3). Live tree carbon estimates using disturbance adjusted wood gravity,  $C_{\text{sim}}$ , are significantly lower compared to live tree carbon estimates based on constant wood gravity, especially in more disturbed plots that are characterized by lower carbon stocks (table S2, figure S2). Hence, estimates of the importance of deadwood carbon,  $C_{\text{sim\_imp}}$ , are higher using live tree carbon estimates with disturbance adjusted wood gravity (figure S2, top panel, right). Responses of both live tree carbon and importance of deadwood carbon to disturbance follow similar trend using conservative  $AGB_{\text{live}}$  and  $C_{\text{live}}$  estimates. However, our analyses indicate a more rapid decline of  $C_{\text{sim}}$  at plot level and a more rapid increase in the importance of deadwood,  $C_{\text{sim\_imp}}$ , with increasing disturbance (figure 3).

In young oil palm plantations (OP1 and OP2) much of the CWD mass comes from dead tree remains with only marginal contributions from cut palm fronds (mean  $\pm$  SE =  $0.11\% \pm 0.06$ ). In the mature oil palm stand, a larger amount of the CWD mass is contributed by palm fronds ( $34.9\% \pm 13.0$ ). We emphasize that moisture may have been left in the oil palm fronds after drying potentially leading to slight overestimates in the amount of CWD carbon and in the importance of CWD carbon in mature oil palm plots.

#### 3.2. Linking CWD stocks to plot environments

In forest stands, CWD volume, CWD carbon and the proportion of carbon stored in deadwood,  $C_{\text{sim\_imp}}$ , increased significantly with disturbance ( $P < 0.01$ ) in single predictor linear mixed effects models.  $C_{\text{sim\_imp}}$





also decreased with increasing terrain steepness ( $P = 0.057$ ). However, that effect disappeared after accounting for disturbance impacts. The proportion of carbon stored in deadwood was significantly higher in forest plots with skid trails ( $P < 0.001$ ), which also have significantly lower live tree carbon stocks ( $P < 0.05$ ). The proportion of carbon stored in deadwood was significantly higher in plots located on ridges as compared to plots in gullies ( $P < 0.05$ ; Tukey HSD), but showed no other patterns in response to plot attributes. We also found significantly higher  $C_{sim}$  stocks on plots without rivers ( $P < 0.05$ ), but this does not propagate into effects on  $C_{sim\_imp}$ .

Final models predicting  $C_{sim\_imp}$  retained forest blocks as significant random effect ( $P < 0.01$ ) and disturbance ( $P < 0.001$ ) with an interaction effect between presence of skid trails and gulliness ( $P = 0.05$ ) as significant fixed effects. Final models predicting CWD volume or CWD carbon only retained land use as significant fixed effect each ( $P < 0.01$ ).

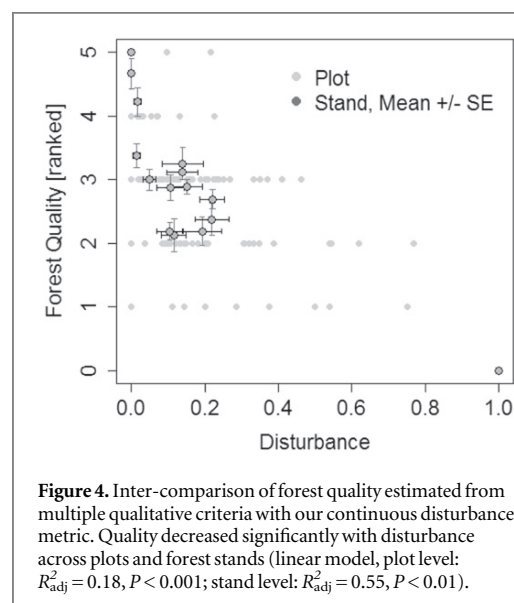
### 3.3. Validating tree heights and disturbance metric

Canopy closure did not show a trend with the disturbance index at plot or stand level (excluding heavily managed oil palm stands). The forest quality score decreased significantly with disturbance across plots and forest stands (linear model, plot level:  $R^2_{adj} = 0.18$ ,  $P < 0.001$ ; stand level:  $R^2_{adj} = 0.55$ ,  $P < 0.01$ ) (figure 4). Modelled average tree heights were higher than measured average tree heights but not significantly so (see figure S1 in electronic supplementary material in supporting information), thus validating the visual estimates of height made in the field.

## 4. Discussion

### 4.1. Above-ground carbon changes

Our estimates of CWD stocks for primary forest sites at SAFE (mass: 21.6 and 57.1 Mg ha<sup>-1</sup>) lie within the spectrum recorded for lowland tropical forests (Baker



et al 2004) and are similar to estimates of  $\sim 26$  (Saner et al 2012) and 41 (Gale 2000) Mg ha<sup>-1</sup> previously found for lowland forests in North Borneo. Gale (2000) estimated CWD mass for pieces with  $\geq 20$  cm diameter to be  $\sim 45$  mg ha<sup>-1</sup> (Belalong),  $\sim 41$  Mg ha<sup>-1</sup> (Danum) and  $\sim 69$  Mg ha<sup>-1</sup> (Andalau). Deadwood mass in undisturbed moist tropical forests has been estimated to be less than 10% (Delaney et al 1998, Saner et al 2012), 15% (Uhl et al 1988) and 19% (Saldarriaga et al 1988) of total above-ground biomass stocks. This is in line with our findings for the proportion of deadwood carbon in primary and lightly-logged forest stands. However, our analyses clearly show that the importance of deadwood carbon stocks increase with forest disturbance to around 20 or 30% for twice-logged forest stands and to more than 30 or 40%, and as high as 64% in salvage-logged forest stands. This indicates that carbon storage and emissions in logged forests may be markedly different to those in primary forests.

The increase in the importance of deadwood carbon with disturbance was caused, not by increases in CWD mass, but primarily by a significant reduction in the above-ground biomass and carbon of living trees (figure 3). Borneo's lowland rainforests are living carbon density hotspots (Ruesch and Gibbs 2008). At SAFE, carbon storage in living trees of unlogged forests is around 229 and 190 Mg C ha<sup>-1</sup>. This is similar to earlier findings for lowland rainforests in Borneo (~229 Mg C ha<sup>-1</sup>) and considerably higher compared to the Amazonian average of ~144 Mg C ha<sup>-1</sup> (Slik et al 2010) or to conservatively-estimated stocks in unlogged forests at nearby Danum Valley of 91.9 Mg C ha<sup>-1</sup> (Saner et al 2012). Logging removed large trees at SAFE and caused residual logging damage, thereby significantly reducing above-ground carbon stocks in live trees to 20–30 Mg C ha<sup>-1</sup> in some of the logged forest stands (7–10 years post-logging). Our findings imply that logging impacts on live tree carbon stocks may be stronger than the 28.6% reduction 22 years post logging previously reported for Sabah's lowland forests (Saner et al 2012). To verify that assumption, we are currently re-measuring biomass annually in the 193 vegetation plots to obtain estimates of biomass recovery over time.

There was only a weak significant relationship between absolute CWD stocks and disturbance. CWDs stocks at SAFE, as elsewhere, are likely to be caused by a balance between input rates and rates of decomposition. Assuming that input rates in unmodified forests are a function of living biomass and do not vary strongly from year to year (Baker et al 2007), the lack of a relationship between AGB<sub>live</sub> and CWD mass in our study suggests that current CWD stocks may reflect pre-logging stocks, which are now slowly decomposing. However, mean residence time of deadwood carbon is assumed to be around six to nine years (Chambers et al 2001, Rice et al 2004) and the last logging events in the SAFE area took place in the early to mid-2000s, suggesting that most CWD should have already decomposed. An alternative hypothesis is that human activities during selective logging have generated CWD that offsets naturally low rates of CWD production. This may help explain the high relative deadwood carbon stocks observed in some of the forest stands characterized by a very low amounts of living biomass. Furthermore, some species decay much slower than others, and species composition may have changed post-logging. Either way, our finding that disturbed forests increasingly store carbon as dead wood are likely to impact on carbon flux estimates because of subsequent decomposition (Blanc et al 2009), which may temporarily offset carbon sequestration from the growth of new and surviving trees.

We detected some environmental factors that influenced the relative amount of carbon stored in CWD; terrain steepness, land use and the presence of old logging trails were linked to higher deadwood carbon ratios. However, environmental factors other

than disturbance measured at SAFE do not appear to drive absolute CWD carbon stocks, but rather affect above-ground live tree carbon, highlighting the complex patterns of topography and disturbance that underlie spatial variation in above-ground carbon at landscape scale (Gale 2000, Vieira et al 2011). Given the potential impact of species composition on CWD stocks, including biological drivers into models of CWD stock variation will be the subject of future studies.

#### 4.2. Implications for carbon budgets

Forest degradation through selective timber harvesting is increasing in frequency and extent (Curran et al 2004, Asner et al 2005) and has now probably become a more extensive cause of land use change than outright deforestation (Asner et al 2009). Satellite monitoring has revealed the progression of logging through Central Africa (Laporte et al 2007), the Amazon (Asner et al 2005), Borneo (Gaveau et al 2014) and other humid tropical forest regions.

The impacts of widespread logging have recently regained the attention of conservation ecologists, as meta-analyses suggest that selectively-logged forests retain substantial biodiversity, carbon and timber stocks, with once-logged forest stands retaining 76% of their above-ground carbon stocks one year after logging (Putz et al 2012). However, large, landscape-scale assessments of above-ground carbon changes along a disturbance gradient in tropical forests are rare (Berenguer et al 2014). Carbon change studies typically focus on assessments of either live tree or deadwood carbon (Keller et al 2004, Malhi et al 2006, Blanc et al 2009, Lewis et al 2009). The few studies that quantify both living and dead carbon stocks have often been carried out in primary forest stands alone (Nascimento and Laurance 2002, Pereira et al 2002, Rice et al 2004, Malhi et al 2009), or along comparatively small transects. For example, Saner et al (2012) sampled along linear transects covering just 1 ha in both selectively logged forests and primary forests and ignored fallen dead wood, which represented the majority of deadwood carbon in our plots (>65% in all forest stands except in LF1, where it was 54.1%).

Our analyses show that deadwood carbon stocks can represent a large proportion (>50%) of above-ground carbon stocks in human-modified forests. We acknowledge that our estimates contain uncertainties. For example, we use a global algorithm to estimate above-ground biomass in live trees (although trends remain stable using different biomass algorithms). However, we do account for possible changes in mean stand-level tree wood density over time with disturbance that might occur as the high-density commercial timber species are removed and more light-wooded successional species become more dominant. And we show that those factors are not changing our

clear results, which highlight the need for carbon stock studies to include CWD estimates in their calculations.

Forest degradation can alter the balance between carbon emissions and sequestration in tropical forests. A global assessment of carbon sinks in the world's forests estimate a 'near-sink' in tropical forests as carbon emissions from tropical deforestation ( $\sim 3$  and  $2.8 \text{ Pg C yr}^{-1}$ ) are counterbalanced by carbon sequestration in intact forests combined with forests re-growing after disturbance ( $\sim 2.9$  and  $2.7 \text{ Pg C yr}^{-1}$ ) (Pan et al 2011). This assessment was criticized for overestimating carbon sequestration, as the authors overlooked tree re-census data and mismatched between sources used for estimates of forest area (Wright 2013). The authors based their analyses on biomass data taken in old-growth forests and up-scaled to regions. In addition, for the tropics they had only sparse ground-based data on deadwood carbon stocks and none from disturbed and re-growing forests. Our results imply that for logged forests, at least in Southeast Asia, they may have underestimated carbon emissions from dead wood and overestimated carbon storage in live trees.

The patterns found at the SAFE landscape may ultimately be representative of tropical forests in Southeast Asia and human-modified tropical forests elsewhere. Detrimental effects of disturbance may be less severe in selectively logged tropical forests compared to outright deforestation and agroforestry (Gibson et al 2011, Putz et al 2012). However, lower carbon storage in live biomass and higher temporary carbon storage in deadwood across degraded forest stands may have important implications for global assessments of carbon sources and sinks such as those by Pan et al (2011), as logged forests now represent more than 30% of all standing tropical humid forests, implying a strong, time-delayed human footprint.

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